

Spermatozoal Ultrastructure and Phylogeny in the Parasitic Platyhelminthes

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ABSTRACT

The ultrastructure of spermiogenesis and spermatozoon is briefly described and illustrated in fifteen species: nine Digenea, *Proisorchis ghanensis*, *Apatemon graciliformis*, *Spirorchis* sp., *Aphalloides coelomicola*, *Proctoeces maculatus*, *Aporocotyle spinosicanalis*, *Schistosoma* sp., *Haematoloechus* sp. and *Echinostoma togoensis*, two Monogenea Polyopisthocotylea, *Heteraxinoides* sp. and *Diplozoon gracile*, two Monogenea Monopisthocotylea, *Cleitharcticus* sp. and *Furnestinia echeneis*, and two Eucestoda, *Moniezia* sp. and *Echeneibothrium* sp. Most of these species have their spermatozoon described for the first time. The literature shows that sperm ultrastructure is now known in about 140 genera (almost 200 species) of parasitic Platyhelminthes (= Aspidogastrea, Digenea, Monogenea, Amphilinidea, Gyrocotylidea, and Eucestoda). The general structure (two 9+1 axonemes, microtubules only dorsal and ventral in the principal region of the spermatozoon) originates from a process of proximo-distal fusion and is found in the Aspidogastrea, Digenea, Gyrocotylidea and Amphilinidea, with, however, a few variations in the first two groups. The Monogenea Polyopisthocotylea are differentiated by the presence of additional lateral microtubules. The Monogenea Monopisthocotylea are characterised by the loss of certain structures and a general trend towards a simpler spermatozoon. The Eucestoda are characterized by the loss of the mitochondrion and show some other deviations. The genus *Schistosoma*, belonging to the Digenea, has a spermatozoal structure completely different from the general structure found in the two supposedly closely related families of blood-flukes, the Spirorchidae and Sanguinicolidae, and the spermatozoon is considered "progenetic". A precise identification of the outgroup for the parasitic Platyhelminthes is needed for a more reliable cladistic analysis of spermatozoal characters.

RÉSUMÉ

Ultrastructure des spermatozoïdes et phylogénie des Plathelminthes parasites

L'ultrastructure du spermatozoïde et de la spermiogénèse est décrite brièvement et illustrée chez quinze espèces: neuf Digenea, *Proisorchis ghanensis*, *Apatemon graciliformis*, *Spirorchis* sp., *Aphalloides coelomicola*, *Proctoeces maculatus*, *Aporocotyle spinosicanalis*, *Schistosoma* sp., *Haematoloechus* sp. et *Echinostoma togoensis*, deux Monogenea Polyopisthocotylea, *Heteraxinoides* sp. et *Diplozoon gracile*, deux Monogenea Monopisthocotylea, *Cleitharcticus* sp. et *Furnestinia echeneis*, et deux Eucestoda, *Moniezia* sp. et *Echeneibothrium* sp. Le spermatozoïde est décrit pour la première fois dans la plupart de ces espèces. Les données bibliographiques montrent que l'ultrastructure du spermatozoïde est maintenant connue chez approximativement 140 genres (presque 200 espèces) de Plathelminthes parasites (= Aspidogastrea, Digenea, Monogenea, Amphilinidea, Gyrocotylidea, et Eucestoda). La structure générale (deux axonèmes 9+1, microtubules seulement dorsaux et ventraux dans la région principale du spermatozoïde) résulte d'un processus de fusion proximo-distale et est rencontrée chez les Aspidogastrea, Digenea, Gyrocotylidea et Amphilinidea, avec toutefois quelques variations dans les deux premiers groupes. Les Monogenea Polyopisthocotylea se différencient de

la structure symplésiomorphe par la présence de microtubules latéraux additionnels. Les Monogenea Monopisthocotylea sont différenciés par la perte de nombreuses structures et une tendance générale vers un spermatozoïde plus simple. Les Eucestoda sont caractérisés par l'absence de la mitochondrie et montrent d'autres déviations. Le genre *Schistosoma*, appartenant aux Digenea, a un spermatozoïde à structure totalement différente de la structure générale qui est pourtant retrouvée dans les familles supposées proches (Spirorchidae et Sanguinicolidae), et son spermatozoïde est considéré comme "progénétique". L'outgroup des Platyhelminthes parasites doit être identifié de manière précise pour une analyse cladistique plus fiable des caractères du spermatozoïde.

The phylum Platyhelminthes represents an exemplary case of the use of comparative spermatology for the understanding of phylogeny, because it combines several characteristics: 1. absence of fossils, necessitating that characters may be sought only in living taxa; 2. small size of organisms, which have directed the interest of researchers toward electron microscopy from the onset of this technique; 3. sperm morphologies which, although they follow a general ground plan, are extremely variable; 4. in most parasitic Platyhelminthes, an enormous development of the reproductive apparatus and a constant fecundity, making the work of the electron microscopist easier.

Moreover, some "historical" factors have emphasised the importance of comparative spermatology in the Platyhelminthes. The first is that several schools of research have been created in this field and continue to be investigating actively. Professor EUZET has established, in the seventies, the first of these schools in Montpellier, from which were successively issued the theses of KTARI (1971)[135], MOKHTAR-MAAMOURI (1976)[152], FOURNIER (1980)[60], and JUSTINE (1980) [88], (1985)[95]. The work of SWIDERSKI [58, 209-222] was linked with this school. A second generation of researchers has been formed by the students of EUZET: AZZOUZ-DRAOUI (1985)[6] and NOURY-SRAÏRI (1988)[162]. Xavier MATTEI, commencing with a thesis in the same University of Montpellier on Fish comparative spermatology, went on to establish an active group in Dakar, Senegal, where JUSTINE worked on various Platyhelminthes [88-95, 105-123] and later MARCHAND and BÅ worked on Cestodes [8-21]. Two other independent schools, which are not limited to spermatology but also deal with other ultrastructures, were developed in Australia by Klaus ROHDE (with Nikki WATSON [174, 175, 178, 179, 187-189, 191-193, 233-235, 237-239, 241, 242, 244] and others [140, 141]) and in Germany by Ulrich EHLERS [49-53] (with SOPOTT-EHLERS [202], XYLANDER [250-252], and others). In the past years, several independent teams have begun original works in this field, and the establishment of some researchers in China [40, 65, 142, 143, 199, 255-257] and Korea [2, 82, 83, 201] promises that research on spermatozoa will benefit from the wide diversity of the fauna in these regions.

The second historical factor is that spermatozoal ultrastructure was recognised relatively precociously as a source of characters for the cladistic analysis of the phylum Platyhelminthes. As early as 1984-1985, EHLERS [49-51] and later BROOKS [30] used spermatozoal apomorphies for defining *major* groups of the phylum. The Trepaxonemata Ehlers, 1984 was defined on the basis of an ultrastructural character of spermatozoa (the 9+"1" axoneme). This a striking example of the importance of comparative spermatology for the cladistic analysis of the Platyhelminthes: such a definition would have been impossible ten years before, but it remains unquestioned ten years later. Several groups of Platyhelminthes such as the Temnocephalida [77, 98, 129], the Prolecithophora [53], the Cercomeridea [98] or others [50, 51, 97, 98] have also been defined on the basis of spermatozoal ultrastructural characters.

Table 1 is a list of genera studied for sperm ultrastructure. Comparison with a similar Table published in 1991 [98] shows that the number of genera studied for sperm ultrastructure in the parasitic Platyhelminthes has increased from 98 to 141 (representing almost 200 species) in four years, thus giving an idea of the vitality of these studies in the past years.

This chapter includes new results from several species and a general presentation of sperm ultrastructure in the various taxa of the parasitic Platyhelminthes. The term "parasitic Platyhelminthes" refers in this study to the major taxa (Aspidogastrea, Digenea, Monogenea,

Gyrocotylidea, Amphilinidea and Eucestoda) which include only parasitic species. This study excludes, however, the various parasitic species (see [182]) which belong to the "Turbellaria". The parasitic Platyhelminthes defined above are considered monophyletic in all modern analyses, but are called the Cercomeridea [30] or the Neodermata [181] according to the position assigned to the Udonellidea. Data concerning the "Turbellaria" and Eucestoda are detailed in others chapters of this book by WATSON & ROHDE [232] and BÂ & MARCHAND [21], respectively. The results of the cladistic analyses of the Platyhelminthes previously performed by the author [97-99, 102] will not be repeated here.

MATERIAL AND METHODS

Observations are presented here on the following parasitic species, for which results have not previously been published or have been published in a very incomplete form. Digenea: *Prosorthis ghanensis* Fischthal et Thomas, 1972, Sclerodistomatidae, from the fish *Acanthurus monroviae* Steindachner, 1876, Dakar; *Apatemon graciliformis* Szidat, 1928, Strigeidae, from the bird *Cairina moschata*, Guadeloupe, French West Indies; *Spirorchis* sp., Spirorchidae, from the turtle *Pelusios adansonii*, Lac de Guiers, Senegal; *Aphalloides coelomicola* Dollfus, Chabaud et Golvan, 1957, Cryptogonimidae, from the fish *Gobius micropus*, Mediterranean, France; *Proctoeces maculatus* (Loos, 1901) Odhner, 1911, Fellodistomatidae, from the fish *Crenilabrus cinereus*, Mediterranean, France; *Aporocotyle spinosicanalis* Williams, 1958, Sanguinicolidae, from the fish *Merluccius merluccius* L., 1758, Mediterranean, France; *Echinostoma togoensis* Jourdan et Kulo, 1978, Echinostomatidae, from mice, strain from Togo; *Haematoloechus* sp., Haematoloechidae, from the amphibian *Rana* sp., Dakar, Senegal (spermiogenesis has already been described [111] in this species but one micrograph is added here for comparison); *Schistosoma* sp., Schistosomatidae, from sheep or cattle, Dakar, Senegal (this species has been referred to as *S. bovis* in publications concerning sperm [90, 108] but it has been shown later that certain specimens could belong to *S. curassoni* [3]); Monogenea: *Furnestinia echeneis* (Wagener, 1857), Diplectanidae, from the fish *Sparus aurata* L., Mediterranean, France; *Cleitharcticus* sp., Ancyrocephalidae, from the fish *Acanthurus monroviae* Steindachner, 1876, Dakar; *Heteraxinoides* sp., Heteraxinidae, from the fish *Pomadasys incisus*, Dakar (the spermatozoon has already been described in *Heteraxinoides* sp. from an other fish [123], but not in these specimens); *Diplozoon gracile*, Diplozoidae, from the fish *Gobio gobio*, small river near Montpellier, France (sperm in this species has been described [106, 107] but a micrograph is presented here for comparison); Cestodes: *Moniezia expansa* Rud., 1810, Anoplocephalidae, from sheep, Dakar; cestode, probably *Echeneibothrium* sp., Phyllobothriidae, from the fish *Raja miraletus* L., 1758, Dakar.

Living specimens were placed in cold (4 °C) fixative consisting of 2% glutaraldehyde in a buffer solution of 0.1 M sodium cacodylate, 0.1 M sucrose, and 0.2 mM CaCl_2 , at pH 7.2 at 4°C for 1 h. After washing in the same buffer, worms were postfixed for 1 h in 1% osmium tetroxide in the same buffer, dehydrated in ethanol and propylene oxide, and embedded in Epon. Ultrathin sections were contrasted with uranyl acetate and lead citrate, and observed with a Siemens Elmiskop 101 or a Hitachi H600 electron microscope.

OBSERVATIONS

Conventions and orientation

Antero-posterior orientation, or "where is the head?" Platyhelminthes spermatozoa are filiform and it is impossible to recognize a "head" or a "tail", in contrast to many other groups. For the orientation of the spermatozoon, some authors have chosen to consider the nucleus as anterior, by analogy to most animal spermatozoa. However, in the Platyhelminthes there is a fundamental antagonism between the orientation of the axonemes and that of the nucleus. In most animal spermatozoa, the anterior extremity of the axoneme, the centriole, pushes the nucleus forward and thus the orientation of the nucleus (considered as anterior in the sperm) and that of the axoneme are the same. In the parasitic Platyhelminthes, the nucleus is located at the non-centriolar extremity of the axonemes. Some limited observations about movement show that the axonemes are motile at the anterior part and that the nucleus is dragged at the posterior part [111]. Observations of fertilization [118, 125] show that the nucleus is the last part of the spermatozoon to enter the oocyte. Therefore, it is more logical to use the antero-posterior orientation in a

TABLE 1. — List of the genera of parasitic Platyhelminthes in which sperm ultrastructure has been studied.

Subclass Trematoda		<i>Choricotyle</i>	[135, 230]
Infraclass Aspidobothrea		<i>Concinnocotyla</i>	[244]
<i>Aspidogaster</i>	[22, 71, 72, 197]	<i>Diclidophora</i>	[67, 68, 135, 144, 231]
<i>Lobatostoma</i>	[182, 183, 193]	<i>Diplozoon</i>	[106, 107]
<i>Multicotyle</i>	[175, 233, 239]	<i>Erpocotyle</i>	[135, 231]
<i>Rugogaster</i>	[235]	<i>Gastrocotyle</i>	[196]
Infraclass Digenea		<i>Gonoplasius</i>	[191]
<i>Alaria</i>	[75]	<i>Gotocotyla</i>	[121, 178]
<i>Apatemon</i>	[94]	<i>Heteraxine</i>	[123]
<i>Aphalloides</i>	This study	<i>Heteraxinoides</i>	[123], This study
<i>Aporocotyle</i>	[94, 227-229], This study	<i>Hexostoma</i>	[119]
<i>Brachylaimus</i>	[254]	<i>Kuhnia</i>	[120]
<i>Bucephaloides</i>	[57]	<i>Lagarocotyle</i>	[73]
<i>Clonorchis</i>	[82, 83, 151]	<i>Metamicrocotyla</i>	[23]
<i>Collyricloides</i>	[94]	<i>Microcotyle</i>	[120, 135, 230, 231, 253]
<i>Corrigia</i>	[173]	<i>Neopolystoma</i>	[241]
<i>Cotylophorum</i>	[75]	<i>Octomacrum</i>	[69, 70]
<i>Cryptocotyle</i>	[171]	<i>Plectanocotyle</i>	[135, 230]
<i>Dicrocoelium</i>	[42, 160]	<i>Polylabroides</i>	[192]
<i>Didymozoon</i>	[115, 116]	<i>Polystoma</i>	[26]
<i>Echinostoma</i>	[78, 94], This study	<i>Polystomoides</i>	[174, 177]
<i>Eurytrema</i>	[63]	<i>Pricea</i>	[244]
<i>Fasciola</i>	[65, 80, 204-206]	<i>Protomicrocotyle</i>	[196]
<i>Fibricola</i>	[201]	<i>Pseudodiplorchis</i>	[36]
<i>Fischoederius</i>	[143]	<i>Pseudomazocraes</i>	[120]
<i>Ganeo</i>	[198]	<i>Pterinotrema</i>	[94]
<i>Gonapodasmius</i>	[89, 109, 118]	<i>Pyragraphorus</i>	[120]
<i>Gorgodera</i>	[75, 78]	<i>Sphyrnura</i>	[97]
<i>Gynaecotyle</i>	[43]	Cohort Monopisthocotylea	
<i>Haematoloechus</i>	[28, 32-35, 78, 111], This study	<i>Acanthocotyle</i>	[103, 149, 223]
<i>Maritrema</i>	[74]	<i>Amphibdella</i>	[105, 127]
<i>Meiogymnophallus</i>	[48]	<i>Amphibdelloides</i>	[113]
<i>Metagonimus</i>	[2]	<i>Anoplodiscus</i>	[234]
<i>Metorchis</i>	[142]	<i>Caballeroctyla</i>	[105, 126]
<i>Microphallus</i>	[38, 39, 48]	<i>Calceostoma</i>	[105, 124]
<i>Neochasmus</i>	[47, 81]	<i>Calicotyle</i>	[225, 238]
<i>Paragonimus</i>	[62, 63, 76, 151, 164, 165, 194, 255]	<i>Cichlidogyrus</i>	[54]
<i>Pharyngostomoides</i>	[66]	<i>Cleithrarticus</i>	[94, 110], This study
<i>Podocotyle</i>	[64]	<i>Dionchus</i>	[105, 125, 126]
<i>Postharmostomum</i>	[40, 143]	<i>Diplectanum</i>	[110, 117]
<i>Proctoeces</i>	[94], This study	<i>Encotyllabe</i>	[97, 128]
<i>Prosorchis</i>	This study	<i>Entobdella</i>	[224, 226]
<i>Pycnopus</i>	[143]	<i>Euzetrema</i>	[60, 61]
<i>Quinqueserialis</i>	[249]	<i>Furnestinia</i>	[105], This study
<i>Schistosoma</i>	[4, 5, 45, 55, 56, 79, 84, 88, 90, 100, 104, 108, 131, 151, 166-168, 203, 257], This study	<i>Gyrodactylus</i>	[134]
<i>Spirorchis</i>	[94], This study	<i>Heterocotyle</i>	[110, 112]
Subclass Cercomeromorphae		<i>Isancistrum</i>	[150]
Infraclass Monogenea		<i>Lamellodiscus</i>	[105]
Cohort Polyopisthocotylea		<i>Loimosina</i>	[105, 122]
<i>Atriasier (Atriasier)</i>	[101]	<i>Macrogyrodactylus</i>	[195]
<i>Atriasier (Atrispinum)</i>	[94, 97]	<i>Megalocotyle</i>	[91, 114, 126]
<i>Axine</i>	[120]	<i>Monocotyle</i>	[238]
<i>Cemocotyle</i>	[123]	<i>Myxinidocotyle</i>	[103, 149]
		<i>Pseudodactylogyrus</i>	[139, 151, 195]
		<i>Tetraonchoides</i>	[128]
		<i>Tetraonchus</i>	[94]
		<i>Trochopus</i>	[135, 231]

TABLE 1. — continued.

Infraclass Cestodaria		<i>Hymenolepis</i>	[1, 10, 58, 130, 151, 172, 208, 211, 216]
Cohort Gyrocotylidea		<i>Inermicapsifer</i>	[13, 14, 210, 214]
<i>Gyrocotyle</i>	[250, 252]	<i>Lacistorhynchus</i>	[58, 212, 217]
Cohort Cestoidea		<i>Mathevotaenia</i>	[16]
Subcohort Amphilinidea		<i>Moniezia</i>	[9, 209], This study
<i>Amphilina</i>	[250]	<i>Monobothrium</i>	[151]
<i>Austramphilina</i>	[182, 187, 188]	<i>Monoecocetus</i>	[145]
Subcohort Eucestoda		<i>Nematotaenia</i>	[157]
<i>Acanthobothrium</i>	[152, 154, 155, 158, 216]	<i>Onchobothrium</i>	[158]
<i>Aporina</i>	[15]	<i>Oochoristica</i>	[222]
<i>Avitellina</i>	[14, 18]	<i>Phyllobothrium</i>	[153]
<i>Bothrimonus</i>	[145]	<i>Proteocephalus</i>	[58, 215, 219]
<i>Bothriocephalus</i>	[221]	<i>Pseudanthobothrium</i>	[145]
<i>Catenotaenia</i>	[210]	<i>Railletina</i>	[14, 17, 169]
<i>Cotugnia</i>	[14]	<i>Retinometra</i>	[12, 218]
<i>Cylindrotaenia</i>	[86, 87]	<i>Sandonella</i>	[19]
<i>Diphyllobothrium</i>	[29]	<i>Stilesia</i>	[11]
<i>Duthiersia</i>	[96]	<i>Taenia</i>	[59]
<i>Echeneibothrium</i>	[159], This study	<i>Tetrabothrius</i>	[207]
<i>Echinobothrium</i>	[6, 7, 58, 156]	<i>Thysanetia</i>	[20]
<i>Echinococcus</i>	[24, 160, 199]	<i>Trilocularia</i>	[148]
<i>Glaridacris</i>	[58, 216, 220]		
<i>Haplobothrium</i>	[146, 147]		

functional way rather than follow an unjustified analogy with spermatozoa of other groups which have a completely different ontogeny. The nucleus should be considered as *posterior*, and the extremity of the spermatozoon which is thinner, more motile, and devoid of nucleus should be considered *anterior*, because it contains the centrioles.

Dorso-ventral orientation. There are no functional arguments here. The usage follows the purely arbitrary orientation chosen by SATO *et al.* (1967) [194]: mitochondrion ventral, nucleus dorsal. Note that the antero-posterior and dorso-ventral orientations together allow recognition of a right side and a left side for the spermatozoon, a notion important for unilateral organelles such as undulating membranes [121].

Observations on spermiogenesis of some Digenea (Figs 1-3)

Spermiogenesis in Prosorthis (Fig. 1). Spermiogenesis in *Prosorthis* exemplifies the usual process found in most Digenea. The early spermatid, with round nucleus, has a short protuberance (termed zone of differentiation) from which two flagella grow in opposite directions (Fig. 1a). Later, the zone of differentiation elongates (Fig. 1b). The two centrioles are each associated with a striated root (Fig. 1b), and an intercentriolar body is located between them (Fig. 1a). The zone of differentiation has three processes elongating from its distal extremity: a median cytoplasmic process and two free flagella. Transverse sections show that the two flagella have the 9+“1” structure diagnostic of the Trepaxonemata, and that the median cytoplasmic process has dorsal and ventral microtubules. Attachment zones are visible and indicate the place where the flagella will fuse with the median process (Fig. 1c). The process of fusion is proximo-distal, i.e. it begins near the common cytoplasmic mass and ends at the elongating tip of the spermatid. After this fusion, the elongating spermatid (Fig. 1d) shows the same structure as mature spermatozoa: transverse sections show two axoneme, microtubules, and the mitochondrion. In addition, a section of the nucleus is visible in the nuclear region (Fig. 1e).

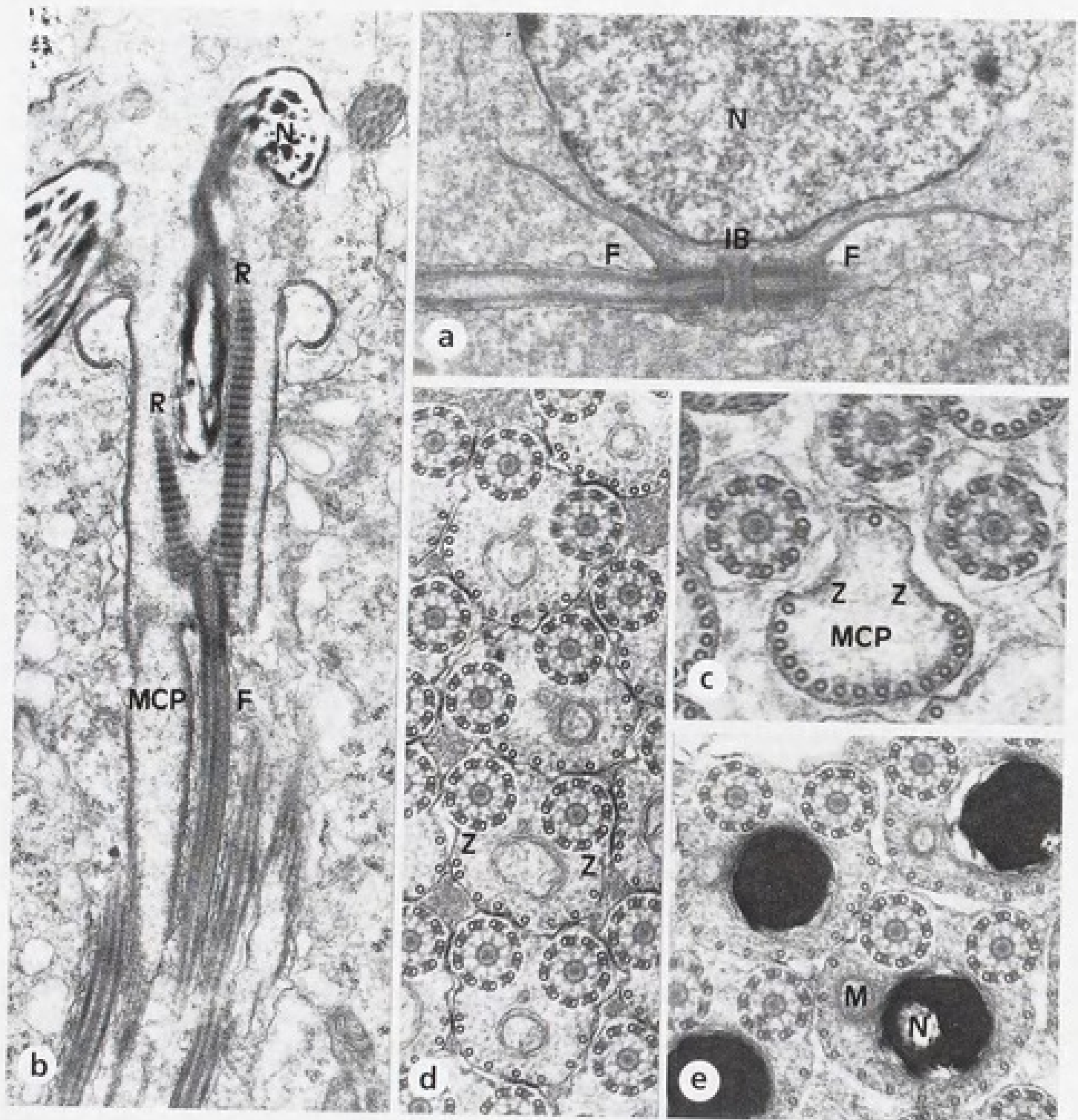


FIG. 1. — Spermiogenesis in the Digenea, exemplified in *Prosorhynchus ghanensis*. Note the 9+1 structure of axonemes and microtubules restricted to the dorsal and ventral side of spermatozoa. a: Early spermatid, with early zone of differentiation from which two flagella grow in opposite direction. IB, intercentriolar body. b: Mature zone of differentiation. The nucleus passes through the zone of differentiation, which bears three elongating processes: the median cytoplasmic process (MCP) and two flagella (one visible here). Each centriole has a striated root (R). c: Transverse section in median cytoplasmic process (MCP) and associated flagella. Note attachment zones (Z) where the flagella will later fuse with the MCP. d: Transverse section of elongating spermatids, after the fusion; attachment zones (Z) still visible. e: Transverse section of elongating spermatid, showing nucleus and mitochondrion. a, x 20 000; b, d, e, x 24 000; c, x 90 000. For all figures: F, flagellum; M, mitochondrion; N, nucleus.

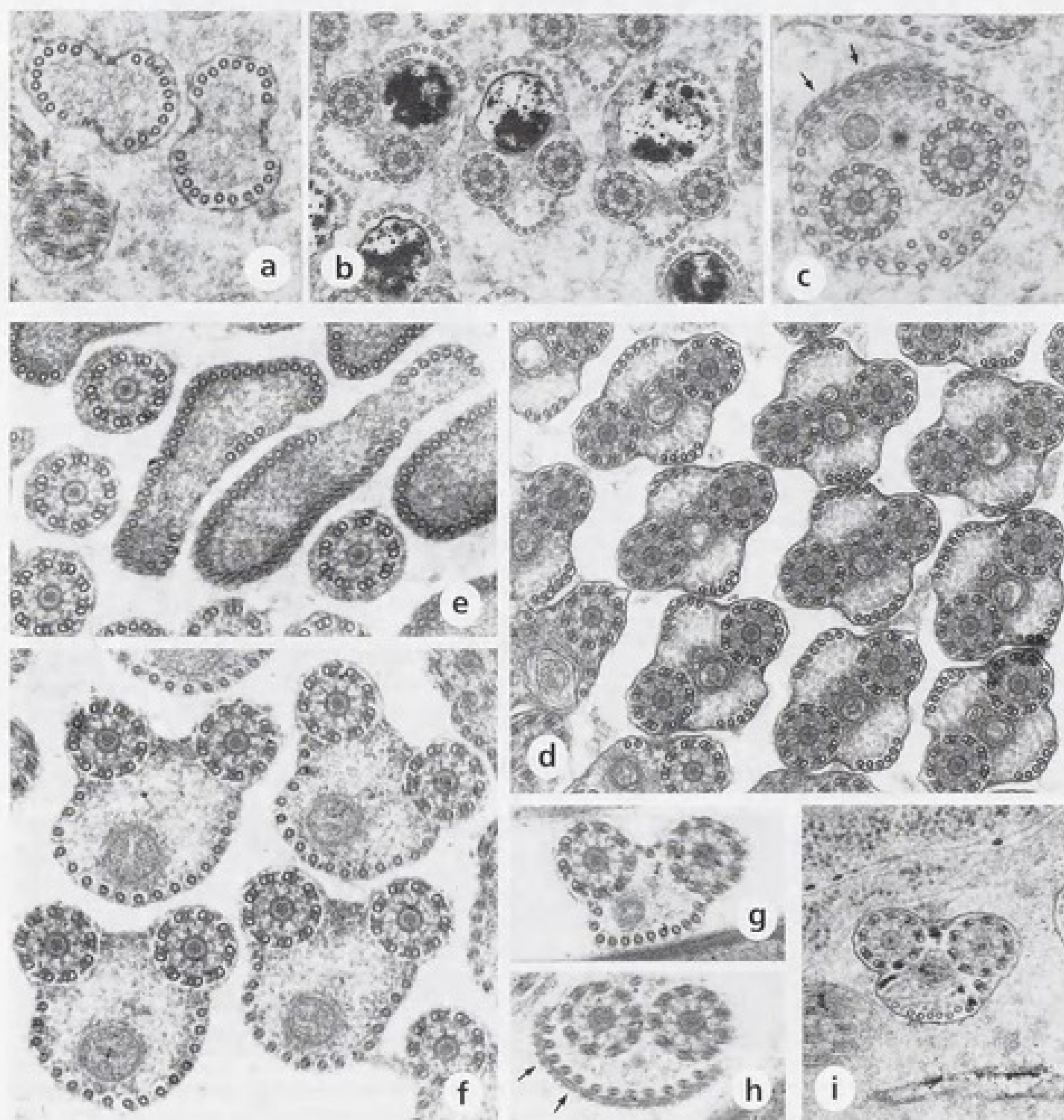


FIG. 2. — Homogeneity of spermiogenesis and spermatozoon structure in the Digenea. a-c: *Proctoeces maculatus*. d: *Haematoloechus* sp. e, f: *Apatemon graciliformis*. g, h: *Aphalloides coelomicola*. i: *Echinostoma togoensis*. a, e: Median cytoplasmic process of spermatid. d, f, g, i: Transverse section of spermatozoa in the mitochondrial region. b: Transverse section of spermatozoa in the principal region, containing the nucleus. c, h: Transverse section in a region (probably anterior) showing ornamentation (arrows) on the membrane. a, c-h, x 60 000; b, x 36 000; i, x 48 000.

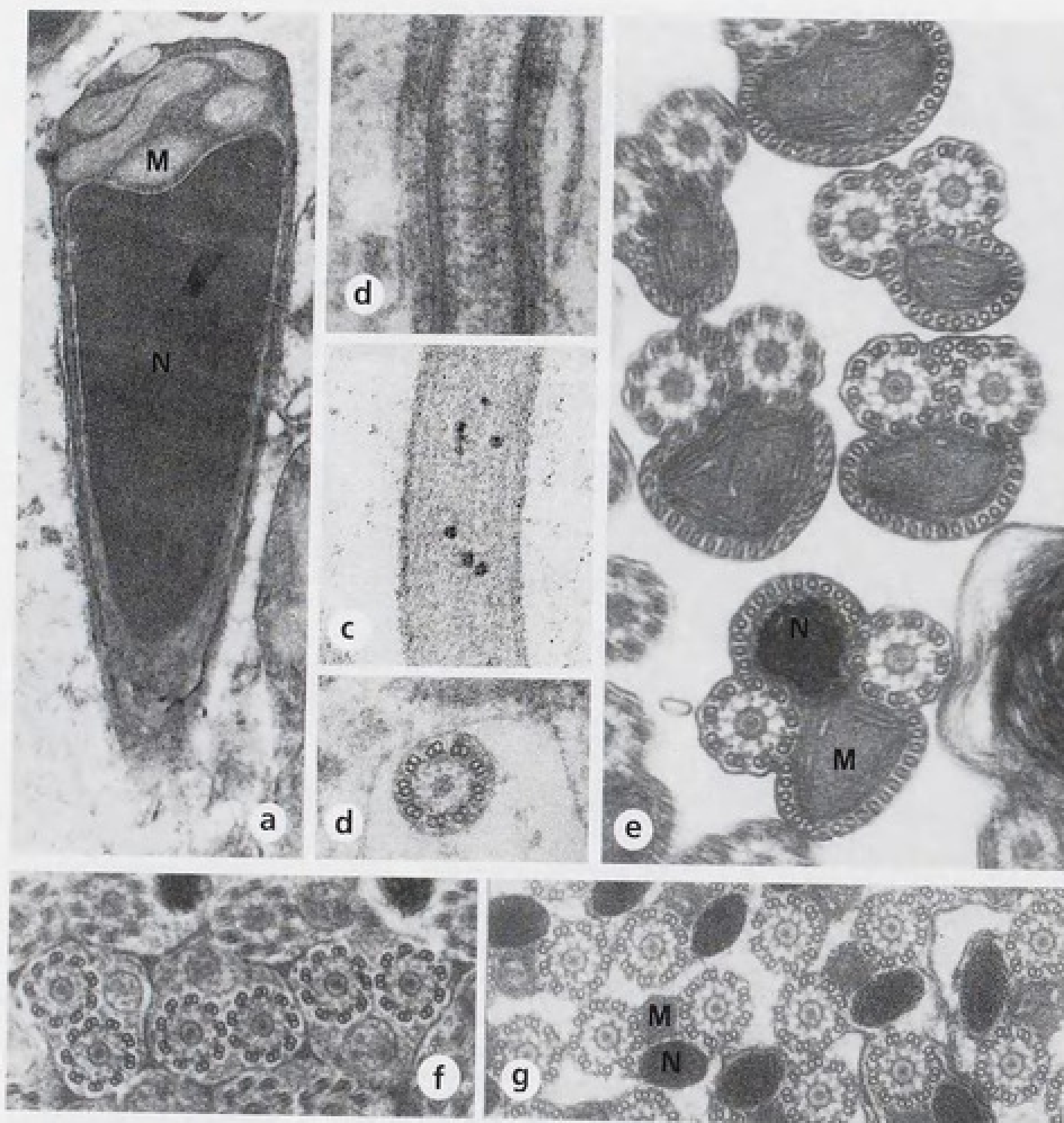


FIG. 3. — Spermatozoa in Schistosomes and other blood flukes. **a-d**: *Schistosoma* sp. (Family Schistosomatidae, blood flukes of mammals). **a**: longitudinal section of sperm body, with mitochondria at the anterior extremity and pyriform nucleus. **b**: longitudinal section of flagella. **c**: glycogen demonstrated in flagella by Thiéry's method. **d**: Transverse section of flagellum, showing a structure which is not a trepaxonematan $9+1$. **e**: *Spirorchis* sp. (Family Spirorchidae, blood flukes of turtles). Transverse section at various levels. **f, g**: *Aporocotyle spinosicanalis* (Family Sanguinicolidae, blood fluke of fishes). Transverse section at the mitochondrial level (**f**) and nuclear level (**g**). The spermatozoon of schistosomes is not threadlike and is similar to the zone of differentiation found in spermatids of the other Digenea ("progenetic spermiogenesis"[100]). In contrast, the spermatozoon of the other blood flukes is threadlike and similar to that of other Digenea in having two $9+1$ trepaxonematan axonemes. **b-d**, modified from [108]. **a**, x 24 000; **b, c, e**, x 90 000. **d, f, g**, x 60 000.

Spermiogenesis in Proctoeces (Fig. 2 a-c). The median cytoplasmic process (Fig. 2 a) has a similar as in *Prosorchis*, with its attachment zones clearly visible. Transverse section of spermatozoa in the testis show the usual structure with two axonemes, microtubules, mitochondrion and nucleus. As usual in the Digenea, the microtubules are only dorsal and ventral, and the lateral faces, along the axonemes, are devoid of microtubules (Fig. 2b). However, some transverse section (Fig. 2c) show a continuous microtubule row at the periphery of the spermatozoon. These sections also show external ornamentation associated with the membrane. These sections correspond with the anterior extremity of the spermatozoon, which originates from the zone of differentiation.

Spermatozoon of Haematolechus (Fig. 2d). This genus, which is easily collected from frogs, has been widely used for the early studies of spermiogenesis in the Digenea (see Table 1) and has become a standard. Sections of spermatozoa are displayed here to show the similarities of the other species with this standard. Sections show the mitochondrion and a small circular profile of two membranes, which probably represents the extreme anterior extremity of the nucleus.

Spermiogenesis in Apatemon (Fig. 2e, f). The median cytoplasmic process (Fig. 2e) shows the usual structure, but the number of microtubules is relatively high. Transverse sections of spermatid after the fusion still show the attachment zones (Fig. 2f).

Spermatozoa of Aphalloides (Fig. 2g, h) and Echinostoma (Fig. 2i). Spermatozoa show the usual structure, including a zone with external ornamentation in *Aphalloides* (Fig. 2h).

Spermatozoa in Schistosomes (mammal blood-flukes) and other blood-flukes: Sanguinicolidae or fish blood-flukes (Aporocotyle) and Spirorchidae of turtle blood-flukes (Spirorchis) (Fig. 3). Schistosomes show an aberrant sperm structure [90, 100, 104, 131]. The spermatozoon is not filiform (Fig. 3a), and there is one single axoneme, which has not the 9+“1” trepaxonematan structure. Instead, the axoneme shows 9 doublets and a central poorly contrasted structure, termed 9+0 or 9+“1” [108], and is devoid of dynein arms (Fig. 3 b-d). The phyletic interpretation of this aberrant structure is difficult and requires a study of the families considered as close to the schistosomes, i.e. the other blood-flukes, the spirorchid and sanguinicolids. In the spirorchid *Spirorchis*, the spermatozoon (Fig. 3e) is filiform and shows the usual structure found in the Digenea, with two 9+“1” axonemes and dorso-ventral microtubules. In the sanguinicolid *Aporocotyle*, the spermatozoon (Fig. 3 f-g) is filiform and shows two 9+“1” axonemes, but the peripheral microtubules are absent in most sections, although a few microtubules can be seen in some rare sections.

Observations on spermatozoa of the Monogenea Polyopisthocotylea (Figs 4-6)

Spermatozoon of Heteraxinoides (Fig. 4). Observations are briefly reported to exemplify the homogeneous structure found in most polyopisthocotylean monogeneans. The spermatozoon shows two 9+“1” axonemes, the nucleus and mitochondrion (Fig. 4). The fundamental difference from the Digenea is that the microtubule row, in the principal region of the spermatozoon, makes a complete circle around the sperm cell, i.e. it is not interrupted at the axoneme level.

Spermatozoon of Diplozoon (Fig. 5). The spermatozoon is highly aberrant [105-107]: it is elongate, aflagellate and contains several hundreds of parallel longitudinal microtubules (Fig. 5b). A view of the animal is presented (Fig. 6a) for the purpose of the discussion.

Spermatozoon of Gotocotyla (Fig. 6). This species has the general pattern found in the polyopisthocotylean monogeneans but shows an outstanding additional structure: a lateral undulating membrane, which contains a large number of parallel microtubules. The ultrastructure of the spermatozoon has been described previously [121], but Fig. 6 is an unpublished artist's view of the mature spermatozoon drawn from micrographs.

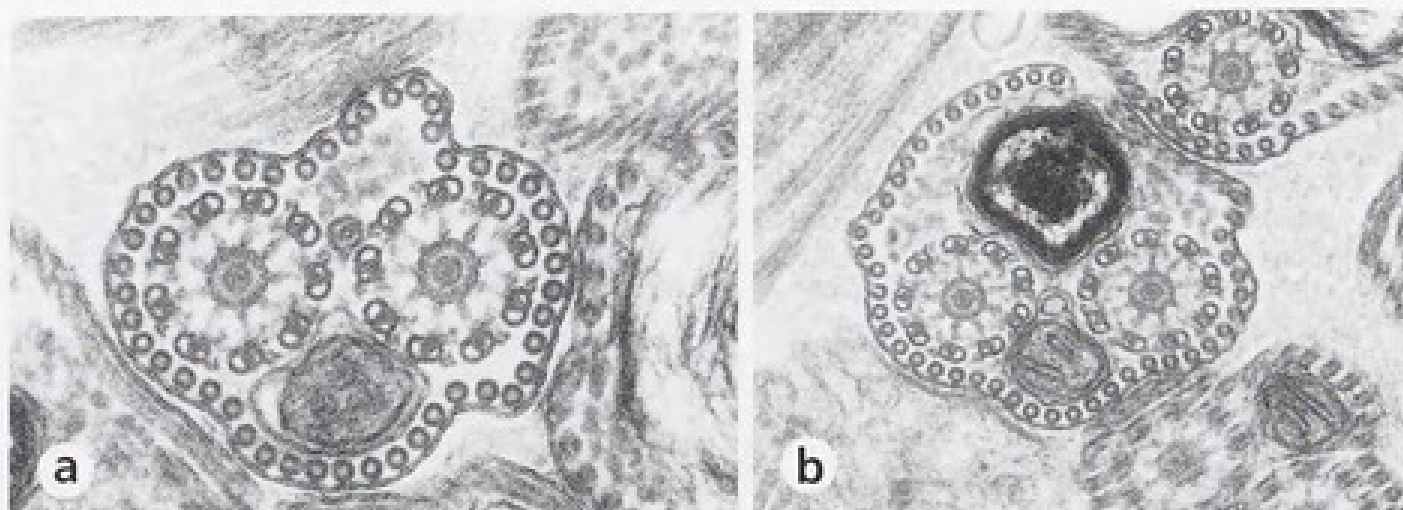


FIG. 4. — Spermatozoa in the Monogenea Polyopisthocotylea, exemplified by *Heteraxinoides* sp. **a, b**: Transverse sections showing two 9+1 axonemes, mitochondrion and nucleus. Note that the microtubules form a complete row around the spermatozoon (synapomorphy for the Polyopisthocotylea [97, 98]). **a**, x 90 000; **b**, x 120 000.

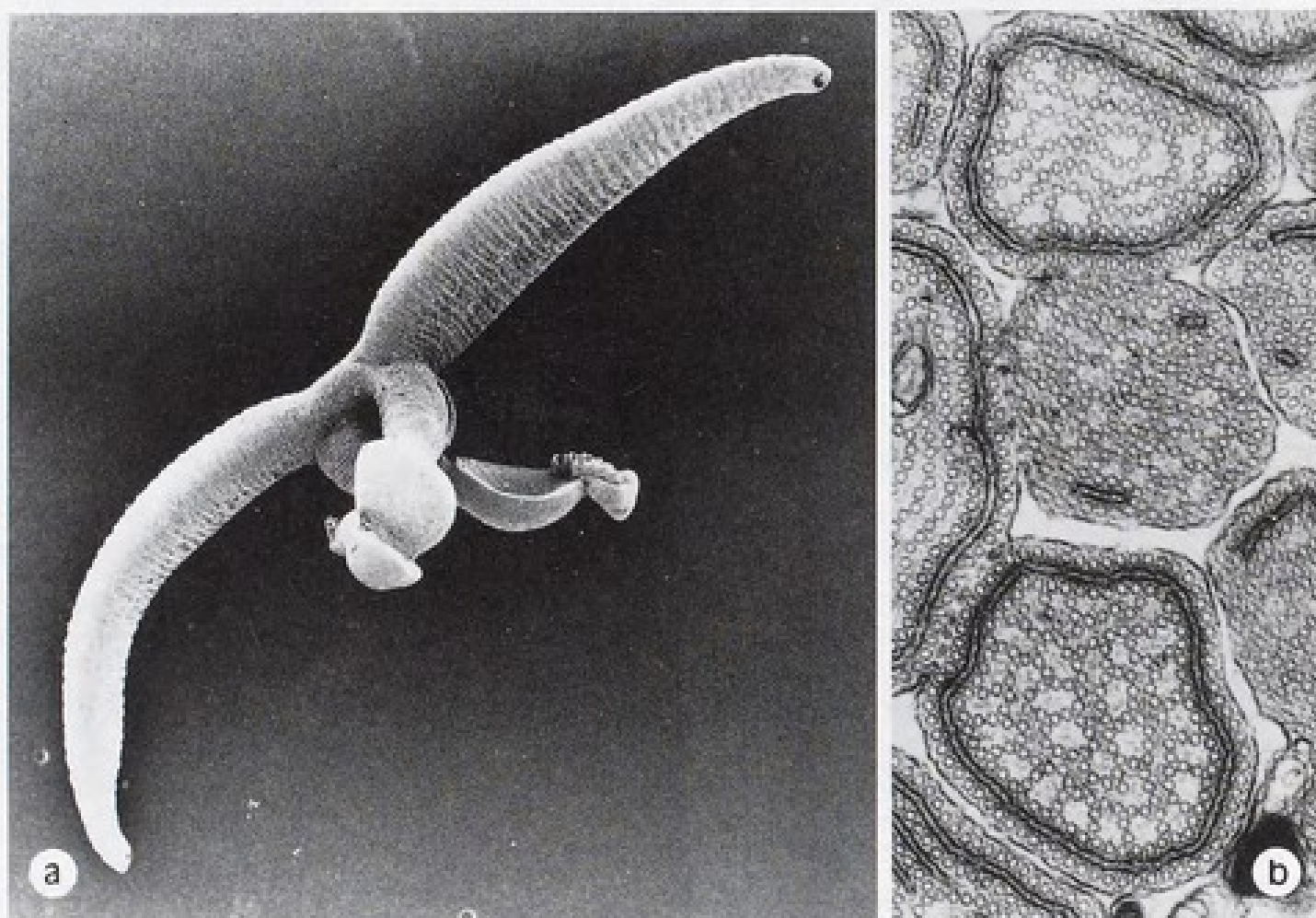


Fig. 5. — The aberrant case of *Diplozoon* (Monogenea Polyopisthocotylea). **a**: The two member of a pair are permanently fused. Scanning electron microscope photograph of *Diplozoon nipponicum* by Nathalie LE BRUN. **b**: Transverse section of spermatozoa of *Diplozoon gracile*, showing numerous parallel longitudinal microtubules (modified from [106]). This is the only known case of aflagellate spermatozoon in the parasitic Platyhelminthes, and this aberrant pattern is linked with the exceptional biology of reproduction.

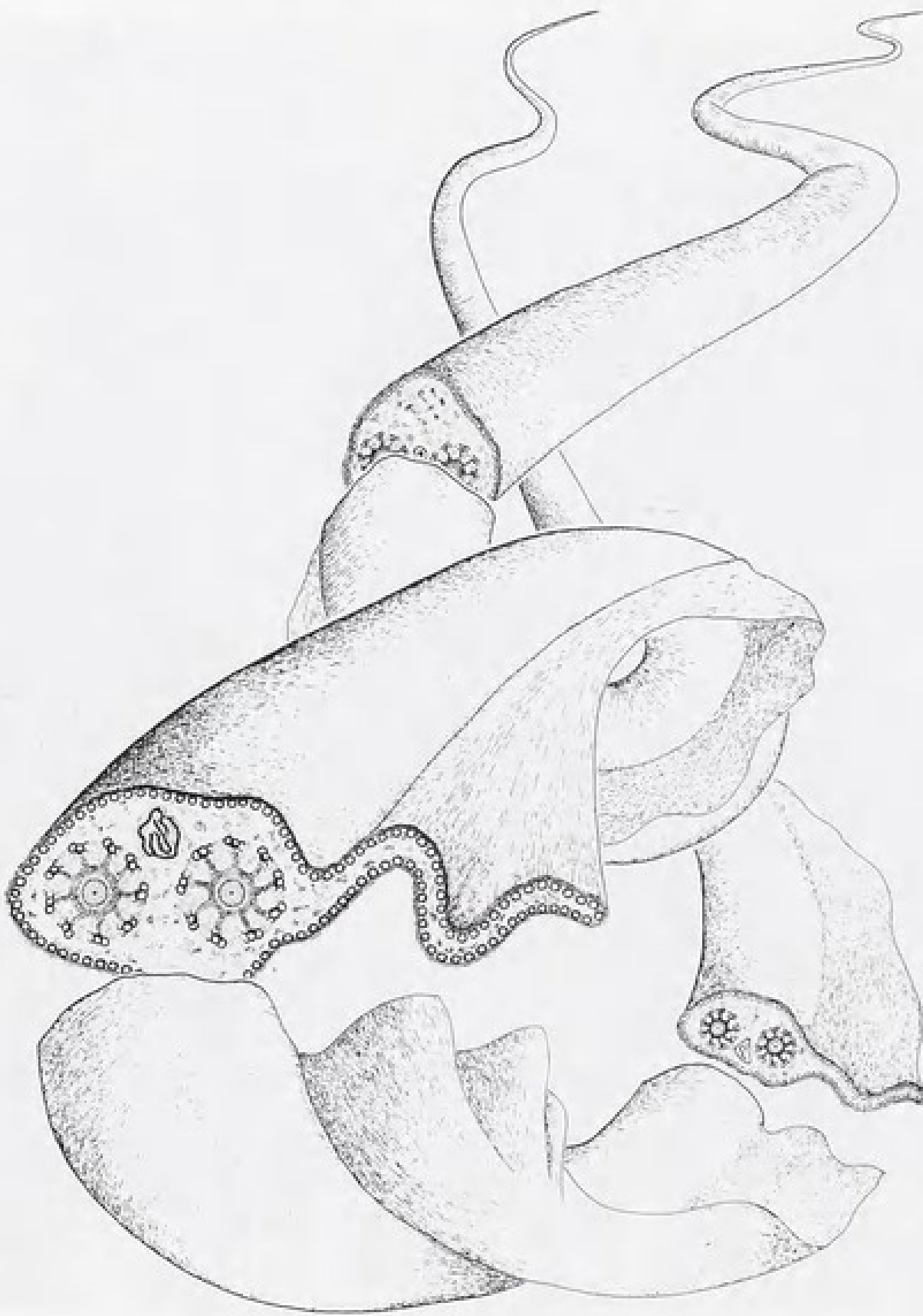


FIG. 6. — An artist's view of the spermatozoon of *Gotocotyla acanthura* (Monogenea Polyopisthocotylea), drawn from micrographs published in [121]. The spermatozoon has an undulating membrane along part of its length. The undulating membrane is an autapomorphy for this species. However, the general sperm structure is similar to the classic pattern found in the parasitic Platyhelminthes. Drawing by Nathalie LE BRUN.

Observations on spermiogenesis of the Monogenea Monopisthocotylea (Figs 7, 8)

The Monopisthocotylea show a variety of sperm structures. Observations reported here concern two species in which the spermatozoon has one single axoneme, and thus has the maximum deviation from the Digenea or the Polyopisthocotylea.

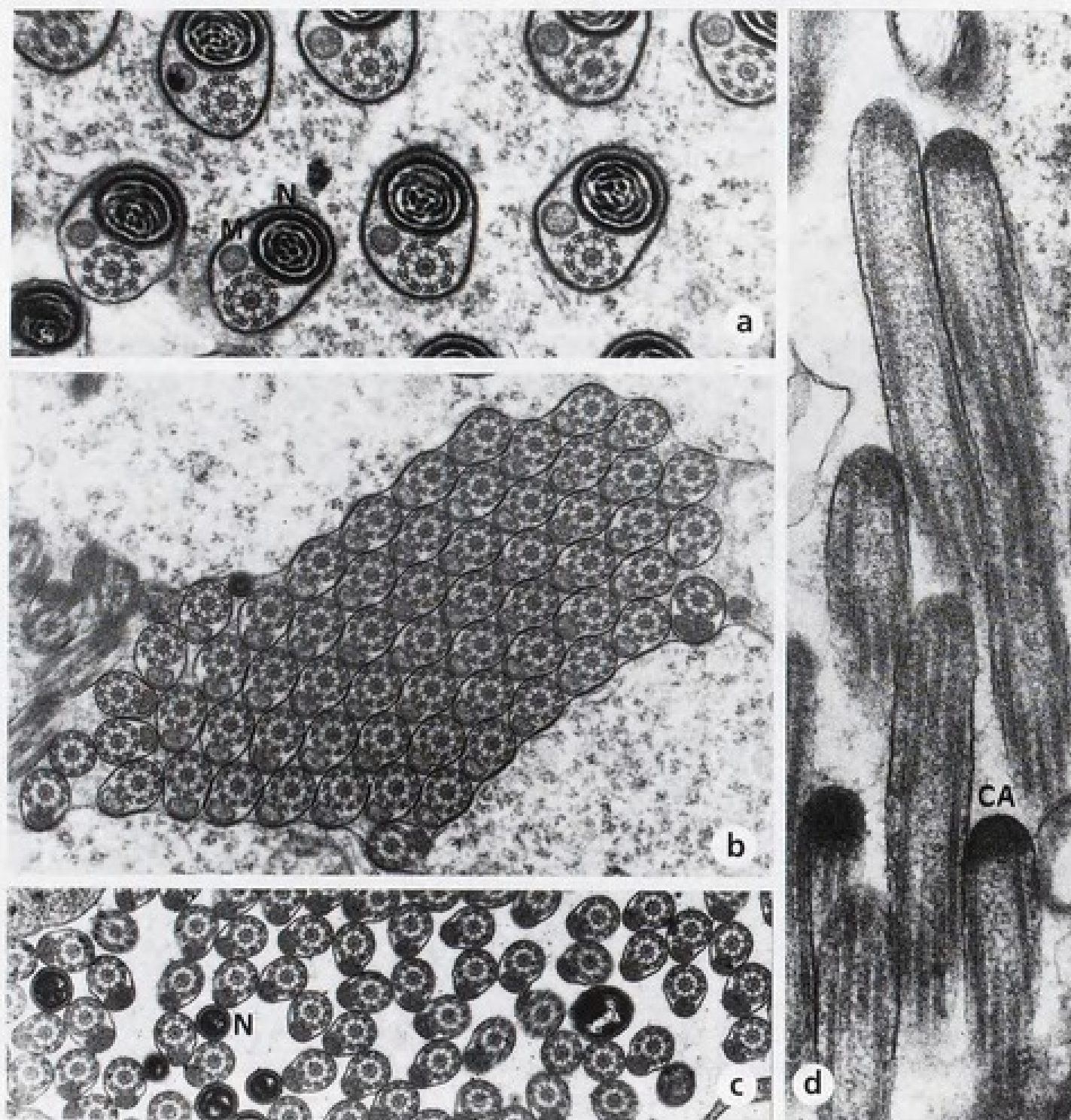


FIG. 7. — Spermiogenesis in *Furnestinia echeneis*, a Monogenea Monopisthocotylea with uniflagellate spermatozoon. a: Transverse section of zones of differentiation embedded in the common cytoplasmic mass (modified from [105]). b: Isogenic group with 64 spermatids; c: Mature spermatozoa have only one axoneme, and the nucleus is located in a region devoid of any other organelles. d: centriolar adjunct. a, d, x 48 000; b, c, 30 000.

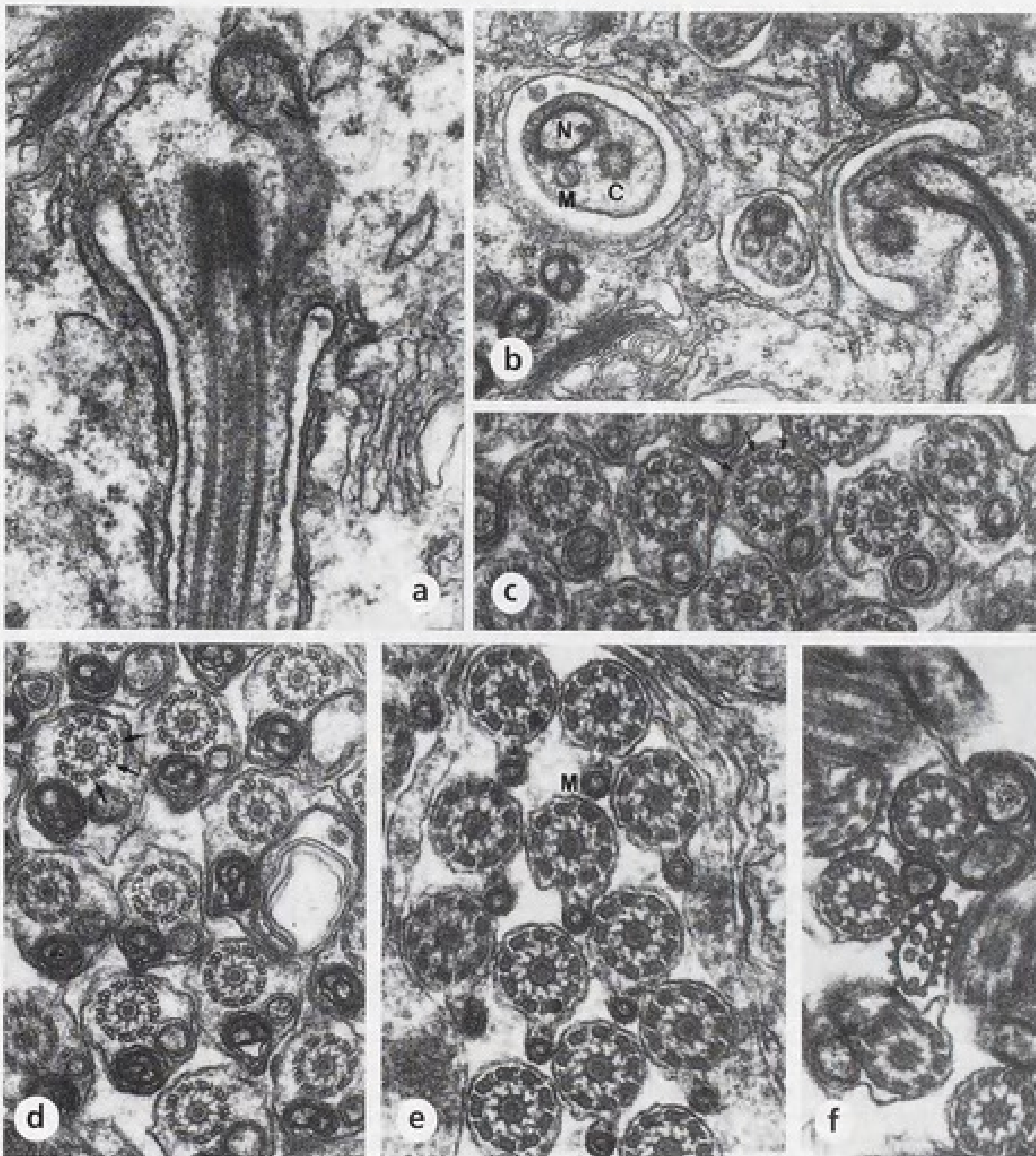


FIG. 8. — Spermiogenesis in *Cleithareticus* sp., a Monogenea Monopisthocotylea with uniflagellate spermatozoon. a: Longitudinal section of zone of differentiation containing one single axoneme. Note absence of intercentriolar body and striated roots (compare with Fig. 1a, b). b: Transverse section of zones of differentiation, showing single centriole and migrating nucleus and mitochondrion. c, d: Axonemes in growing spermatids show an incomplete tubule b (arrows) in the axoneme. e: Mature spermatozoa, however, have complete tubules b in their axoneme. f: Region with external ornamentation located at one extremity of the spermatozoon. a, d, x 48 000; b, x 30 000; c, e, f, x 60 000.

Spermiogenesis in Furnestinia (Monopisthocotylea) (Fig. 7). During spermiogenesis, the zone of differentiation is deeply embedded in the common cytoplasmic mass, and shows one single axoneme, the migrating nucleus and mitochondrion (Fig. 7a). It is not possible to recognize the proximo-distal fusion in this species, since only one element exists from the beginning to the end of spermiogenesis. Isogenic groups of spermatids comprise 64 elements (Fig. 7b). Mature spermatozoa in genital ducts show a relatively simple structure, with a region showing the axoneme and mitochondrion, and an other region showing the nucleus with no accompanying element (Fig. 7c). The anterior extremity contains a centriolar derivative (Fig. 7c). Cortical microtubules are absent at all stages of spermiogenesis.

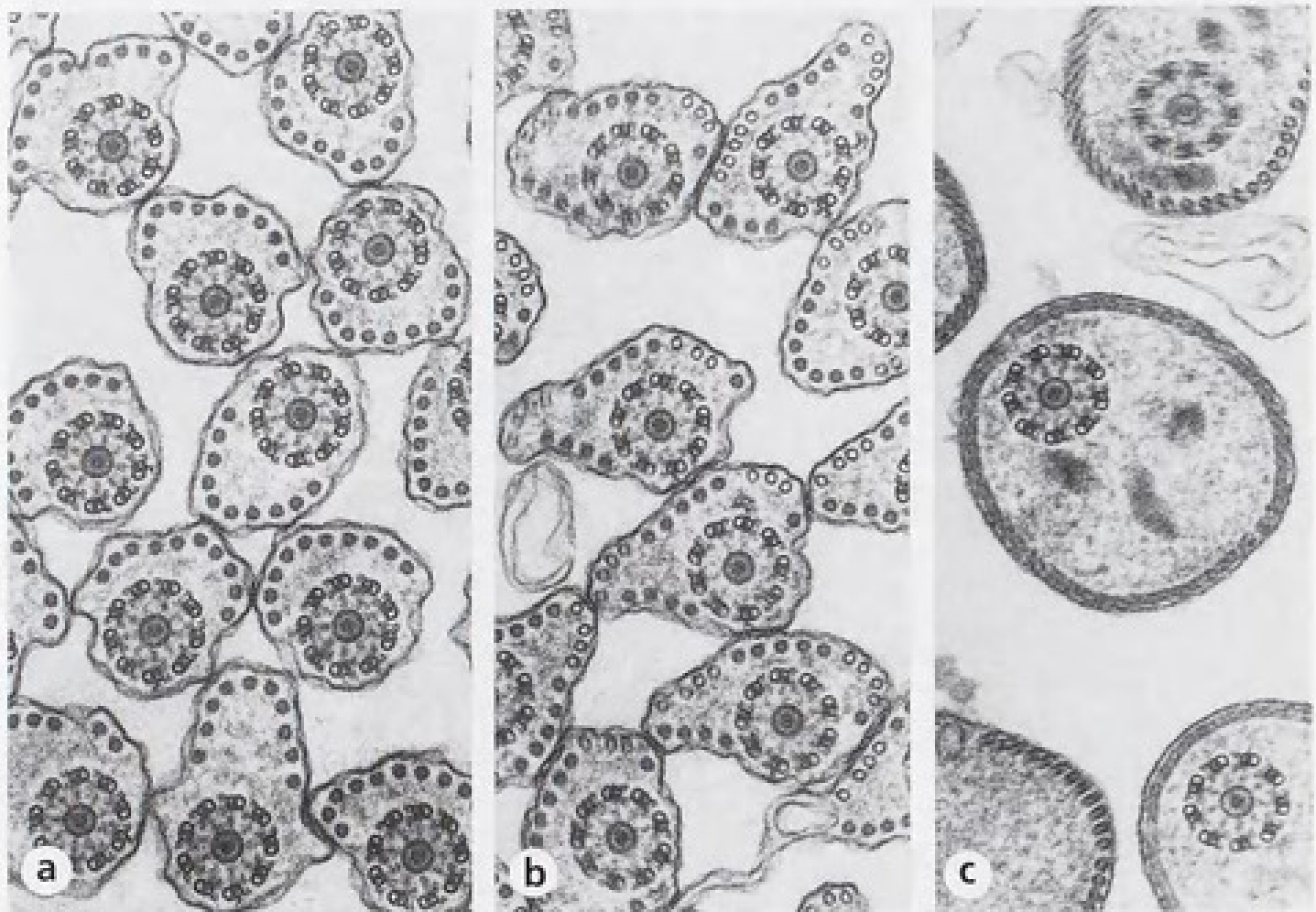


FIG. 9. — Spermatozoa of Eucestoda. Note the absence of mitochondrion, a synapomorphy for the Eucestoda. a, b: *Echeineibothrium* sp. Microtubules and axonemes are at focus on the same section. Note presence of two kinds of microtubules, with thin wall and thick wall. c: *Moniezia* sp. Note that the axoneme and the peripheral microtubules are not in perfect cross section on the same sections, because of the peripheral microtubules twisting, a synapomorphy for the Cyclophyllidea [98]. a-c, x 60 000.

Spermiogenesis in Cleitharecticus (Monopisthocotylea) (Fig. 8). The zone of differentiation (Fig. 8a) is deeply embedded in the cytoplasmic mass and shows one single centriole; the intercentriolar body and striated roots found in the Digenea are absent. As for *Furnestinia*, it is not possible to recognize the proximo-distal fusion in this species. In maturing spermatids, the axoneme shows incomplete b tubules (Fig. 8c, d), but these are complete in the mature sperm

cells (Fig. 8e, f). Mature sperm cells show one single axoneme, the nucleus and mitochondrion, and are devoid of cortical microtubules (Fig. 8f). Some rare sections (Fig. 8f) show external ornamentation on the membrane and may, with analogy with the Digenea, be considered as anterior, although this has not been fully demonstrated.

Observations on spermatozoa of the Eucestoda (Fig. 9)

A few observations are reported here to demonstrate the major characters of spermatozoa. The two species shown have a single axoneme, but others have two axonemes.

Spermatozoa of Echeneibothrium (Fig. 9a, b). Transverse sections show one single axoneme of the 9+“1” structure. The nucleus, not cut at the levels shown here, is present in other sections. Sections never show a mitochondrion. An interesting feature is the co-existence of two kinds of microtubules, either with thin wall and thick wall.

Spermatozoa of Moniezia (Fig. 9c). The spermatozoon has a single axoneme and is devoid of mitochondrion. Transverse sections of sperm never show both the peripheral microtubules and the axoneme perfectly transverse because the microtubules are twisted around the sperm body.

DISCUSSION

Structure of the spermatozoon in the major groups of parasitic Platyhelminthes

The basic structure: Digenea, Amphilinidea, Gyrocotylidea. The basic structure is here described for the Digenea but appears to be similar in the Amphilinidea and Gyrocotylidea. This structure is a synapomorphy for the Cercomeridea [98]. However, within the Cercomeridea, other structures have evolved from this basic pattern, and this pattern may be considered the symplesiomorphic structure for the parasitic Platyhelminthes.

The spermatozoon is filiform, very long, and therefore can be described only from transverse sections. It is composed of two main regions: the principal region, posterior, originating from the fusion of the three processes attached to the zone of differentiation of the spermatid; and the anterior region, originating from the zone of differentiation itself [98]. Transverse sections of the spermatozoon in the principal region (which contains the nucleus) show two axonemes, the mitochondrion and nucleus, and peripheral longitudinal microtubules limited to the ventral and dorsal faces. The microtubules are not twisted along the long axis of the sperm and are parallel. The anterior region is much shorter than the principal region. It generally shows a continuous microtubule row, not interrupted at the axoneme level, and is often marked by external ornamentations on the membrane.

It should be emphasized that, although the structure found in the principal region is remarkably homogeneous, a greater variety of structure is found in the anterior region. The anterior region of *Proctoeces* (Fig. 2c) has the structure described above, but *Aphalloides* (Fig. 2h) has ornamentation in a region which lacks a complete row of microtubules. In *Haematoloechus*, the two regions (anterior and principal) are separated by a “collerette” or collar which is visible with the light microscope [111]. The variations of the anterior region and its associated membrane ornamentation would probably be valuable for the understanding of phylogeny, because the principal region is too homogeneous to be useful. However, transverse sections of the anterior region often represent only a small proportion of the sections available, and sub-optimal fixations do not allow observation of the membrane ornamentation.

Variation in the Digenea. Sperm structure in the Digenea is homogeneous and variations are relatively rare.

In the didymozoids, deviations from the classic pattern have been found in *Gonapodasmius* and *Didymozoon*. *Gonapodasmius* has a relatively short spermatozoon, and the intercentriolar

body is lacking during spermiogenesis, but the ultrastructure of the spermatozoon is "classical" and the morphology is filiform. *Didymozoon* has a filiform spermatozoon, but the two axonemes show a 9+0 pattern and peripheral microtubules are absent.

In the Schistosomes (genus *Schistosoma*) the deviation from the sympleiomorphic pattern is extreme (Table 2).

TABLE 2. — Characteristics of spermiogenesis in the schistosomes and other Digenea (See Table 1 for references)

Characteristic	Digenea	<i>Schistosoma</i>
Shape of spermatid	great elongation, spermatozoon filiform	no elongation
Centrioles	migration from distal extremity of zone of differentiation to proximal extremity	no migration
Median cytoplasmic process	lengthening	abortion of process growth
Free flagella	lengthening, up to 400 μ m	moderate lengthening (20 μ m)
Shape of nucleus	successively round, pyriform and eventually very long and filiform	successively round and pyriform; no further elongation
Migration of nucleus	nucleus migrates to a region posterior to the centriolar region	no migration; nucleus remains in a position anterior to the centriolar region
Shape of mitochondria	mitochondria gather to fuse and form a single filiform and much elongated mitochondrion	mitochondria remain ovoid and do not fuse
Migration of mitochondria	the single mitochondrion migrates to a region posterior to the centriolar region	mitochondria remain anterior to centriolar region (and to nucleus)
Evolution of striated roots	striated roots, originally conspicuous, disappear at the end of spermiogenesis	striated roots remain in mature spermatozoa
Centriole ultrastructure	originally 9 triplets in spermatids, simplifies to 9 singlets	9 triplets in spermatid and in spermatozoon
Axoneme structure	in early spermatid, axonemes are sometimes observed without trepaxonematan core (9+0 structure); trepaxonematan 9+"1" in all other stages including spermatozoon	central trepaxonematan core absent in all stages
Separation of germ cells	spermatocytes form clusters; spermatids remain grouped in a common cytoplasmic mass until the very end of spermiogenesis	germ cells separate early in spermatogenesis; no clusters, no cytoplasmic mass

Sperm structure in the schistosomes and its deviation from the classic pattern is difficult to interpret if only a comparison between mature spermatozoa is performed. However, a comparison of the spermiogenetic processes shows that the mature sperm of schistosomes can be compared to a mature zone of differentiation in other Digenea. Spermiogenesis in the schistosomes therefore may be considered "progenetic" (i.e. the mature spermatozoon is a spermatid's zone of differentiation having precociously reached maturity) [100]. In addition, this zone of differentiation has one single axoneme instead of two.

It is interesting to note that the deviation in sperm pattern found in *Schistosoma* is not found in the other blood-flukes, the spirorchids and the sanguinicolids. These families, however, are considered to be closely related to the schistosomes in most phyletic schemes of the Digenea [31, 37, 44, 136, 200], but a different opinion was recently expressed [25]. The schistosomal sperm pattern is therefore restricted to the family Schistosomatidae. Moreover, in the genus *Schistosomatium*, a member of the family Schistosomatidae, light microscope observations have shown that there are clusters and that the spermatozoon is filiform, with two free flagella at one extremity [161]. Thus, the schistosome aberrant pattern appears to be restricted to the genus *Schistosoma* but is similar in all species of the genus [104].

The link between phylogeny and sperm ultrastructure is thus not obvious for the schistosomatids and related families (spirorchids, sanguinicolids). The influence of the biology of fertilization is probably important, and is discussed below.

Sperm ultrastructure in the Aspidogastrea. The Aspidogastrea are considered the most primitive group of Neodermata by ROHDE [183]. Indeed, their spermatozoa correspond to the classic, symplesiomorphic pattern, with two 9+"1" axonemes and dorso-ventral microtubules. However, some deviations from the plesiomorphic pattern do exist in the Aspidogastrea and are listed in Table 3 for three species; information available on *Aspidogaster* is scarce and therefore not included. The dense region could be considered a synapomorphy for the Aspidogastrea [235]. The undulating membrane of *Lobatostoma* [176, 193] and *Multicotyle* [239] is similar to that of the monogenean *Gotocotyla* [121] and should be considered a case of convergence.

TABLE 3.— Deviation from the basic pattern of the Cercomeridea found in the Aspidogastrea.

Characteristic	<i>Multicotyle</i>	<i>Lobatostoma</i>	<i>Rugogaster</i>
Dense region	Present	Present	Present in spermatid, not seen in mature sperm
Undulating membrane	Present	Present	Absent (but see Fig. 27)
Reference	[233, 239]	[193]	[235]

Spermatozoon structure in the Monogenea Polyopisthocotylea. The deviation from the symplesiomorphic pattern in the Polyopisthocotylea is the acquisition of supplementary microtubules on the lateral faces of the mature spermatozoon. This has been proposed as a synapomorphy for this group [97]. The Polyopisthocotylea are relatively homogeneous in their sperm structure, but some original features have been found in a few cases. These are generally restricted to one species and thus should be considered only as autapomorphies [101]. *Diplozoon*

has an aberrant spermatozoon with more than 400 parallel longitudinal microtubules and no axonemes. This represents the only case of aflagellate sperm in the parasitic Platyhelminthes, but aflagellarity has also evolved several times in the "Turbellaria" ([163, 190, 202]; see also [232]). The case of *Diplozoon* is dealt with below, in the paragraph on biology of fertilization.

Sperm structure in the Monogenea Monopisthocotylea. The Monopisthocotylea are characterised by synapomorphies such as the loss of the dorso-ventral microtubules, loss of striated roots, loss of intercentriolar body. A general evolutionary trend in this group is a tendency to shorter and simpler spermatozoa. Simplification of sperm includes the loss of one axoneme and the loss of peripheral microtubules, with the result that the sperm cell contains only three components, the nucleus, mitochondrion and one axoneme. A general cladistic analysis of sperm structure has been performed on the Monopisthocotylea [97] and updated [102]. These analyses, among other results, have allowed the erection of the group Monoaxonematidea Justine, 1991 (etymology: one single axoneme) for several families which have uniflagellate spermatozoa [97]. Since new information has been acquired recently on several Monogenea (see Table 1), this cladistic analysis should be updated. This would, however, exceed the scope of this general review.

The recent literature shows that DNA studies generally accord with spermatology concerning the systematic relationships within the Monogenea. JUSTINE (1991) [97, 98] insisted that synapomorphies can be defined for the Monopisthocotylea and for the Polyopisthocotylea, but not for the Monogenea as a whole (= Monopisthocotylea+Polyopisthocotylea). Subsequently, several DNA studies have also concluded that no argument could be given to support monophyly of the Monogenea [27, 46, 183-185]. The position of the Gyrodactylids within the Monopisthocotylea or the Polyopisthocotylea is uncertain in studies based on morphology [137] but they are clearly assigned to the Monopisthocotylea on spermatological evidence [97, 105]; this has been recently confirmed in a study of 18S DNA [46].

The convergence found between the Monopisthocotylea and the Eucestoda has received little comment. Both groups, and these groups alone, within the parasitic Platyhelminthes, have filiform spermatozoa with one single axoneme. This emphasizes a striking feature of the Platyhelminthes: the plesiomorphic sperm in the parasitic group is biflagellate, and these two groups have evolved toward a simpler structure.

Sperm structure in the Eucestoda. The Eucestoda are characterized by a synapomorphy accepted by all authors [21, 30, 50], the absence of mitochondrion. This clearly apomorphic condition separates the Eucestoda from the two other groups of the Cestodaria, the Amphilinidea and Gyrocotylidea. These two groups have apparently kept the basic structure of the Cercomeridea. This character-state "absence of mitochondrion" requires some comments. Characters defined by "absence" are generally considered, in systematics and particularly in cladistics, as less reliable than the acquisition of new structures. However, in this case, one may note that the absence of mitochondrion is probably correlated with the acquisition of other enzymatic systems in the spermatozoon, which are not revealed by ultrastructural methods. Another comment is that researchers interested in the inheritance of paternal mitochondrial DNA should perform a comparative study between a digenean, in which the volume of the spermatozoal mitochondrion is important, and a member of the Eucestoda.

Other synapomorphies of Eucestoda spermatozoa include the twisting of peripheral microtubules, a synapomorphy for the Cyclophyllidea [98] exemplified in the present paper. BÂ & MARCHAND have detailed propositions of other synapomorphies in their chapter in this volume [21].

Number of spermatids in an isogenic group (32 or 64), and value of this character for phylogenetic studies

Table 4 gives a list of some references concerning the number of spermatids in isogenic groups, i.e. groups of cells originating from a single spermatogonium, and fused together until the separation of the mature spermatozoa. XYLANDER [250] has given some phylogenetic value to this character, and considered that a group of 64 was a synapomorphy for the Amphilinidea+Gyrocotylidea+Eucestoda. However, some problems make this character difficult to use. The number is not homogeneous in the Monogenea Monopisthocotylea nor in the Aspidogastrea. Also, it is difficult to polarise this character since the outgroup for the parasitic Platyhelminthes is not precisely known. This character cannot be used at the present time owing to these uncertainties.

TABLE 4. — Number of spermatids in an isogenic group

Group	Species	Number of spermatids	Reference
Aspidogastrea	<i>Rugogaster</i>	64	[235]
	<i>Multicotyle</i>	32	[233, 239]
Digenea		32	many, see Table 1
Monogenea Polyopisthocotylea	<i>Diclidophora</i>	32	[67]
	<i>Gastrocotyle</i>	64	[196]
	<i>Gonoplasius</i>	64	[191]
	<i>Protomicrocotyle</i>	64	[196]
	Several (see Table 1)	64	[135]
Monogenea Monopisthocotylea	<i>Calceostoma</i>	32	[124]
	<i>Calicotyle</i>	64	[238]
	<i>Diplectanum</i>	64	[117]
	<i>Macrogyrodactylus</i>	32	[195]
	<i>Megalocotyle</i>	64	[114]
	<i>Myxinidocotyle</i>	64	[103]
	<i>Pseudodactylogyrus</i>	32	[195]
	<i>Pseudodiplorchis</i>	32	[36]
Gyrocotylidea	<i>Gyrocotyle</i>	64	[250]
Amphilinidea	<i>Amphilina</i>	64	[250]
Eucestoda	many	64	Table 1, [21]

Organelles absent in parasitic Platyhelminthes but present in free-living Platyhelminthes ("Turbellaria"): dense bodies and 25 nm granules

As for other characters mentioned above, the apomorphic character of the parasitic Platyhelminthes is the absence of structures which are present in the plesiomorphic taxa.

Membrane-bound dense bodies. These are absent in all parasitic Platyhelminthes examined. Several categories of granules are present in the same spermatozoon in the Acoela [170]. In other taxa of the "Turbellaria", one or two categories are found, or dense bodies are absent (see Table 1 in [232]). The absence of membrane-bound granules has been considered a synapomorphy for the Neodermata by EHLERS [50, 51].

Cortical non-membrane bound 25-nm granules. These have been found in the Temnocephalidea [77, 180, 240, 243, 245, 246] and in some Dalyellioida [41, 163, 202]. Detailed bibliographical information can be found in the chapter by WATSON & ROHDE in this volume [232]. These granules have been discussed by several authors [77, 163, 202, 232]. It is pertinent to this chapter that they have never been found in any parasitic Platyhelminthes. In our present state of knowledge, it does not appear valid to attribute to the presence of these granules the value of a synapomorphy for a specific taxon of the "Turbellaria" because their presence is not regular in all taxa of a given group. However, they could have an important physiological role, which apparently does not exist in any parasitic Platyhelminthes.

Spermatozoal structure and the biology of fertilization

The question of the relationships between spermatozoal structure and the biology of fertilization in Platyhelminthes has been discussed before [98] but new data make it more precise. It is impossible to link the aberrant structure found in *Schistosoma* (Digenea) and in *Diplozoon* (Monogenea) with the assumed respective phylogeny of these two taxa. For the schistosomes, the present study shows that related families have the plesiomorphic structure. For *Diplozoon*, a recent study [70] has shown that the Octomacridae, considered very close to the Diplozoidae, have the symplesiomorphic structure. All spermatologists know that the biology of fertilization may affect the morphology of spermatozoa: in a taxonomic group, the species which evolve toward a different biology of fertilization may be expected to acquire new sperm structures. Functional interpretation of these new structure is sometimes possible. In the case of the parasitic Platyhelminthes, functional interpretation is not easy. Individuals of schistosomes (male and female) live in permanent pairs, and they have acquired small and simple spermatozoa. Individuals of *Diplozoon* also live in permanent pairs [138] (Fig. 5a), are fused, and the genital ducts communicate, and they have acquired a long and very complicated spermatozoon. Similar factors in *Schistosoma* and *Diplozoon* seem to have produced an evolution of the sperm structure in two completely opposite directions. The answer to this puzzling problem could be found if we consider that in both cases, the permanent pairing implies the absence of inter-individual sperm competition. The fact that the pair is made up of one male and one female in *Schistosoma* and of two hermaphrodites in *Diplozoon* does not seem to have an influence. Thus, in both cases, spermatozoa have not been subjected to selection in terms of performance such as speed or fertilization efficiency, and evolution could diverge in different directions.

The problem of an outgroup for the cladistic analysis of the parasitic Platyhelminthes

The problem of the recognition of a correct outgroup is central for the polarisation of characters. I will here concentrate on the interpretation of characters emerging from sperm studies, although it is clear that other structures may be highly useful. JUSTINE [98] has used, for defining an outgroup, the general system of EHLERS [50, 51]. The taxon Typhloplanida, which has spermatozoa with non-incorporated axonemes, was used as an outgroup for the Doliopharyngiophora, which comprise the Temnocephalidea, Dalyelliida, Udonellidea and Cercomeridea. It was noted [98] that the Dalyellioida have a very heterogeneous structure.

WATSON & ROHDE have systematically tried to find the outgroup for the Neodermata in the past year. *Pterastericola*, which has two incorporated axonemes was first proposed as an outgroup for the Neodermata [85]. Later, the analysis of spermiogenesis demonstrated that the fusion is not proximo-distal [242] and this hypothesis has been abandoned. DNA studies also concluded that Pterastericolidae are not the sister-group for the Neodermata [185].

Kronborgia (family Fecampiidae) was suggested as the outgroup [236, 237]. The spermatozoon of *Kronborgia* has two incorporated axonemes and a continuous row of cortical microtubules [237, 247, 248] and thus resembles that of the Monogenea Polyopisthocotylea. *Kronborgia* has a spermiogenesis with proximal centrioles, as in the parasitic Platyhelminthes. However, the proximo-distal fusion is not observed, there are no free flagella nor median cytoplasmic process, and the two axonemes grow within the elongating spermatid. The presence of a dense body makes its spermiogenesis close to most "Turbellaria". It is not certain that *Kronborgia* represents the taxon closest to the parasitic Platyhelminthes in term of ultrastructure of spermiogenesis. Should *Kronborgia* be considered the outgroup of the parasitic Platyhelminthes, this would require a re-examination of the polarity of certain characters, including the lateral microtubules (synapomorphy for the Polyopisthocotylea) which are present in *Kronborgia* and thus would become the plesiomorphic pattern. Recently, a study of 18s ribosomal RNA [186] has indicated that *Kronborgia* was not the sister-group of the Neodermata and could even be widely separate from them. However, this need confirmation from longer RNA sequences.

Udonella has a spermiogenesis with proximal centrioles, but there is no median cytoplasmic process nor fusion [189, 133, 189, 251]. This spermiogenesis is in fact similar to that of *Kronborgia*. However, the mature spermatozoon of *Udonella* has no microtubules [105]. Spermiogenesis in *Udonella* and *Kronborgia* resembles that found in certain Monogenea such as capsalids [114] or certain didymozoid digeneans [116] where a fusion is not observed because the axonemes grow within the elongating zone of differentiation. In these two latter cases, this characteristic should be interpreted as secondary reduction. The phyletic position of the Udonellidea is a matter of controversy: either outgroup for the Cercomeridea [30], or close to the Monopisthocotylea [183].

In a strictly spermatological point of view, we have, at present, no candidate for the role of outgroup of the parasitic Platyhelminthes. The proximo-distal fusion, with typical zone of differentiation, median cytoplasmic process and free flagella, is found only in the Aspidogastrea, Digenea, Monogenea Polyopisthocotylea, Gyrocotylidea, Amphilinidea, and certain Eucestoda. The analogies of the zone of differentiation in the Monogenea Monopisthocotylea [97, 98] and in certain Eucestoda [21] with the basic structure of the parasitic Platyhelminthes suggest that, although they lack a true proximo-distal fusion, these taxa may be considered closely related. However, the proximo-distal fusion has not been found in any taxon more primitive than the Cercomeridea.

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