

**The Ultrastructure of the Spermatozoon of  
*Dromidiopsis edwardsi* Rathbun, 1919  
(Crustacea : Brachyura : Dromiidae):  
Confirmation of a Dromiid Sperm Type**

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*Abstract*

The dromiid spermatozoon, as exemplified by *Dromidiopsis edwardsi*, *Stimdromia* (= *Petalomera*) *lateralis* and *Dromidia antillensis*, accords with that of the Homolidae and differs markedly from spermatozoa of other crabs (the raninid-heterotreme-thoracotreme assemblage) in the discoidal form of the acrosome and the capitate form of the perforatorium. Dromiids differ from homolids in the greater depression of the acrosome and the form of the head of the perforatorium, thus exhibiting a distinctive dromiid sperm type. The head is bilaterally prolonged in *D. edwardsi* and also shows bilateral symmetry, though this is less pronounced in *S. lateralis*. In homolids the head of the perforatorium has the form of a horizontally disposed spiked wheel. Centrioles are unknown in dromiid sperm but are present in homolids. Nuclear arms in *D. edwardsi*, as in homolids, have the form of three small radial vertices. Dromiids, homolids, raninids, higher heterotremes and thoracotremes differ (homoplasically?) from lower heterotremes in lacking microtubules in the nuclear arms. Dromiid sperm lack the posterior median process of the nucleus seen in homolids, anomurans and lower heterotremes. The sperm of *D. edwardsi* differs from other investigated dromiid sperm in the asymmetrical location of the opercular perforation relative to the longitudinal axis of the sperm, and in more complex zonation of the acrosome vesicle. The acrosome is deeply embedded in the nucleus in *D. edwardsi* whereas in *S. lateralis* it is superficial on the nucleus. Both have an apical protuberance of subopercular material through the opercular perforation, known elsewhere only in dynomenid crabs. Sperm structure in the Dromiidae thus differs significantly from that in the Eubrachyura.

**Introduction**

The use of spermatozoal ultrastructure for taxonomy and phylogeny is now widely accepted as it has proved effective in resolving hitherto intractable problems of taxonomic placement and relationship. A striking endorsement of its validity is the recent ratification from molecular biology of Abele *et al.* (1989) of placement of the Pentastomida in the Crustacea from consideration of spermatozoal ultrastructure by Wingstrand (1972), confirmed by Storch and Jamieson (1992). There are many other examples of groups in which analysis of sperm ultrastructure has produced significant advances in phylogenetic reconstruction, for which only a few references can be mentioned here: anthozoan coelenterates (Schmidt and Zissler 1979); Platyhelminthes (Justine, many papers, e.g. 1991) and, with the erection of a higher taxon, the Trepaxonemata, on sperm ultrastructure (Ehlers 1985); Nematoda (Baccetti *et al.* 1973); Polychaeta (Jamieson and Rouse 1989); Oligochaeta (Jamieson 1981, 1983; Jamieson *et al.* 1987); Clitellata (Ferraguti 1983); Mollusca (Healy, many papers, e.g. 1988); insects and other Hexapoda (references in Jamieson 1987); Myriapoda (Baccetti 1978); Crustacea (Pochon-Masson *et al.* 1970; Jamieson 1991a);

Chelicerata (Alberti 1990); Urochordata (Holland 1989); Echinodermata, protochordates and fish, including the erection of a new Order, the Esciformes (Jamieson 1991*b*); fish (Mattei 1991); Amphibia (Pugin-Rios 1980; Jamieson *et al.* 1992; Lee and Jamieson 1992); Reptilia (Furieri 1970); Aves (Phillips and Asa 1986; Baccetti *et al.* 1991); Marsupialia (Harding *et al.* 1986; Temple-Smith 1987); Eutheria (Roldan *et al.* 1991; Rouse and Robson 1986); and many phyla (Franzén, 1970; Afzelius 1979; Wirth 1991).

In the present study we investigate the sperm of the dromiid *Dromidiopsis edwardsi* with a view to further defining a dromiid sperm type which has been established for *Dromidia antillensis* by Brown (1966) and Felgenhauer and Abele (1990) and for *Stimdromia* (= *Petalomera*) *lateralis* by Jamieson (1990). The spermatozoon is described for its interest *per se* and to aid resolution of brachyuran phylogeny.

The Dromiidae is a family of marine crabs that are commonly referred to as masked or sponge crabs because they often carry sponges or ascidians over the carapace, giving concealment and protection. Objects are held in position by the subchelate fifth pereopods (Abele and Felgenhauer 1982). The family has traditionally been placed in the Dromioidea *sensu lato* (represented in living crabs by the superfamilies Dromioidea and Homoloidea). The Dromioidea has widely been regarded as the plesiomorphic sister-group of the remaining Brachyura (Warner 1977 and references therein) which collectively comprise the Eubrachyura of de Saint Laurent (1980) but, as shown below, the constitution of the Dromioidea and the phylogenetic position of its families has been the subject of controversy.

Guinot (1978) divided the Brachyura into three sections on the basis of the location of the male and female pores: the Podotremata, the Heterotremata and the Thoracotremata. Jamieson (1991*a*) pointed out that the coxal positions of male and female pores and isolation of the spermathecae from the oviducts characterising the podotremes were symplesiomorphies that left the validity of the Podotremata in some doubt. The Podotremata, as diagnosed by Guinot, contain not only the Dromioidea and Homolodromioidea (both comprising the subsection Dromioidea) but also the Homoloidea, Raninoidea and Cyclodorippoidea (= Tymoloidea) (the latter three groups comprising a subsection Archaeobrachyura that Guinot admitted was artificial). The Heterotremata (Dorippoidea, Calappoidea, Corystoidea, Portunoidea, Xanthoidea, Majoidea, Parthenopoidea, Bellioidea and Leucosioidea) and Thoracotremata (Gecarcinoidea, Grapsoidea, Mictyroidea, Pinnotheroidea, Hexapodoidea, Ocypodoidea and Hymenosomatoidea) are synapomorphic in the sternal location of the female pores and development of the spermatheca as a diverticulum of the oviduct. The Thoracotremata are further apomorphic in the sternal location of the male pores, though this is seen in some heterotremes. Although Guinot (1978) was confident of the brachyuran status of those podotremes that she placed in the Archaeobrachyura she was uncertain that dromiids were true crabs. Jamieson (1990, 1991*a*), from sperm ultrastructure, suggested that dromiids should be excluded from the Brachyura and that they might be more basal than the paguroid Anomura, as had been suggested by studies of larval morphology (Williamson 1974; Guinot 1978). The Dromioidea have been attributed an origin near or from the Thalassinidea, and therefore at a level more primitive than most Anomura, by several workers (for instance, Gurney 1942; Pike and Williamson 1960; Burkenroad 1963; Williamson 1965, 1974; Rice 1980, 1983) (see also discussions in Stevcic 1971; Guinot 1978). The Dromioidea have been excluded from the Brachyura by Williamson (1965, 1974) and Rice (1980, 1983), who retain the Homoloidea in the true crabs. Nevertheless, Warner (1977) implies monophyly of the Dromioidea with other brachyurans, stating that the morphology of the Dromioidea is crab-like and that they are 'clearly the ancestors of modern crabs'.

In a landmark paper on the molecular biology of crabs, using 18S rRNA, Spears *et al.* (1992) confirmed that the Podotremata could not be retained in the Brachyura. Additionally, they found the Dromiidae to be diphyletic, as *Hypoconcha* grouped closely with the hermit crab *Clibanarius* while *Dromidia* formed a separate branch below the Brachyura. They did not, however, examine the RNA sequences and phylogenetic position of homolids. Guinot

*et al.* (1993) have shown the sperm of three investigated homolids to share features (there regarded as synapomorphies) with the dromiid *Stimdromia* (see Jamieson 1990), namely a capitate form of the perforatorium and depression of the acrosome, which suggested a close relationship of homolids and dromiids that would contraindicate severance by Guinot (1978) of homolids from dromiids and placement of the former with raninids in the Archaeobrachyura. Homolids differed from dromiids, and were autapomorphically united, in the spiked-wheel form of the head of the capitate perforatorium. The following description of the sperm of *D. edwardsi* will contribute to a cladistic analysis of brachyuran sperm that is in preparation.

### Materials and Methods

A specimen of *D. edwardsi* was trawled at 20 m in the Turtles Group of reefs, Great Barrier Reef, Queensland, Australia (14°42'S., 145°11'E.) in November 1992. Portions of the 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; washed in buffer, retained in buffer, with a trace of glutaraldehyde (c. 0.2%), for two weeks, including transportation to this laboratory; postfixed for 80 min in similarly buffered 1% osmium tetroxide; 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-stabilised, colloidal-coated, 200- $\mu$ m-mesh copper grids, rinsed in distilled water, stained for 30 s in Reynold's lead citrate, then in 6% aqueous uranyl acetate for 60 s and for a further 30 s in lead citrate before final rinsing. Electron micrographs were taken on an Hitachi 300 electron microscope at 75 kV and a Jeol 100-s electron microscope at 60 kV.

### Results

#### General

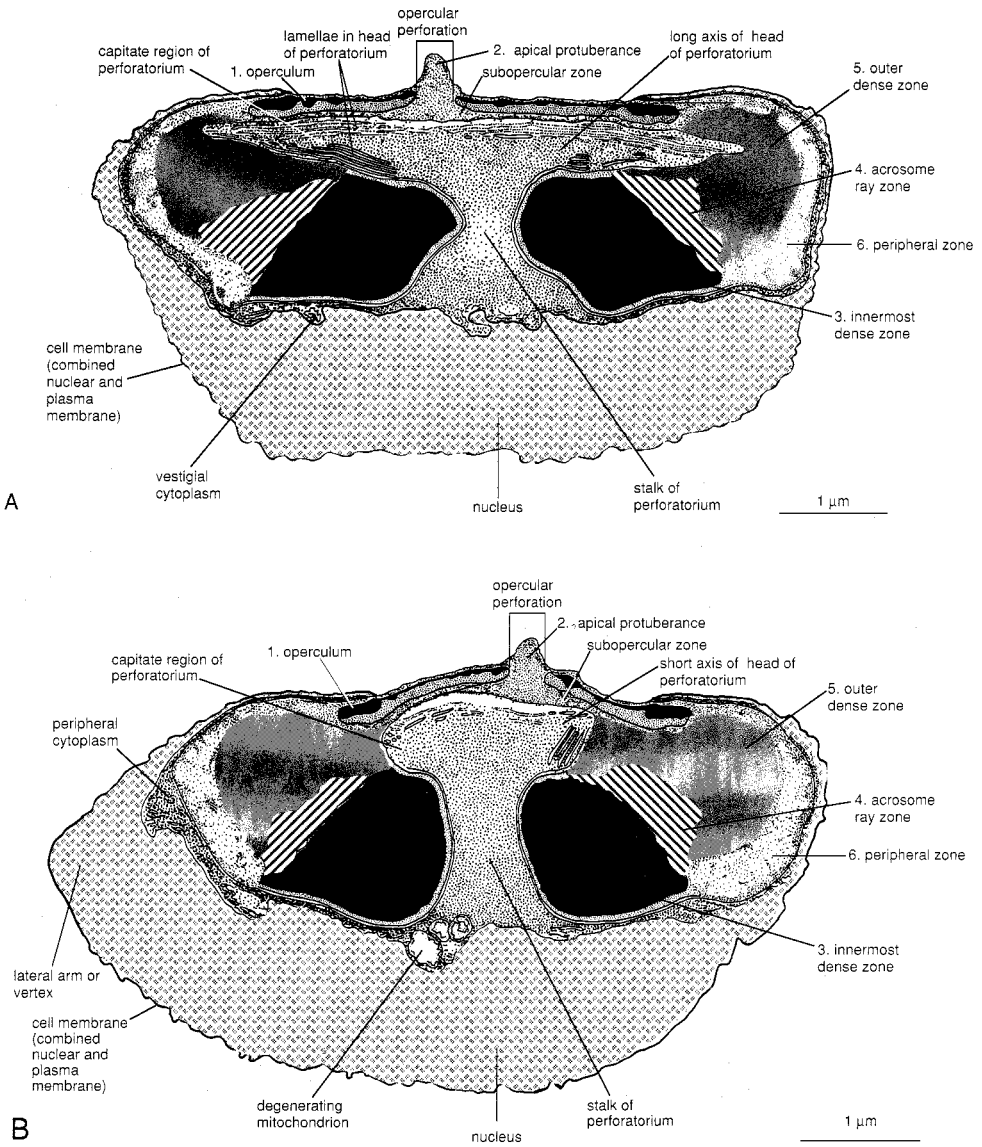
The male ducts contain numerous subspheroidal, thin-walled spermatophores, each containing many spermatozoa. The bulk of the spermatozoon (Fig. 1A, B) consists of an ellipsoidal acrosome, with the form of a thick discus, bordered posteriorly by the electron-pale nucleus in which it is embedded except for its anterior face (the opercular region). A very small amount of cytoplasm, chiefly apparent by the presence of degenerating mitochondria, adheres to the posterolateral aspects of the acrosome. The longitudinal axis of the spermatozoon is occupied by a wide, cylindrical, anteriorly narrowing column, identified as a perforatorium, that is capitate anteriorly by virtue of a large lateral expansion near its tip, giving the perforatorium the form of a symmetrical anvil. The expansion forms a continuous flange that is wider in one radius than in that at right angles (Figs 1A, B, 2B, C); this bilateral symmetry is seen, although not as pronounced, in *Stimdromia*. In dromiids this perforatorial head is not subdivided into radial horizontal spikes as it is in homolids.

A low dome-shaped, almost flat, dense layer, with a narrow apical interruption, covers the anterior limit of the perforatorium and extends laterally over much of the anterior aspect of the acrosome vesicle; this layer is identifiable with the operculum of the sperm of anomurans, other dromiids, homolids, raninids and higher crabs. It is covered by the general acrosome membrane and the plasma membrane of the sperm cell.

Nuclear arms are recognisable in transmission electron micrographs of transversely sectioned spermatozoa and in light microscopy. Each spermatozoon, when viewed from the anterior pole, is seen to have three angular protuberances or vertices representing rudimentary nuclear arms (Figs 2A, 3A). Spermatozoa are 5.29–7.69  $\mu$ m wide (mean of 13 = 6.38  $\mu$ m) and 2.14–4.23  $\mu$ m thick in anteroposterior section (mean of 9 = 3.49  $\mu$ m).

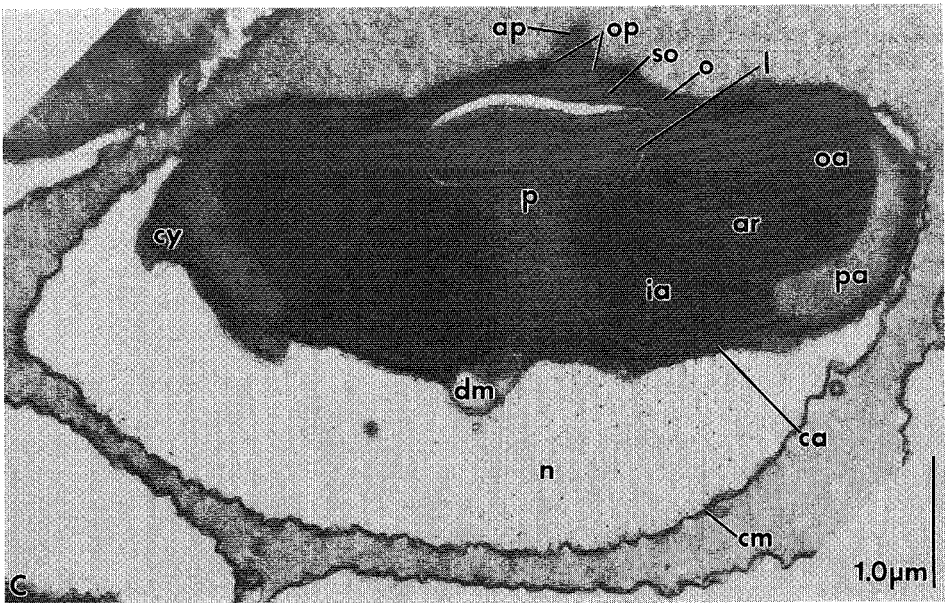
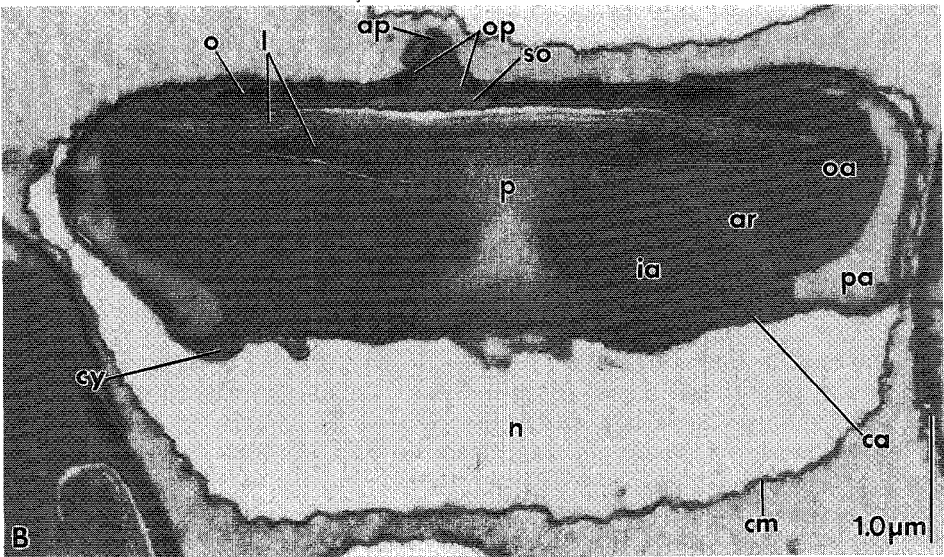
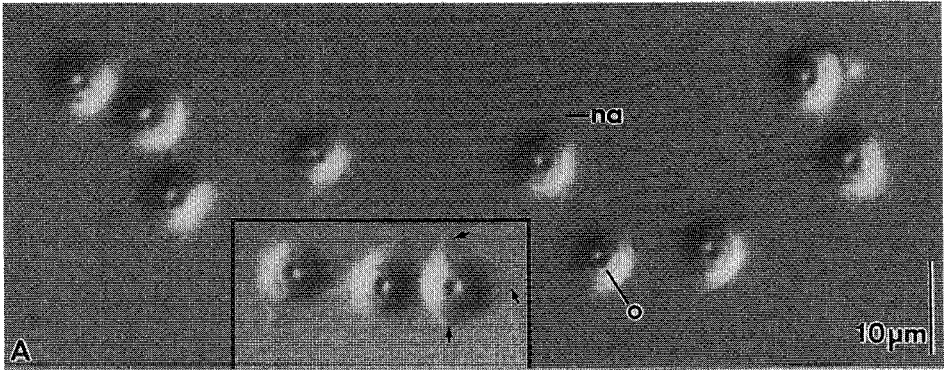
#### Acrosome

The acrosome is a thick disc (Figs 1A, B, 2B, C). Its anterior surface is very gently domed or almost flat over the operculum, which occupies about half of its total width



**Fig. 1.** *Dromidiopsis edwardsi*. Semidiagrammatic vertical longitudinal sections of the spermatozoon traced from transmission electron micrographs. *A*, Through the greater width of the capitata perforatorium; *B*, through the lesser width of the capitata perforatorium.

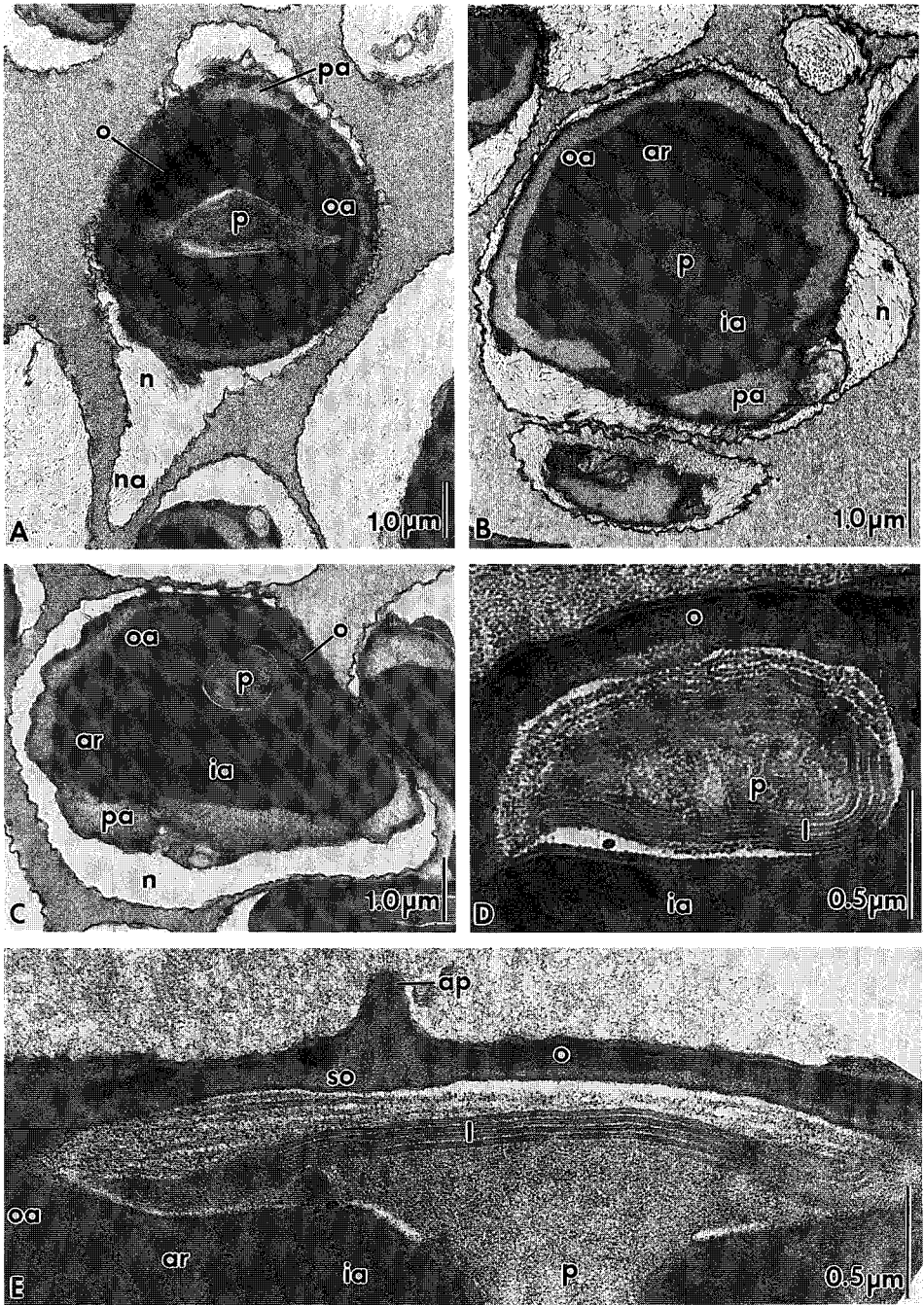
**Fig. 2.** *Dromidiopsis edwardsi*. *A*, Light micrograph of glutaraldehyde-fixed spermatozoa by Nomarski contrast (inset, arrows show the three nuclear arms or vertices). *B*, *C*, Transmission electron micrographs of vertical longitudinal sections of the spermatozoon, through the greater (*B*) and lesser (*C*) width of the capitata perforatorium. ap, apical protuberance; ar, acrosome ray zone; ca, capsule; cm, cell membrane; cy, cytoplasm; dm, degenerating mitochondrion; ia, inner acrosome zone; l, lamellae; n, nucleus; na, nuclear arm, o, operculum; oa, outer acrosome zone; op, opercular perforation; p, perforatorium; pa, peripheral acrosome zone; so, subopercular zone.



(Fig. 2*B, C*). The width of the acrosome vesicle, in sagittal longitudinal section, is 4.57–6.80  $\mu\text{m}$  (mean of 15 = 5.83  $\mu\text{m}$ ); its anteroposterior thickness is 1.15–2.57  $\mu\text{m}$  (mean of 12 = 2.20  $\mu\text{m}$ ). The vesicle is bounded by a unit acrosomal membrane. Internal to this, a thick, electron-dense layer possibly equivalent to the usual brachyuran acrosomal capsule is recognisable only around the base of the perforatorium (Fig. 2*B, C*) and is well developed where it becomes the wall of the basal invagination that forms the subacrosomal or perforatorial chamber. The terminally bulbous, finger-like extensions of the capsule that extend in *Stimdromia* sperm into the underlying nucleus are absent in *Dromidiopsis*. The contents of the acrosome vesicle, peripheral to the axial perforatorium (described below), show a more complex zonation (Figs 1*A, B, 2B, C*) than in *Stimdromia* and the zonation that is horizontal in *Stimdromia* and the homolids is in *Dromidiopsis* more nearly concentric. Six zones or regions are discernible in the acrosome contents, including the operculum (enumerated in Figs 1*A, B, 2B C*). (1) The operculum, which is 2.45–4.06  $\mu\text{m}$  wide (mean of 15 = 3.30  $\mu\text{m}$ ), appears in vertical section as a very thin strongly electron-dense layer with bead-like swellings at irregular intervals underlain by a moderately electron-dense plate. It is thickest at its outer rim. The beaded layer and the plate are interrupted, somewhat eccentrically, by a perforation that has been reported also for *Stimdromia* and the homolids. (2) In *D. edwardsi*, and to a lesser extent in *Stimdromia*, moderately dense material protrudes from below the operculum through the perforation as an apically rounded cone. The layer of which the protuberance is an extension is here termed the subopercular zone, though homology with a zone of the same name in other brachyurans is uncertain. The subopercular zone directly overlies the capitate expansion of the perforatorium. The four remaining zones of the acrosome vesicle will be described in concentric sequence from the wall of the perforatorial chamber towards the periphery. (3) The innermost zone, immediately surrounding the wall of the perforatorial chamber, is the most electron-dense layer of the acrosome excepting the operculum. It fills the region of the acrosome vesicle between the capitate expansion of the perforatorium and the posterior limit of the vesicle and extends laterally for almost half of the width of the vesicular contents of its side. In vertical section on each side of the perforatorium this inner dense zone is about as long anteroposteriorly as it is laterally. Its outer margins converge anteriorly and it forms in totality a thick torus, or doughnut-shaped ring around the perforatorium. Two zones (4 and 5) abut on the lateral margin of the inner dense zone. (4) This zone in longitudinal section of the acrosome is approximately triangular with its median margin lying along the outer edge of the inner dense zone almost as far as the posterior end of the latter and its outer margin extending obliquely outwards. The contents of this zone have the appearance of a maze of tortuous dense lines separated by paler lines (tubules?) and appear to be identifiable with the acrosome ray zone of the sperm of *Stimdromia* and probably with that of paguroids and heterotreme Brachyura. The acrosome ray zone could be considered part of (5) a moderately electron-dense homogeneous zone, here termed the outer dense zone, extending laterally almost to the periphery of the acrosome. This zone borders the posterior aspect of the perforatorial expansion and extends around the lateral margin of this to cover its anterolateral margin where it extends medianly to contact the subopercular zone. (6) An electron-pale zone, here termed the peripheral zone, lies posterior to the acrosome ray zone, narrowly abuts the inner dense zone, and invests the posterolateral aspect of the outer dense zone,

The centre of the acrosome vesicle is penetrated by a stout vertical column of dense material that widens apically so as to appear approximately T-shaped in sagittal section (Figs 1*A, B, 2B, C*), consistent with its possessing a capitate structure, the whole being the putative perforatorium. Its stalk is circular in cross-section (Fig. 3*B*). The head of this capitate structure is approximately bilaterally symmetrical (Fig. 3*A*): the long axis of the head is 3.18–5.10  $\mu\text{m}$  wide (mean of 8 = 4.20  $\mu\text{m}$ ), while the shorter axis is 1.26–1.91  $\mu\text{m}$  wide (mean of 5 = 1.62  $\mu\text{m}$ ).

The anterior expansion or head of the perforatorium is filled for at least its anterior half



**Fig. 3.** *Dromidiopsis edwardsi*. *A*, Transverse section (TS) through the head of the perforatorium showing bilateral prolongation. *B*, TS through the stalk of the perforatorium. *C*, *D*, Longitudinal section (LS) through the lateral prolongation of the head of the perforatorium; *D*, showing contained lamellae. *E*, LS through the anterior pole of the spermatozoon, showing lamellae in the head of the perforatorium, the operculum with opercular perforation and the apical protuberance. ap, apical protuberance; ar, acrosome ray zone; ia, inner acrosome zone; l, lamellae; n, nucleus; na, nuclear arm; o, operculum; oa, outer acrosome zone; p, perforatorium; pa, peripheral acrosome zone; so, subopercular zone.

with horizontal parallel-stacked membranes with a granular appearance suggestive of rough endoplasmic reticulum (Figs 1A, 2B, 3E). The cross-section of the lateral extension of the head of the perforatorium (Fig. 3C, D) is approximately circular to oval. In such sections (Fig. 3D), the parallel membranes tend to form a concentric whorl following the external margin of the extension.

### Nucleus

The nucleus (Figs 1A, 2B) forms an approximately ellipsoid structure only a little wider than the acrosome, which surmounts but is embedded in it. Its contents consist of a pale matrix containing a reticulum of fine putative DNA fibrils (Fig. 2B, C). The nuclear material is in direct contact with the cell membrane and a discrete nuclear membrane is not visible. However, the cell membrane surrounding the nucleus is not a simple unit membrane and in places is seen to consist of apposed membranes, presumably the nuclear envelope and the plasma membrane. The cell membrane continues apically over the surface of the acrosome to which it is closely adherent, without the intervention of cytoplasm (Figs 1A, B, 2B, C).

### Centrioles and Other Organelles

As in *S. lateralis*, no centrioles have been detected but, unlike that species, some mitochondria, still with recognisable cristae though degenerate, are present in the cytoplasm, posterolateral to the acrosome and projecting into the nucleus (Figs 1B, 2C). The mitochondria are embedded in almost negligible amounts of cytoplasm.

### Discussion

The dromiid spermatozoon, as exemplified by *Dromidiopsis edwardsi* (this study), *Stimdromia lateralis* (Jamieson 1990) and *Dromidia antillensis* (Brown 1966; Felgenhauer and Abele 1990), accords with that of the Homolidae (Guinot *et al.* 1993) and differs markedly from spermatozoa of other crabs (the raninid-heterotreme-thoracotreme assemblage) in the discoidal form of the acrosome and the capitate form of the perforatorium. Dromiids differ from homolids in the greater depression of the acrosome and the form of the head of the perforatorium, thus exhibiting a distinctive dromiid sperm type. The head is bilaterally prolonged in *D. edwardsi* and also shows bilateral symmetry, though this is less pronounced, in *S. lateralis*. Brown (1966) does not discuss symmetry in *D. antillensis*. In *S. lateralis* there is no certain equivalent of the lamellae within the *Dromidiopsis* head. In *Stimdromia* the head of the perforatorium contains tortuous profiles, most abundant peripherally, that are interpretable as parallel tubules or threads. It is possible that the tubular elements in the head of the *Stimdromia* perforatorium are equivalent to the microtubules that fill the axis of the perforatorial column in eubrachyurans such as xanthids and portunids (Jamieson 1989b, 1989c). In homolids the head of the perforatorium, though capitate as in dromiids, differs in having the form of a horizontally disposed spiked wheel (Guinot *et al.* 1993).

The acrosome contents in *D. edwardsi* show more complex zonation than in *S. lateralis*. In *S. lateralis* there is a major dense zone, constituting most of the contents of the vesicle, extending from the perforatorium to the periphery of the vesicle and, above this zone, a zone that consists of a dense matrix. A row of interconnecting electron-pale lacunae that separates the dense matrix from the capsule anteriorly, peripheral to the apical dome, is possibly the homologue of the peripheral acrosome zone of *Dromidiopsis*. A region in *Stimdromia* identified as the acrosome ray zone is presumably but not certainly homologous with the zone of that name in *Dromidiopsis*. The inner or proximal electron-dense layer in *D. antillensis* is composed of material very similar to that of the true acrosomal ray zone of the sperm of heterotremes, astacids and hermit crabs (Brown 1966; Jamieson 1990; Tudge 1992), though homology remains tentative.

Centrioles are unknown in dromiid sperm but are present in those of homolids. Nuclear arms in *D. edwardsi*, as in homolids, have the form of three small radial vertices. The 'three



stubby radial arms', lacking microtubular bundles, observed in *D. antillensis* (Brown 1966) were presumably identical with the three vertices. In *S. lateralis*, although the ellipsoidal-to-subspherical nucleus frequently shows irregularities or distortions, no discrete arms were reported (Jamieson 1990) but presence of three vertices cannot be discounted as no cross-sections of the sperm were obtained. Whether the weak development of arms is plesiomorphic in dromiids is debatable. To regard this condition as plesiomorphic would, parsimoniously, demand that dromiids be regarded as nearer the ancestral stock of the Decapoda than are the Palinura, Astacidea, Anomura and Brachyura in which the presence of well-developed nuclear arms, with or without microtubules, is a synapomorphy. This view is, however, weakened by the presence of relatively extensive nuclear arms, with or possibly as outgrowths of the three nuclear vertices, in the sperm of the Homolidae, a family regarded as being, spermatologically at least, close to the Dromiidae (Guinot *et al.* 1993). The lateral arms, known only in shrimps and prawns for the carid shrimp *Rhynchocinetes typus* (Barros *et al.* 1986), are questionably homologous with dromiid through brachyuran nuclear arms. Arms are absent from the supposed adelphotaxon (sister-group) of the Decapoda, the Euphausiacea (Jamieson 1991a), from the Syncarida, the Stomatopoda and the Peracarida (see Jamieson 1989a). The arms of branchiopods and Phyllocarida do not involve prolongation of the nuclear membrane and are therefore probably not homologous with the thus characterised arms of decapods.

Dromiids, homolids, raninids, higher heterotremes and thoracotremes differ (homoplasically?) from lower heterotremes in lacking microtubules in the nuclear arms. Dromiid sperm lack the posterior median process of the nucleus seen in homolids, anomurans and lower heterotremes. The sperm of *D. edwardsi* differs from other investigated dromiid sperm in the asymmetrical location of the opercular perforation (and the apical protuberance) relative to the longitudinal axis of the sperm, and in more complex zonation of the acrosome vesicle. Protuberance of subopercular material through the opercular perforation is seen also in *Paradynomene tuberculata* (Jamieson *et al.* 1993). The acrosome is deeply embedded in the nucleus in *D. edwardsi* whereas in *S. lateralis* it is superficial on the nucleus. Cytoplasm, though meagre, is better developed in *D. edwardsi* and, particularly, in *D. antillensis* than in *S. lateralis* in which it consists of a very small amount of moderately electron-dense material surrounding or adjacent to some of the finger-like extensions of the capsule and underlies the acrosome in places; occasionally, scroll-like or lamellar structures are present in this cytoplasm. In *D. antillensis*, sandwiched between the nucleus and the acrosomal region there is a thin lamellar region that consists of membrane arrays in certain areas.

Dromiids resemble homolids in the shared depressed acrosome and capitate perforatorium (bilateral in dromiids, radial in homolids) but resolution of the question of whether these are synapomorphies or homoplasies awaits parsimony analysis of a wide range of brachyurans in this laboratory. The phylogenetic position of raninoids, placed with homolids in an archaebachyuran section of the Podotremata by Guinot (1978), similarly requires further analysis. Although the existence of a distinctive and unified dromiid sperm type has been demonstrated here, it remains to be seen whether the sperm of the dromiid *Hypochocha*, which rRNA sequences place closer to the anomuran *Clibanarius* than to *Dromidia* (Spears *et al.* 1992), will be found to conform to the dromiid sperm type. It may be pertinent that, in view of its apparent relationship with shell-inhabiting anomurans, *Hypochocha* is a shell-carrier whose relationship with other sponge-carrying dromiids is difficult to establish (McLay 1993).

#### Acknowledgments

The authors are grateful to the Queensland Department of Primary Industries, the staff of their Northern Fisheries Research Centre, Cairns, and the crew of their research vessel, 'Gwendolynne May', for assisting in the collection and fixation of the specimen of

*D. edwardsi* used in this study. Peter Davie (Queensland Museum) is thanked for identifying the specimen. Mrs L. Daddow (Zoology Department, the University of Queensland) gave excellent technical assistance. This work was made possible by Australian Research Council funding to B. Jamieson.

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