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Spermatozoal ultrastructure in four genera of Homolidae (Crustacea, Decapoda): exemplified by *Homologenus* sp., *Latreillopsis* sp., *Homolomannia sibogae* and *Paromolopsis boasi*

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ABSTRACT: The spermatozoa of *Homologenus* sp., *Latreillopsis* sp., *Homolomannia sibogae* and *Paromolopsis boasi* confirm characteristics of a distinctive homolid spermatozoon previously established for *Homola* sp., *Paromola* sp. and *Paromola petterdi*. Homolid features are (1) moderate anteroposterior depression of the acrosome (ratio of length: width 0.4–0.6) as in lyreidine raninids (0.5), depression being greater in dromiids and dynomenids (both 0.3); (2) the capitate form of the perforatorium, shared with dromiids, dynomenids and lyreidine raninids; (3) the autapomorphic spiked-wheel form of the anterior expansion of the perforatorium; (4) horizontal zonation of the acrosome is possibly a unique synapomorphy of homolids with dromiids and dynomenids, and therefore an autapomorphy of the dromioid-homolid assemblage. In dromiids the posterior zone is proportionately the larger, while in homolids the anterior zone is the larger. The anterior zone is complexly subdivided in dynomenids; (5) the autapomorphic presence of numerous radial arranged extensions of the acrosomal operculum into the perforatorium; (6) presence of nuclear arms, a symplesiomorphy of all investigated crabs, but small or questionably sometimes absent in Dromiidae; (7) absence of microtubules from the nuclear arms, as in dromiids, raninids, higher heterotremes and thoracotremes; (8) transient presence of a posterior median process of the nucleus. The process is not seen in dromiids but occurs in anomurans and lower heterotremes; (9) apical perforation of the operculum, also seen, apparently symplesiomorphically, in dromiids, raninids, and lower heterotreme families; (10) absence of an acrosome ray zone, probably homoplasic with absence in raninids; (11) location of most of the cytoplasm, including tortuous membranes and degenerating mitochondria, below the acrosome,also seen in *Lyreidus*; (12) presence, in at least some species, of centrioles, unknown in dromiids and raninids and variable in occurrence in heterotremes.

INTRODUCTION

Guinot et al. (1993) defined a distinctive homolid sperm type on the basis of a study of sperm ultrastructure in homolids collected off New Caledonia, *Homola* sp., *Paromola* sp., and a new genus erected to receive *Paromola* (formerly *Latreillopsis*) *petterdi* (Grant, 1905). The three taxa are described taxonomically by Guinot & Richer de Forges (1994).

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Collection of a further four homolid species, each in a genus not hitherto examined for sperm ultrastructure, from New Caledonian waters, allows confirmation of characteristics which are diagnostic of the Homolidae. The species examined in the present account are *Homologenus* sp., *Latreillopsis* sp., *Homolomannia sibogae* Ihle, 1912, and *Paromolopsis boasi* Wood-Mason, 1981. A generalized homolid sperm has been illustrated semidiagrammatically by Guinot et al. (1993).

MATERIALS AND METHODS

Specimens of the four homolid species were collected by B. Richer de Forges during the BATHUS 1 Cruise on the east coast of New Caledonia in March, 1993. Collecting stations were: *Homologenus* sp. (CP660), *Latreillopsis* sp. (CP667, 669), *Homolomannia sibogae* (CP695) and *Paromolopsis boasi* (CP658, CP657). Portions of the testes and male ducts were fixed in 3 % glutaraldehyde in 0.1 M sodium phosphate buffer (pH 7.2), with 3 % sucrose, at 4 °C for 2 h and despatched in the fixative to Brisbane by air-mail for further processing. On receipt in Brisbane they were washed in buffer; post-fixed for 80 min in similarly buffered 1 % Osmium tetroxide; washed in three 15-min changes of buffer; dehydrated through an ethanol series; and infiltrated and embedded in Spurr's epoxy resin. Sections were cut with diamond knives on an LKB 2128 UM IV microtome. Thin sections, 50–80 nm thick, were collected on carbon stabilized colloidin-coated 200 mesh copper grids, stained for 30 sec in lead citrate, rinsed in distilled water, stained for 1 min in 6 % aqueous uranyl acetate, rinsed in distilled water, and stained for a further 30 sec in lead citrate before final rinsing. Electron micrographs were taken on an Hitachi 300 electron microscope at 75 kV and a JEOL 100 at 60 kV.

RESULTS

General. The sperm of *Latreillopsis* sp. is illustrated semidiagrammatically in Figure 1 which serves to show the main features of homolid spermatozoa. The bulk of the spermatozoon in each of the four species examined in the present study consists of an ellipsoidal acrosome bordered posteriorly by the irregular nucleus. By light microscopy the nucleus may exhibit three radial arms and a (putative) posterior median process (Fig. 3A) or, in the same individual, one or more of these projections may be withdrawn, or there may be additional arms. A thick zone of cytoplasm, containing degenerating mitochondria and tortuous membranes, intervenes between the acrosome and nucleus. The longitudinal axis of the spermatozoon is occupied by a wide cylindrical, anteriorly widening column, the perforatorium, which is capitate anteriorly by virtue of lateral expansion near its tip. The expansion is subdivided into laterally directed horizontal spikes, radiating in the form of a spiked-wheel, or the ribs of an umbrella, and contained within the anterior material of the acrosome. A low dome-shaped dense layer, the operculum, with a wide apical interruption, covers the anterior limit of the perforatorium and its spikes and extends laterally over much of the anterior aspect of the acrosome vesicle. It is covered by the general acrosome membrane and the plasma membrane.

Species are illustrated in the account below as follows: *Homologenus* sp. Figure 2; *Latreillopsis* sp. Figures 1, 3A–E; *Homolomannia sibogae* Figures 4A–E, and *Paramolopsis boasi* Figures 5A–E.

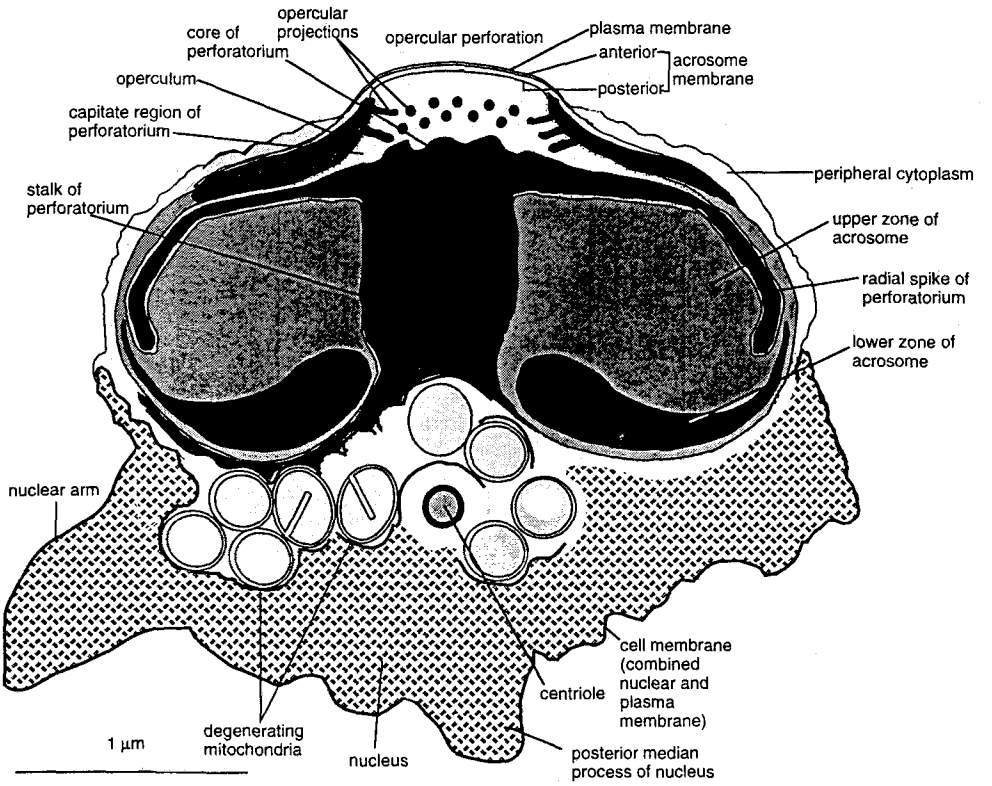


Fig. 1. Semidiagrammatic longitudinal section of the spermatozoon of an homolid, *Latreillopsis* sp.

Acrosome. The acrosome is a thick disc, domed centrally at its free, polar surface (Figs 1, 2A, 3B, 4A, 5A). Dimensions of the acrosome for the four species investigated in this work and in three previously described (Guinot et al., 1993) are given in Table 1. The small samples relate to the difficulty in obtaining a true sagittal section of the spermatozoon.

The acrosome vesicle is bounded by a generally thin acrosomal membrane which is most clearly distinguished as a crenulate or (some *Homologenus* sperm) straight dense membrane bounding the anterior end of the perforatorium. The membrane covering the perforatorium may be referred to as the posterior acrosome membrane, as it results from the basal invagination which forms the perforatorial chamber. Anterior to this, and in close proximity, is the anterior acrosome membrane which is the portion of the acrosome membrane covering the anterior aspect of the acrosome and underlying the plasma membrane (Figs 2, 3B, 4A, 5A). The operculum is bounded above by the anterior acrosome membrane and below by the posterior acrosome membrane. A thin, moderately pale layer underlies the acrosome membrane and, with it, bounds the acrosome vesicle, extends from the posterior limit of the operculum, around the sides and posterior face of the acrosome vesicle and is invaginated posteriorly along the posterolateral walls of the perforatorium (Figs 1, 2, 3B, 4A, 5A). This pale layer may be equivalent to the capsule

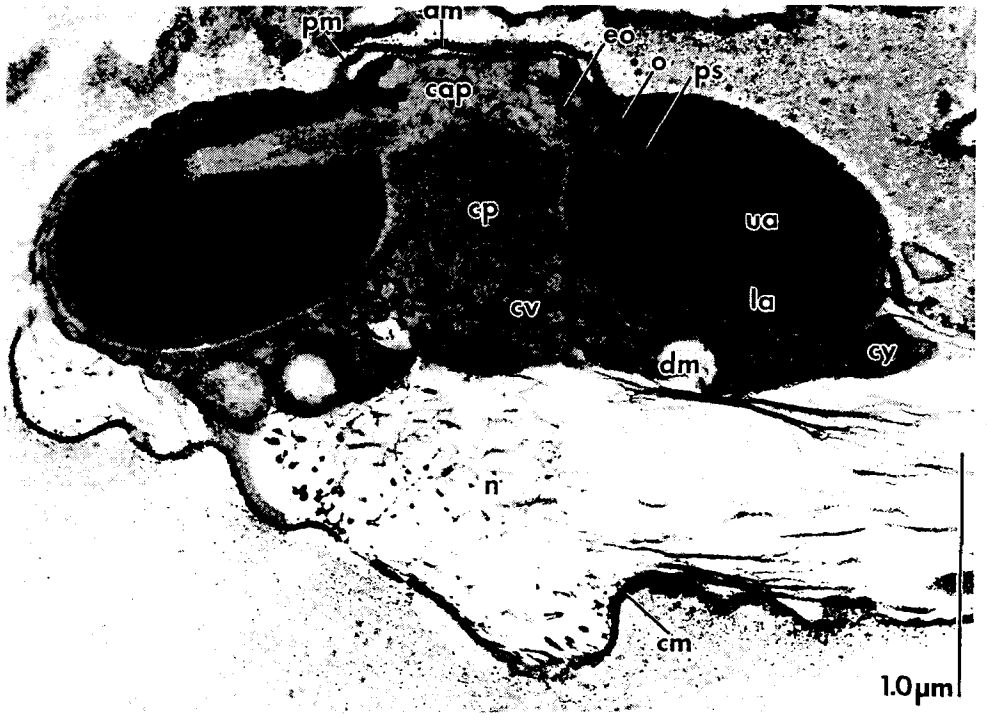


Fig. 2. *Homologenus* sp. Longitudinal section of a spermatozoon. am – acrosome membrane; cap – capitate region of perforatorium; cm – cell membrane; cp – core of perforatorium; cv – convoluted membranes; cy – cytoplasm; dm – degenerating mitochondrion; eo – extensions of the operculum into head of perforatorium; la – lower acrosomal zone; n – nucleus; o – operculum; pm – plasma membrane; ps – perforatorial spike; ua – upper acrosomal zone

observed in the acrosomes of other crab sperm. The posterior acrosome membrane and a very thin continuation of the pale layer invests each of the perforatorial spikes (see below).

The bulk of the contents of the acrosome vesicle form an inflated ring surrounding the axial perforatorial chamber. The substance of the ring is subdivided into an upper, large, moderately electron-dense zone, constituting most of its thickness, and a lower strongly electron-dense zone which in vertical section is approximately crescent-shaped with the concavity anterior (Figs 1, 2, 3B, 4A, 5A). In *Paromolopsis boasi* an additional peripheral zone is discernible (Figs 5A, D, E).

The spikes of the perforatorium lie near the anterior surface of the upper pale zone of the acrosome and are overlain by the operculum. In all four species the operculum sends dense extensions into the substance of the perforatorium in the vicinity of the base of the spikes (Figs 1, 2, 3B, 4A, 5A). These extensions are numerous, and have an approximately radial orientation (Figs 3D, 4C, 5B).

The centre of the acrosome vesicle is penetrated by a stout vertical column of dense material which widens subapically in a capitate configuration (as seen in vertical section), composed of the radiating spines or spikes, the whole constituting the putative per-

foratorium (Figs 1, 2, 3B, 4A, 5A). Its stalk is circular in cross-section (Figs 4D, E, 5D, E). The material of the stalk and head of the perforatorium has a dense core in *Homologenus* (Fig. 2) and *P. boasi* (Figs 5A, B, C) but is more uniform in *Latreillopsis* sp. (Figs 1, 3B) and *Homolomannia sibogae* (Fig. 4A).

The radial spikes extend far laterally. In *Homolomannia sibogae* (Fig. 4D) and *P. boasi* (Fig. 5D), their tips are visible in transverse sections at the level of the stalk of the perforatorium, indicating that they bend posteriorly, and they are much longer in *Latreillopsis* sp. (Fig. 3B), in which they curve around the inner aspect of the vesicle almost to its base. Their full lateral extent has not been determined for *Homologenus* sp. but they appear normal in longitudinal section (Fig. 2). In all four species the spikes are supported by fibrous cores which radiate from the central core of the perforatorium where a core is defined, as in *Paromolopsis* (Fig. 5C). The number of spikes, seen in cross sections of the sperm, is in the order of 12, though accurate counts were not possible. The radial arrangement, as seen in transverse sections of the head of the perforatorium, is not entirely regular (Fig. 5C).

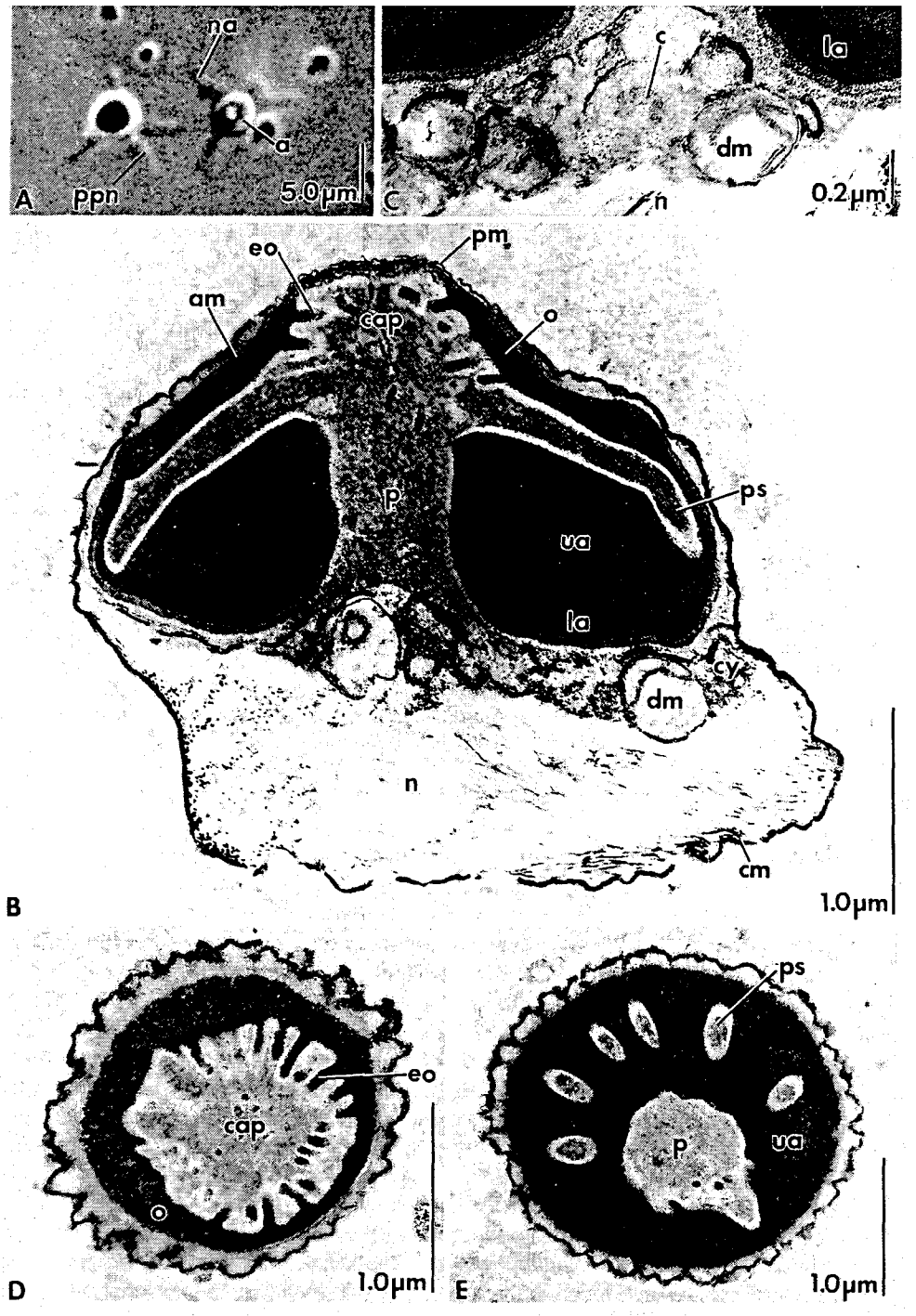
Table 1. Dimensions of the acrosome in seven homolid species

Species	Length/ width	Length (μm)	Mean length	Width (μm)	Mean width	n
Homola sp.	0.50	1.7–2.7	2.1	3.6–5.1	4.2	8
Homolomannia sibogae	0.47	1.6–2.1	1.9	3.7–4.5	4.0	4
Homologenus sp.	0.39	1.3–1.4	1.4	3.5	3.5	2
Latreillopsis sp.	0.57	1.6–1.8	1.7	2.9–3.1	3.0	3
Paromola sp.	0.49	1.8–2.3	2.0	3.5–4.8	4.1	8
Paromola petterdi	0.56	1.9–2.0	2.0	3.5–3.7	3.6	3
Paromolopsis boasi	0.39	1.5–1.9	1.7	3.8–4.9	4.4	4

Nucleus. The nucleus posteriorly cups the acrosome-cytoplasm portion of the sperm (Fig. 1). Its form is clearly highly labile and its thickness varies in longitudinal sections of the spermatozoa of the same species from about one third of the thickness of the acrosome to an equal thickness. Its variability by transmission electron microscopy (Figs 2, 3B, 4A, 5A) reflects that described for light microscopy above (Fig. 3A).

No microtubules are present in the arms or elsewhere in the sperm. The chromatin consists of fine, diffusely arranged putative electron-dense DNA fibrils, but the nucleus consists mostly of electron-lucent "space". The nucleus is in direct contact with the plasma membrane (the combined nuclear-plasma membrane being termed the "cell membrane"). The concavity of the nucleus is separated anterolaterally from the acrosome and, over most of its extent, from the cytoplasm by a thick, dense wavy or irregular membrane (Figs 2, 3B, 4A, 5A).

Cytoplasm centrioles and other organelles. The cell membrane continues from the nucleus apically over the surface of the acrosome, as the plasma membrane, to which it is closely adherent. No cytoplasm intervenes between the plasma membrane and the acrosome, but at the anterior pole the plasma membrane is separated from the acrosome membrane, though not widely (Figs 2, 3B, 4A, 5A).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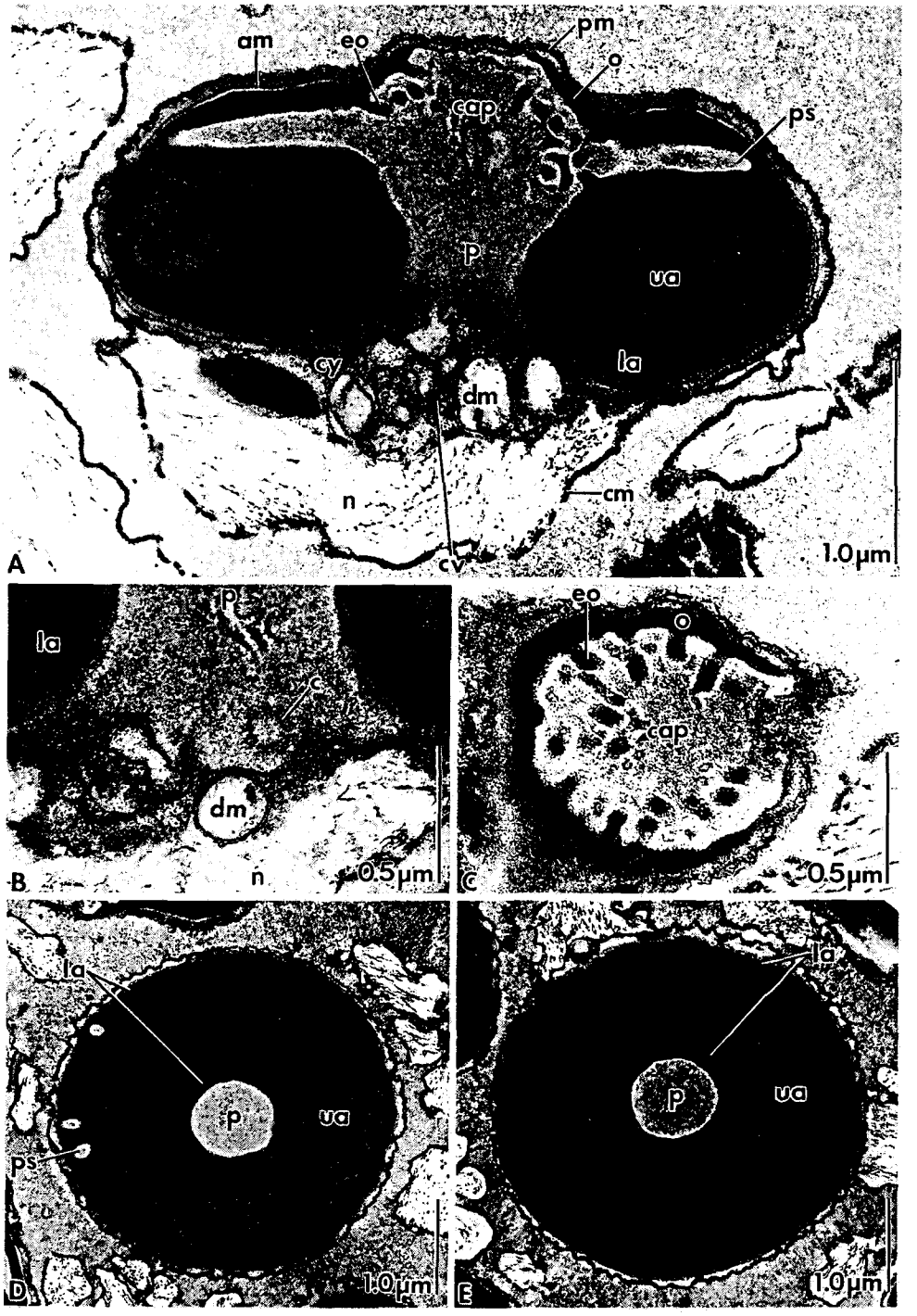
The large mass of cytoplasm lies in the hiatus at the hind end of the perforatorium, extends thinly along the posterior face of the acrosome vesicle and anteriorly for a short distance axially approximately to the equator of the acrosome (Figs 2, 3B, 4A, 5A). It contains posteriorly situated subspherical bodies with dense bounding membranes, some of which have vestigial cristae and are therefore clearly degenerate mitochondria. The dense membranes bounding the degenerate mitochondria are continuous with highly convoluted membranes which fill much of the cytoplasm or convoluted membranes may be only weakly, or not appreciably, developed. The cytoplasm is separated from the perforatorium and acrosome by a similar dense membrane which is itself frequently infolded as part of the tortuous membranes and of those limiting the putative mitochondria. Centrioles are probably normally present in the cytoplasm as one (presumably of a pair) has been seen in an area of the cytoplasm devoid of convoluted membranes in *Latreillopsis* (Fig. 3B), in which it appears to consist of 9 doublets, and in *Homolomannia sibogae* at the base of the perforatorial chamber (Fig. 4B). When visible it is poorly defined, suggesting that it is degenerating.

DISCUSSION

The above account of the spermatozoa of *Homologenus* sp. *Latreillopsis* sp., *Homolomannia sibogae* und *Paromolopsis boasi* confirms the existence of a distinct homolid sperm type as previously established from examination of the sperm of *Homola* sp., *Paromola* sp., and *Paromola* (formerly *Latreillopsis*) *petterdi* (Guinot et al., 1993). A triradiate arrangement of the arms, observed in some preparations of *Homola* sp. in the previous study, is not apparent in sperm sectioned for transmission electron microscopy in the present study, nor has a distinct posterior median process been observed, but they have been demonstrated in light micrographs. Lability in form of the nucleus is, however, consistent with temporary formation of these structures. A further dubious difference from the previous study is that the plasma membrane is not as widely separated from the underlying acrosomal membrane covering the apical perforation of the operculum, as was the case there. The wide separation in the latter was suspected, probably correctly, of being artefactual. The existence of centrioles in the sperm of at least some homolids is confirmed by demonstration of a centriole in an area of the cytoplasm devoid of convoluted membranes in *Latreillopsis* sp. as formerly demonstrated for *Paromola petterdi*. The doublet construction of the centriole is characteristic of Malacostraca (see Jamieson, 1989a, 1991).

In the previous account (Guinot et al., 1993), it was concluded that the spermatozoa

Fig. 3. *Latreillopsis* sp. A: Light micrograph of spermatozoa, showing three nuclear arms and putative posterior median process. B: Longitudinal section of a spermatozoon, showing the great length of the radial spikes of the perforatorium. C: Higher magnification of the centriolar region. D: Transverse section (TS) of the operculum, showing projections into the perforatorium. E: TS of a spermatozoon, near the tips of the radial spikes of the perforatorium. a – acrosome; am – acrosome membrane; c – centriole; cap – capitate region of perforatorium; cm – cell membrane; cy – cytoplasm; dm – degenerating mitochondrion; eo – extensions of the operculum into head of perforatorium; la – lower acrosomal zone; n – nucleus; na – nuclear arm; o – operculum; p – perforatorium; pm – plasma membrane; ppn – putative posterior median process of nucleus; ps – perforatorial spike; ua – upper acrosomal zone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of homolids shared more synapomorphies with dromiid sperm than with the sperm of *Ranina* (both in the Podotremata) or of the heterotreme-thorocotreme assemblage (see Jamieson, 1991). Nevertheless, a recent examination (Jamieson, Guinot & Richer de Forges, in preparation) of the sperm of the raninid *Lyreidus* reveals two putative spermatozoal synapomorphies of this taxon with homolids: the capitate perforatorium, shared with dromiids and dynomenids but with an "amoeboid" form, possibly related to the radiate spiked-wheel structure of homolids; and similar proportions of the acrosome in the ratio of length to width. Resolution of relationships of homolids with dromiids and raninids must await cladistic analysis when data on additional taxa are available.

In summation, homolid features of the spermatozoa of *Homologenus* sp., *Latreillopsis* sp., *Homolomannia sibogae, P. boasi* and previously examined homolid species are as follows:

(1) Anteroposterior depression of the acrosome (ratio of length: width in seven homolid species = 0.4–0.6) is less pronounced than that in dromiids and dynomenids (l:w 0.3) and accords with that in *Lyreidus* (l:w 0.5).

(2) The capitate form of the perforatorium is shared with dromiids, dynomenids and lyreidine raninids.

(3) The spiked-wheel form of the anterior expansion of the perforatorium is restricted to the Homolidae, for which it is an autapomorphy. It reaches its extreme development in *Latreillopsis*. The irregular blunt protrusions of the head of the perforatorium in *Lyreidus* are here very tentatively regarded as synapomorphic with the radial homolid spikes.

(4) Horizontal zonation of the acrosome is possibly a unique synapomorphy of homolids with dromiids and dynomenids and therefore an autapomorphy of the dromioid-homolid assemblage. In dromiids the posterior zone is proportionately the larger, while in homolids the anterior zone is the larger. The anterior zone is large and complexly subdivided in dynomenids.

(5) The presence of numerous radially-arranged extensions of the acrosomal operculum into the perforatorium is here established as an autapomorphy of the homolids.

(6) Presence of nuclear arms is symplesiomorphic of all investigated crabs, though they are small or questionably sometimes absent in Dromiidae.

(7) Absence of microtubules from the nuclear arms in homolid sperm is shared with dromiids, dynomenids, raninids, higher heterotremes and thoracotremes. In view of the presence of microtubules in nephropid (e. g. Talbot & Chanmanon, 1980) and paguroid sperm (Tudge, 1992), absence is probably apomorphic, but may be homoplasic rather than synapomorphic in at least some of these taxa (see discussion in Guinot et al., 1993, in press).

(8) A posterior median process of the nucleus in confirmed for homolid sperm, at

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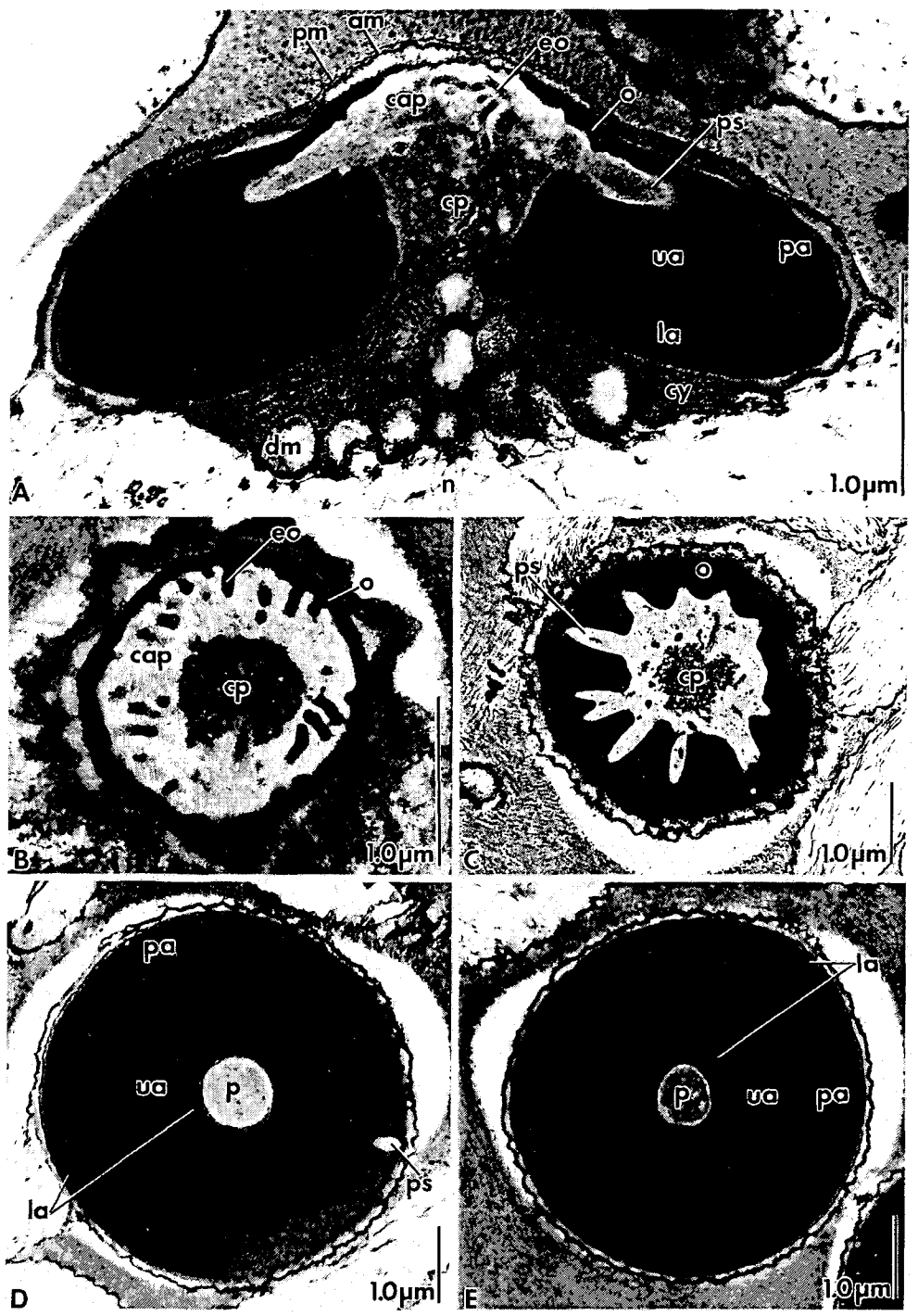
Fig. 4. *Homolomannia sibogae*. A: Longitudinal section of spermatozoon. B: Higher magnification of the centriolar region. C: Transverse section (TS) of the operculum, showing projections into the perforatorium. D: TS of a spermatozoon, near the tips of the radial spikes of the perforatorium. E: TS of a spermatozoon more basally. am – acrosome membrane; c – centriole; cap – capitate region of perforatorium; cm – cell membrane; cv – convoluted membranes; cy – cytoplasm; dm – degenerating mitochondrion; eo – extensions of the operculum into head of perforatorium; la – lower acrosomal zone; n – nucleus; o – operculum; p – peforatorium; pm – plasma membrane; ps – perforatorial spike; ua – upper acrosomal zone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least from light micrographs. Absence or weak development in homolid sperm examined ultrastructurally in the present study may be artefactual or due to transience of this process. The process is not seen in dromiids, but presence is a symplesiomorphy of homolids with anomurans, raninids, and lower heterotremes.

(9) Apical perforation of the operculum is general for homolids. It is also seen, apparently symplesiomorphically, in dromiids (*Petalomera lateralis* [now *Stimdromia lateralis* (Gray, 1831)], *Dromidiopsis*, raninids, and majids and a few other heterotreme families [see Jamieson, 1991]).

(10) Absence of an acrosome ray zone may be a homolid apomorphy (probably homoplasic with absence in raninids). The acrosomal rays also occur in the acrosomes of heterotremes, e. g. xanthids and portunids (Jamieson, 1989 c; Jamieson & Tudge, 1990). Similar rays are, however, visible in published micrographs of the sperm of the astacids, *Pacifastacus leniusculus* (Dudenhausen & Talbot, 1979) and *Cambarus* sp. (Anderson & Ellis, 1967); and are well-known in the sperm of hermit crabs (e. g. Hinsch, 1980; Tudge, 1992; Tudge & Jamieson, 1991). They are therefore possibly plesiomorphic for reptantia.

(11) Location of most of the cytoplasm, including tortuous membranes and degenerating mitochondria, below the acrosome is a homolid feature not seen in the dromiid *Petalomera* (Jamieson, 1990) though seen in *Dromidia antillensis* (Brown, 1966), with an intermediate condition in *Dromidiopsis* (Jamieson, Tudge and Scheltinga, in preparation), nor in *Ranina* (Jamieson, 1989 b), nor *Raninoides* (Jamieson, Guinot and Richer de Forges, in preparation), nor in the heterotreme-thoracotreme assemblage (Jamieson, 1991), but conspicuous in *Lyreidus*. In *Ranina* and *Raninoides* and the heterotreme-thoracotreme assemblage the cytoplasm is predominantly lateral to the acrosome with, in some heterotremes, a trace posteriorly. In *Petalomera* there is the merest vestige of cytoplasm beneath the acrosome. The relatively strong development of cytoplasm posterior to the acrosome in homolids and *Lyreidus* is probably a plesiomorphic condition for decapods.

(12) Centrioles, observed in the cytoplasm posterior to the acrosome in homolid sperm, are unknown in dromiids and raninids, and are variable in occurrence in heterotremes. Presence of short centrioles (they are elongate in the heterotreme *Potamonautes* [see Jamieson, 1993]) is symplesiomorphic for brachyurans, being seen in many other decapods (see Guinot et al., 1993).

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Fig. 5. *Paromolopsis boasi.* A: Longitudinal section of spermatozoon. B: Transverse section (TS) of the operculum, showing projections into the perforatorium. C: TS through the radial spikes of the perforatorium. D: TS through the stalk of the perforatorium and the tip of a radial spike, showing that the spikes extend far posteriorly. E: TS more basally through the stalk of the perforatorium. am – acrosome membrane; cap – capitate region of perforatorium; cp – core of perforatorium; cy – cytoplasm; dm – degenerating mitochondrion; eo – extensions of the operculum into head of perforatorium; la – lower acrosomal zone; n – nucleus; o – operculum; p – perforatorium; pa – peripheral acrosome zone; pm – plasma membrane; ps – perforatorial spike; ua – upper acrosomal zone

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