

Spermatozoal Morphology of Patellogastropoda and Vetigastropoda (Mollusca: Prosobranchia)

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ABSTRACT

The morphologies of the aquasperm of Patellogastropoda and Vetigastropoda are distinctly different, adding further support to the view that these two taxa are not closely related. Within the patellogastropods each family examined to date (Patellidae, Nacellidae, Lottiidae, Acmaeidae) has sperm with distinguishing features and it is therefore possible to recognize members of a family and differentiate between families using sperm morphology. Similarly sperm morphology can be used to differentiate between families of vetigastropods. Although there are a few exceptions, the size (length to breadth ratio) and shape of the nucleus and acrosome of sperm of species within each family are similar. The broad similarities in the morphology of the spermatozoa of the Pleurotomarioidea, Fissurelloidea, Haliotoidea and Trochoidea (with the exception of the Skeneidae) indicate that these taxa are phylogenetically closely related. Some vetigastropods, notably the Lepetodrilidae, Scissurellidae and Skeneidae, have modified spermatozoa which correlates to internal fertilization or fertilization within the mantle cavity. It is suggested that more extensive studies on the sperm from these families as well as other archaeogastropod taxa could provide additional clues to the phylogeny of higher gastropods.

RÉSUMÉ

La morphologie des spermatozoïdes des Patellogastropoda et des Vetigastropoda (Mollusca: Prosobranchia)

La morphologie des aquaspermatozoïdes est différente chez les Patellogastropoda et les Vetigastropoda, ce qui ajoute des arguments à l'opinion que ces taxons ne sont pas proches. Parmi les Patellogastropoda chacune des familles examinées jusqu'ici (Patellidae, Nacellidae, Lottiidae et Acmaeidae) a des spermatozoïdes avec des caractères distinctifs et il est donc possible de reconnaître les membres d'une famille et de différencier les familles en utilisant la morphologie du spermatozoïde. De même, la morphologie du spermatozoïde peut être utilisée pour différencier les familles de Vetigastropoda. En dépit de quelques exceptions, les dimensions (rapport longueur sur largeur) et la forme du noyau et de l'acrosome des spermatozoïdes des espèces d'une même famille sont similaires. La grande ressemblance morphologique des spermatozoïdes des Pleurotomarioidea, Fissurelloidea, Haliotoidea et Trochoidea (à l'exception des Skeneidae) indique que ces taxons sont très proches phylogénétiquement. Quelques Vetigastropoda, en particulier les Lepetodrilidae, Scissurellidae et Skeneidae, ont des spermatozoïdes modifiés qui sont corrélés avec la fécondation interne ou la fécondation à l'intérieur de la cavité palléale. Il est probable que des études plus nombreuses des spermatozoïdes de ces familles et d'autres Archaeogastropodes pourraient fournir des indices supplémentaires pour la phylogénie des Gastéropodes évolués.

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Comparative spermatology has without doubt made significant contributions to a greater understanding of the taxonomic and phylogenetic relationships within and between many taxa. Within the molluscan class Gastropoda, the archaeogastropods are a large assemblage of prosobranchs, the taxonomic status of which has been the subject of considerable debate [5, 6, 9, 16]. Much of this debate is a result of the discovery of new taxa from deep-sea and hydrothermal vent communities [6-9, 31]. Thus in several recent re-evaluations of the Archaeogastropoda (*s. lat.*) [7-9, 16, 30], the assemblage has been split into numerous new orders.

A number of the recent publications have also attempted to reconstruct phylogenetic relationships within the archaeogastropods (*s. lat.*) as well as between archaeogastropods and higher gastropod taxa (e.g. caenogastropods and euthyneurans) [5-7, 16, 17]. To date most of these studies have not incorporated detailed information from sperm morphology (or spermiogenesis), information which may provide valuable insights into archaeogastropod taxonomy and phylogeny.

Two of the recognized orders within the archaeogastropod assemblage are the Patellogastropoda (formally Docoglossa) and Vetigastropoda. Whereas virtually nothing is known about sperm morphology of the recently discovered archaeogastropods, in the last 14 years there have been a number of publications on the structure of the spermatozoa of patellogastropods [1, 18-21, 25-28, 34] and vetigastropods [10, 13-15, 22, 23]. This paper reviews this information, discusses the systematic and phylogenetic implications of the data and highlights gaps in our knowledge.

MATERIALS AND METHODS

Information on the ultrastructure of the spermatozoa of Patellogastropoda and Vetigastropoda was obtained either from published papers (see Table 1 and reference list) or from tissue prepared for transmission electron microscopy. For TEM, small portions of the testis of each species were fixed in 2.5% glutaraldehyde in filtered sea water for 2-3 hours. The exception to this was the hydrothermal vent gastropod *Lepetodrilus fucensis*. This material spent several weeks in the glutaraldehyde fixative. Tissues were post-fixed in 1% osmium tetroxide in 0.1M sodium cacodylate buffer and filtered sea water for 90 minutes, dehydrated in a graded ethanol series, and embedded in a TAAB/Araldite resin mixture via propylene oxide. Thin sections (silver/gold) were stained in 5% aqueous uranyl acetate (30 minutes) and lead citrate (5 minutes) and examined in a JEOL JEM CXII TEM at 80kV.

RESULTS

Patellogastropoda

The spermatozoa of 43 species from four families (Table 2) of Patellogastropoda have been examined or described and all have aquasperm. Results to date suggest that members of each family of patellogastropod have spermatozoa with characteristic morphological features (Fig. 1).

Patellidae. In species of Patellidae (Fig. 1A-E), the acrosome, the contents of which may or may not be differentiated into electron-dense and electron-lucent regions, constitutes <50% of the head length and is deeply invaginated posteriorly. The subacrosomal space does not contain an axial rod. Despite these similarities within the Patellidae five morphological types of spermatozoa can be recognized within the family (Fig. 1A-E). The first type (Fig. 1A) have heads with cylindrical nuclei (usually <5 µm long and "bullet-shaped") which are rounded anteriorly and small cap-like acrosomes, the contents of which are uniformly electron-dense (i.e. undifferentiated) (11 species). The second type (Fig. 1B; 3 species) have very elongate "flask-shaped" nuclei (>12 µm long) which are pointed anteriorly and acrosomes with long anterior extensions. The third type (Fig. 1C; 11 species) have nuclei (about 5 µm long) which have a square-shaped anterior which intrudes into the subacrosomal space giving the nucleus a "bottle-shaped" appearance. Anterior to the nucleus is a relatively large acrosome, the wall of which is bulbous posteriorly and in addition the contents are differentiated into electron-dense and electron-lucent regions. The fourth type (Fig. 1D), have cylindrical nuclei (5-7 µm long) and an acrosome

TABLE 1. — Summary of the morphological features of the spermatozoa of vetigastropod families. * Information available as published diagram only. ** Deep-sea species.

Taxon	Reference	Common features of sperm
Pleurotomarioidea		
Pleurotomariidae		Head: Cylindrical (L:B=3:1).
<i>Perotrochus westralis</i>	[10]	Nucleus: Cylindrical (L:B, 2.5:1) with shallow anterior fossa.
<i>Perotrochus queyanus</i>	[15]	Acrosome: Broadly conical, <20% head length, undifferentiated.
Haliotoidea		
Haliotidae		Head: Cylindrical (L:B>5:1).
<i>Haliotis discus</i>	[33]	Nucleus: Narrow anterior fossa.
<i>Haliotis rufescens</i>	[29]	Acrosome: Comprises 40-50% head length, with posterior invagination in form of narrow canal with axial rod.
<i>Haliotis midae</i>	[22]	
<i>Haliotis diversicolor aquatilis</i>	[28]	
Fissurelloidea		
Fissurellidae		Head: Cylindrical (L:B>4:1).
<i>Fissurella matabilis</i>	[22]	Nucleus: Cylindrical (L:B>3:1). Eumarginulinae with deep U-shaped anterior fossa. Fissurellinae fossa absent but small anterior extension present.
<i>Fissurella natalensis</i>	[22]	Acrosome: usually 20-30% of head length, with deep posterior invagination. Axial rod present in Eumarginulinae.
<i>Dendrofissurella scutellum</i>	[22]	
<i>Amblychelipax javanicus</i>	[14]	
<i>Montfortula conoidea</i>	[14]	
<i>Scutus antipodes</i> *	[14]	
<i>Scutus unguis</i>	[22]	
<i>Scutus sinensis</i> *	[28]	
<i>Macroschisma sinense</i> *	[28]	
<i>Diodora aspera</i>	[21]	
Scissurelloidea		
Scissurellidae		Modified spermatozoa (Ent-aquasperm?).
<i>Sinezona</i> sp.	[14]	Nucleus: Deep anterior and posterior fossae.
		Acrosome: Undifferentiated, very small (13% head length), cap-like.
Trochoidea		
Trochidae		Head: Short cylindrical (L:B <3:1).
<i>Oryzetele variegata</i>	[24]	Nucleus: Usually short (L:B >2:1); U-shaped anterior fossa.
<i>Oryzetele impervia</i>	[24]	Acrosome: Comprises 50% or less of head length, usually undifferentiated internally. Axial rod present.
<i>Oryzetele tabularis</i>	[24]	
<i>Oryzetele sinensis</i>	[24]	
<i>Oryzetele tigrina</i>	[24]	
<i>Gibbula umbilicalis</i>	[2, 3]	
<i>Gibbula tumida</i>	[27]	
<i>Monodonta turbinata</i>	[27, 18]	
<i>Monodonta australis</i>	[22]	
<i>Monodonta labio labio</i>	[28]	
<i>Trochus nigropunctatus</i>	[22]	
<i>Chlorostoma argyrostoma lischkei</i> *	[28]	
<i>Omphalus pfeifferi</i>	[28]	
<i>Tectus pyramis</i>	[28]	
<i>Acstrocochlea obtusa</i>	[11]	
<i>Calliotropis glyptus</i> **	[12]	
Turbinidae		
<i>Turbo coronatus</i>	[22]	Head: Broad cylinder (L:B >3:1).
<i>Turbo sarmaticus</i>	[22]	Nucleus: L:B <1.5:1; Very wide V-shaped anterior fossa.
<i>Turbo cidaris natalensis</i>	[22]	Acrosome: Comprises >50% of head length, differentiated internally with short narrow posterior invagination.
<i>Lunella cinerea</i>	[28]	
<i>Lunella granulata</i>	[28]	
<i>Butillius cornutus</i> *	[28]	
Phasianellidae		
<i>Tricolia capensis</i>	[22]	Head: Short cylinder.
		Nucleus: Short and barrel shaped with U-shaped anterior fossa.
		Acrosome: n-shaped, <30% head length, undifferentiated internally.
Skeneidae		Dimorphic and modified sperm - see Fig. 2.
<i>Zalipais laseroni</i>	[13]	
<i>Microcarina surgetea</i>	[13]	
<i>Liotella parvirota</i>	[13]	
Lepetodriloidae		
Lepetodrilidae		Modified sperm (Ent-aquasperm ?) - see Fig. 2.
<i>Lepetodrilus fucensis</i>	[23]	Nucleus: Elongate cylindrical and rounded anteriorly.
		Acrosome: Modified subacrosomal plate.

TABLE 2. — The species of four families of patellogastropod for which descriptions of the sperm exist. Information obtained from [1, 18-21, 25, 28, 35]. The sperm types of Patellidae (I, II, III, IV, VI) are from [19, 25]. ¹Indicates species of uncertain taxonomic status but initially identified as *P. miniata* from Angola; ²Indicates species of uncertain taxonomic status but initially identified as *P. miniata* from Namibia.

PATELLIDAE	
Sperm Type I:	<i>Patella aspera</i>
<i>Patella aphanes</i>	<i>Patella rustica</i>
<i>Patella obiecta</i>	<i>Patella depressa</i>
<i>Patella barbara</i>	<i>Patella ferruginea</i>
<i>Patella argenvillei</i>	<i>Patella caerulea</i>
<i>Patella tabularis</i>	<i>Patella candei</i>
<i>Patella chapmani</i>	Sperm Type IV:
<i>Patella laticostata</i>	<i>Helcion pectunculus</i>
<i>Patella flexuosa</i>	<i>Helcion pruinosus</i>
<i>Patella cochlear</i>	Sperm Type III:
<i>Patella longicosta</i>	<i>Helcion dunkeri</i>
Sperm Type II:	<i>Helcion pellucidus</i>
<i>Patella granularis</i>	
<i>Patella miliaris</i>	NACELLIDAE
<i>Patella peronii</i>	<i>Nacella delesserti</i>
Sperm Type III:	<i>Cellana capensis</i>
<i>Patella granatina</i>	<i>Cellana testudinaria</i>
<i>Patella oculus</i>	<i>Cellana toreuma</i>
<i>Patella concolor</i>	
<i>Patella cf. miniata</i> ¹	LOTTIIDAE
<i>Patella safiana</i>	<i>Lottia pelta</i>
<i>Patella canescens</i>	<i>Lottia digitalis</i>
<i>Patella compressa</i>	<i>Lottia strigatella</i>
<i>Patella miniata</i>	<i>Tectura scutum</i>
<i>Patella cf. miniata</i> ²	
Sperm Type VI:	ACMAEIDAE
<i>Patella vulgata</i>	<i>Patelloida profunda albonotata</i>
	<i>Patelloida saccharina lanx</i>

which is differentiated internally and has a cylindrical posterior lobe. Finally the fifth type (Fig. 1E; 7 species) consists of a nucleus which is elongate and cylindrical but capped by a short, undifferentiated A-shaped, conical acrosome.

Nacellidae. In the Nacellidae the heads of the spermatozoa are always elongate (length: breadth >7:1) and the nucleus is distinctly conical in shape (Fig. 1F). The acrosome, which constitutes <50% of the head length, has a complex internal differentiation which can take the form of electron-opaque striations (e.g. *Cellana capensis* [19]). An axial rod is always present in the subacrosomal space.

Lottiidae. Lottiidae spermatozoa have a head with a short cylindrical nucleus which is rounded anteriorly (Fig. 1G). Anterior to the nucleus is an elongate acrosome which constitutes >50% of the total head length. The acrosome is invaginated posteriorly, differentiated internally into an outer electron-lucent and inner electron-dense region and has an elongate posterior lobe which protrudes into the sub-acrosomal space. Within this space, the fibrous material is aggregated into an axial rod-like structure. The midpiece has four to five spherical mitochondria (with well developed cristae), which surround the proximal and distal centrioles. Surrounding the anterior portion of the axoneme is an elongate (1 µm) cytoplasmic collar (this structure is much smaller in other patellogastropod taxa).

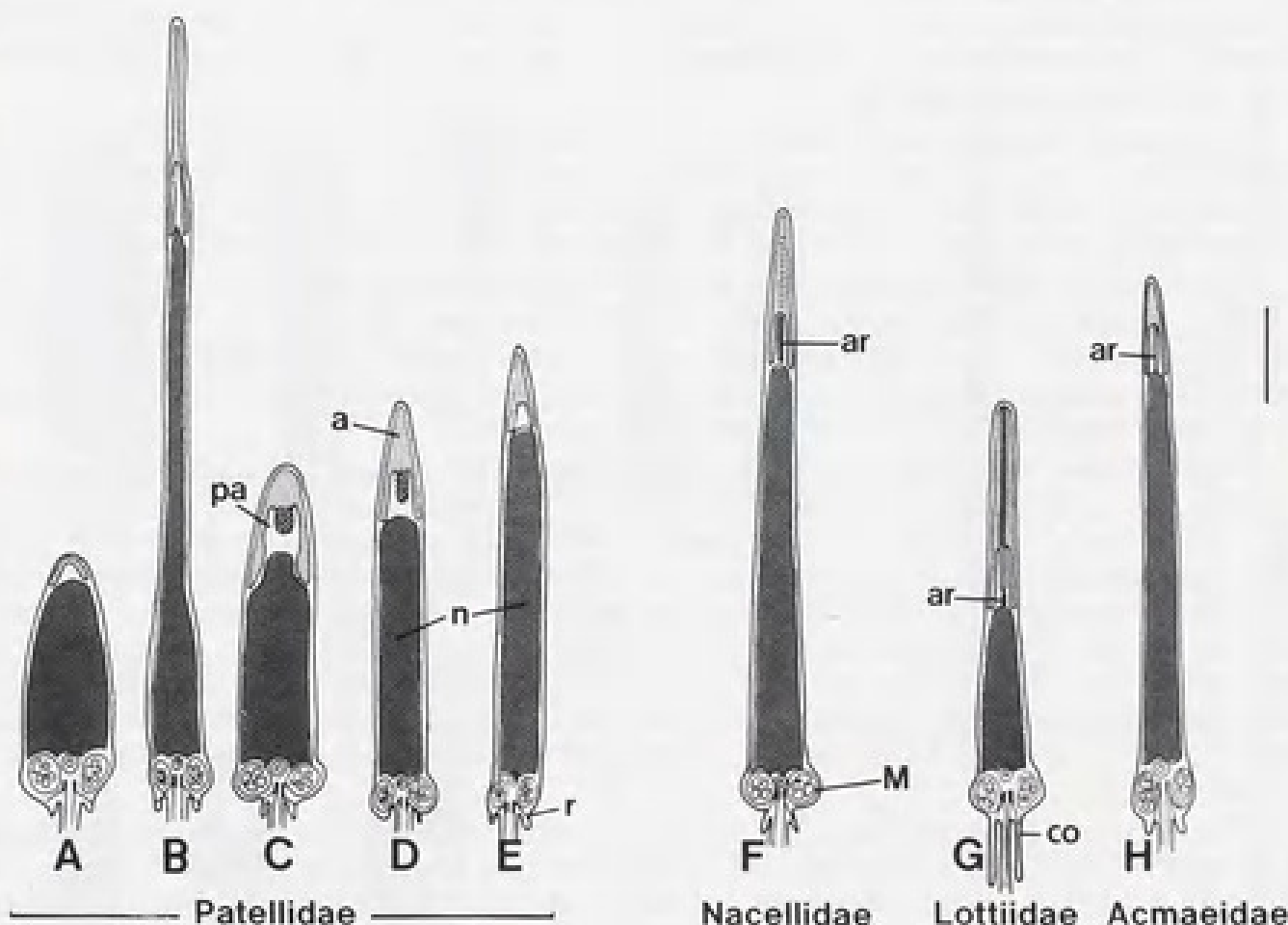


FIG. 1. — Semi-diagrammatic longitudinal sections through the spermatozoa of representative Patellogastropoda. a, acrosome; ar, axial rod; co, cytoplasmic collar; M, mitochondrion; n, nucleus; pa, posterior acrosomal invagination. Diagrams A-C, F, G are modified from [21]. Scale bar = 2 μ m.

Acmaeidae. Only two species, *Patelloida profunda albonotata* [18] and *P. saccharina lanx* [28], have been described from this family, the sperm of the latter species being illustrated diagrammatically only. The sperm have elongate, cylindrical heads (about 5.6 μ m long x 0.3 μ m mid-diameter in *P. p. albonotata* and 5.4 μ m x 0.4 μ m in *P. s. lanx*) (Fig. 1H). The nucleus is cylindrical, tapering towards the rounded anterior, and is capped by a short conical acrosome (about 1 μ m long) the contents of which are undifferentiated. The acrosome has a broad posterior invagination, the subacrosomal space containing an axial rod. The midpiece contains four to five spherical mitochondria (about 0.5 μ m diameter).

Vetigastropoda

With the exception of the Skeneidae which have dimorphic spermatozoa [13], vetigastropods produce only euspermatozoa. Although the majority of species have aquasperm (Fig. 2) each family has spermatozoa with characteristic features (summarized in Table 2).

Pleurotomariidae. Only two species from this family, *Perotrochus westralis* (described as *Pleurotomaria africana*) and *Perotrochus quoyanus* have been examined [10, 15]. Both species have aquasperm. The sperm head is composed of a cylindrical nucleus (length: breadth about 3:1)

which is square anteriorly with a small central invagination. Posteriorly the nucleus has a small but well developed fossa (described as crypt-like by Healy & Harasewych [15]).

Fibrous rootlets extend from the proximal centriole into this fossa. The acrosome is in the form of a rounded cone the contents of which are not differentiated. In addition the acrosome has a deep, narrow posterior invagination.

Haliotidae. The sperm of the Haliotidae all have a head which is cylindrical, with a L:B ratio normally >5:1 (Table 1). The nucleus, which is cylindrical, has a narrow anterior fossa. The acrosome, which constitutes ~40-50% of the total length of the sperm head has a narrow anterior canal containing an axial rod. The acrosomal contents may or may not be differentiated.

Scissurellidae. The spermatozoon of only one species of scissurellid, *Sinezona* sp. has been described [14] and it is of the ent-aquasperm type [32]. The head consists of a cylindrical nucleus which has prominent anterior and posterior invaginations. The anterior invagination houses an axial rod. The small cap-shaped acrosome is undifferentiated internally. The midpiece consists of an axoneme which is surrounded by a sleeve-like mitochondrion.

Fissurellidae. Most fissurellids have a sperm head with a length to breadth ratio of >4:1. The nucleus is cylindrical (L:B 3:1; *Montfortula conoidea* and *Scutus antipodes* are exceptions [14]). Except for *M. conoidea* and *S. antipodes* in which the acrosome comprises 50% of the head length, the acrosome of fissurellids is nearly always small, <35% of the total head length and is deeply invaginated, the invagination penetrating the acrosome as a narrow tube which widens at the anterior. In the subfamily Fissurellinae the nucleus either has a small peg-like anterior extension (includes species of *Fissurella* and *Dendrofissurella*) or there is a shallow anterior nuclear fossa (*Amblychilepas*). By contrast the Eumarginulinae (includes species of *Montfortula* and *Scutus*) all have a large V-shaped anterior nuclear invagination which houses an axial rod.

Trochidae and Phasianellidae. The sperm of species from these two families have a barrel-shaped nucleus (L:B <4:1) which has a U-shaped anterior invagination. In many species the contents of the broadly conical acrosome are uniformly electron-opaque [22], whereas in other species a differentiated acrosome has been noted [10]. The acrosome normally constitutes 50% or less of the total head length and has a narrow posterior invagination. In most trochids there is an axial rod.

Turbinidae. Turbinid spermatozoa are characterised by a nucleus with a length to breadth ratio <1.5:1. The nucleus has a very wide anterior invagination and a relatively large (>50% of the total head length) conical acrosome, the base of which lies within the nuclear invagination. The acrosomal contents are differentiated internally. Posteriorly the acrosome has a short, narrow invagination.

Lepetodrilidae. A preliminary examination of one species (*Lepetodrilus fucensis*) from this taxon, has revealed that they produce only euspermatozoa which are modified [23]. The sperm have an elongate head (about 11 µm long) comprised of a long cylindrical nucleus (about 9 µm long x 0.4 µm mid-diameter) and an anteriorly positioned conical acrosome (about 2 µm long). Between the acrosome and the nucleus is a tube-like structure, the subacrosomal plate (about 0.3 µm long), which is expanded inwards at its base as a small flange. The lumen of this tube is filled with an amorphous material. The acrosome, which sits on the tube, is deeply invaginated posteriorly; the subacrosomal space within the invagination contains an axial rod.

Posteriorly the nucleus has a shallow invagination into which the complex centriolar apparatus protrudes. A single large mitochondrion is sited laterally to the centriolar apparatus. The anterior portion of the axoneme (which emerges from the centriolar complex) is surrounded by a cytoplasmic collar which forms a tube about 2.5 µm long. The cytoplasmic collar contains numerous tubular structures (about 60 nm diameter) which encircle the axoneme.

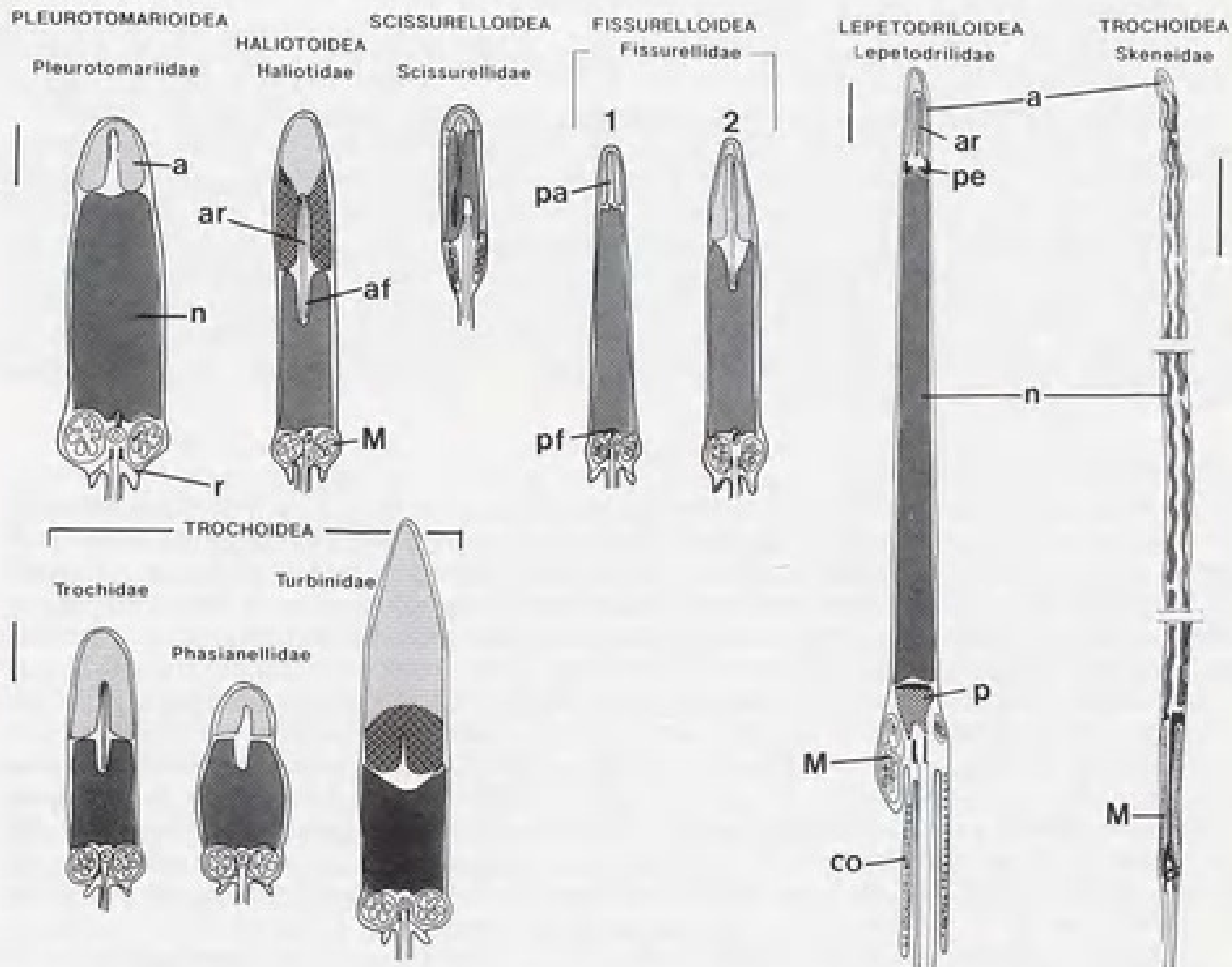


FIG. 2. — Semi-diagrammatic longitudinal sections through spermatozoa of nine families of Vetigastropoda. Examples chosen are thought to typify each family. a, acrosome; af, anterior nuclear fossa; ar, axial rod; co, cytoplasmic collar; M, mitochondrion; n, nucleus; p, proximal centriole; pa, posterior acrosomal invagination; pe, subacrosomal plate; pf, posterior nuclear fossa; r, radial arm. Within the Fissurellidae type 1 sperm are from the Fissurellinae and type 2 from the Eumarginulinae. The diagrams are modified from [13, 22, 23]. Scale bars = 1 μ m.

Skeneidae. The sperm of three species of skeneid have been described [13]. All produce euspermatozoa and one species (*Zalipais laseroni*) has paraspermatozoa. The eusperm are uniflagellate with a long (about 50 μ m in *Zalipais laseroni*), tubular helically coiled nucleus. Anterior to the nucleus of *Z. laseroni* there is a small conical acrosome. The midpiece consists of a mitochondrial sleeve which surrounds an electron-dense rod (about 3 μ m long).

The parasperm of *Z. laseroni* consist of an elongate electron-dense head, a short midpiece of centriolar rods and mitochondria, and a posterior tuft of flagella.

DISCUSSION

Patellogastropod-Vetigastropod relationships

LINDBERG [30] has argued that limpets from the superfamilies Patelloidea, Nacelloidea and Acmaeoidea have morphological features which differ from those of other archaeogastropods. These limpets were therefore removed to a separate order, Patellogastropoda and are regarded as an early holophyletic gastropod offshoot [7, 9]. It is now clear that there are also distinct differences in sperm morphology between the patellogastropods and vetigastropods. Patellogastropods always produce aquasperm, the nuclei of which never have an anterior fossa, whereas in the majority of vetigastropods with aquasperm (the Fissurellinae is an exception) this nuclear feature is present. Furthermore, in patellogastropods the acrosome always has a wide posterior invagination. By contrast in vetigastropods the posterior acrosomal invagination is always in the form of a narrow canal. These small but consistent differences in sperm morphology between patellogastropods and vetigastropods supports the view [7, 30] that these two taxa are distinct from each other.

Patellogastropod relationships

Although information on sperm morphology from families of Patellogastropoda is still incomplete, results to date suggest that each family has a sperm with distinguishing features. As the evolutionary trends and relationships between and within patellogastropods are not certain [30], spermatozoon morphology may eventually provide additional clues to limpet phylogeny when data from outstanding taxa (e.g. Lepetidae) and more detailed information from other taxa (e.g. Nacellidae and Acmaeidae) are forthcoming. Despite the incomplete data base, the information available on sperm morphology invites some speculation on limpet phylogeny. It is suggested that spermatozoa with the most plesiomorphic features are found in the Patellidae, with some species having a sperm with a short "bullet-shaped" nucleus and small undifferentiated acrosome (Fig. 1A). Apomorphic features of sperm of other species of Patellidae, as well as the Nacellidae, Lottiidae and Acmaeidae would therefore include a lengthening of the nucleus (often accompanied by an elaboration of the shape) and an increase in the size and complexity of the acrosome (Fig. 1B-G). Sperm morphology therefore adds further support to the view that within the Patellogastropoda, the patellids are the most primitive taxon [30].

From the few species described to date [18, 21, 28] (Table 2) the spermatozoa of the Lottiidae and Acmaeidae appear to be very similar. It is proposed that of the two taxa, the sperm of the Acmaeidae are more plesiomorphic, having smaller acrosomes which are slightly simpler in morphology (e.g. undifferentiated internally). As the fossil history for *Patelloidea* (Acmaeidae) is greater than that of the Lottiidae [30], it might be expected therefore that the acmaeids would have more plesiomorphic sperm.

The morphology of the spermatozoa of most species of the Patellidae is now known [1, 18-21, 25, 26, 34] and the data have not only provided the first insights into relationships within this family of limpets but have also provided clues to their evolutionary radiation. Most species have one of three unequivocal types of sperm (designated Types I, III and VI by HODGSON *et al.* [25]; Table 2) and it is possible that they represent three lines of patellid radiation which have occurred in separate biogeographic areas. HODGSON *et al.* [25] suggest that species with type I sperm (Fig. 1A) probably had their centre of radiation in the Indo-Pacific, those with type III sperm (Fig. 1C) in the South-East Atlantic and finally those with type VI sperm (Fig. 1E) in the North East Atlantic and Mediterranean.

Vetigastropod relationships

The Vetigastropoda comprise the Pleurotomarioidea, Fissurelloidea, Haliotoidea, Trochoidea, Scissurelloidea and Lepetodriloidae. The broad similarities in the structure of the spermatozoa of the Pleurotomarioidea, Fissurelloidea, Haliotoidea, and Trochoidea add further

support to the contention [7, 10, 22, 24, 28] that these superfamilies are phylogenetically closely related. In particular, the spermatozoa of the pleurotomarids and the those of the Trochoidea (particularly the Trochidae) are very similar [10, 15] suggesting that these two superfamilies have a close relationship. Thus sperm morphology supports similar conclusions based on other morphological features [7, 8, 15].

It is suggested that within the Trochoidea, the most plesiomorphic sperm are found within the Trochidae and Phasianellidae whereas the spermatozoa of the Turbinidae have more apomorphic features. These features include a very wide anterior nuclear invagination and a conical acrosome (differentiated internally), the base of which lies within the nuclear invagination, which has lengthened, constituting >50% of the total head length. Sperm morphology therefore does not accord with other morphological features of the Turbinidae, the turbinids having retained many primitive pleurotomariacean features [17]. However it should be noted that HICKMAN & MCLEAN [17] regard the phasianellids as a subfamily of the Turbinidae. Nevertheless spermatologically the phasianellids are more similar to the trochids than to other turbinids (Fig. 2).

The Skeneidae are unlike other trochoideans in that the species examined to date (*Z. laseroni*) [13] has dimorphic spermatozoa, and in addition the euspermatozoa are of the modified (after FRANZÉN [4]) or introsperm (after ROUSE & JAMIESON [32]) type. Such spermatozoa are found in skeneid gastropods with internal fertilization and it is highly likely that skeneids have internal fertilization. The fact that skeneids have introsperm makes it difficult to use sperm morphology to assess their phylogenetic relationship to most other vetigastropods. However the similarity in the structure of the spermatozoa of the skeneids and some caenogastropods (notably the Cerithioidea) has led HEALY [13] to suggest that despite some morphological incongruities, the vetigastropods are the probable ancestral source of the caenogastropods.

Representative species from two other vetigastropod superfamilies have now been found to have "modified" spermatozoa, the Scissurellidae [14] and Lepetodrilidae [23]. In both cases modifications to sperm morphology can be linked to a modification in the biology of fertilization. The scissurellids do not have organs to facilitate internal fertilization and it has therefore been suggested that fertilization occurs in the mantle cavity [8]. The morphology of the sperm of both the Scissurellidae and Lepetodrilidae are consistent with an ent-aquasperm form (after ROUSE & JAMIESON [32]) supporting the idea of fertilization in the mantle cavity.

Studies on spermatozoon morphology of the Patellogastropoda and Vetigastropoda have provided interesting insights into relationships within and between these taxa. However if information from sperm morphology is to be incorporated into phylogenetic and cladistic studies, descriptions from outstanding taxa are required. Although all patellogastropods and most vetigastropods produce aquasperm which are essentially plesiomorphic, these sperm can yield apomorphic characters [26] making it possible to incorporate characters from sperm into cladistic analyses. Within the Patellogastropoda comprehensive data on the morphology of the sperm of the Patellidae exist, but far less is known about other families. Within the vetigastropods an examination of the sperm of hydrothermal vent and deep sea taxa, such as the Skeneidae may help in furthering an understanding of the evolution of higher gastropods. Finally, urgent attention needs to be given to other archaeogastropod taxa such as the Neolepetopsidae, Cocculiniformia, Peltospiroidea, Neomphaloidea, Seguenzioidea, Cyclophoroidea and Ampullarioidea. An examination of sperm from taxa such as these could contribute to a greater understanding of gastropod phylogeny.

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