JOURNAL OF CRUSTACEAN BIOLOGY, 18(1): 78–94, 1998

COMPARATIVE SPERMATOZOAL ULTRASTRUCTURE OF THE THREE DROMIACEAN FAMILIES EXEMPLIFIED BY *HOMOLODROMIA KAI* (HOMOLODROMIIDAE), *SPHAERODROMIA LAMELLATA* (DROMIIDAE), AND *DYNOMENE TANENSIS* (DYNOMENIDAE) (PODOTREMATA: BRACHYURA)

D. Guinot, B. G. M. Jamieson, B. Richer de Forges, and C. C. Tudge

ABSTRACT

The monophyletic Dromiacea, including *Sphaerodromia lamellata*, *Homolodromia kai*, and *Dynomene tanensis*, here studied, have the following characters: (1) operculum perforate, but lacking the thoracotreme apical button; (2) opercular projections into the subopercular material, diagnostic of homolids, absent; (3) operculum discontinuous with the capsule, unlike raninoids; (4) operculum moderately thick, not extremely thin as in the cyclodorippoids *Tymolus* and *Xeinostoma*; (5) operculum not extremely wide, contrasting with the great width in cyclodorippoids; (6) periopercular rim and (7) accessory opercular ring absent, being variably present in eubrachyurans; (8) subopercular protuberance through operculum well developed (synapomorphy), weak in homolids; (9) true acrosome ray zone absent; (10) peripheral border of outer acrosome zone border not ragged, unlike some xanthoids; (11) anterolateral pale zone of acrosome contents present (autapomorphy); (12) xanthid ring absent; (13) subacrosomal chamber or perforatorium extending preequatorially, unlike *Ranina ranina*; (14) head of perforatorium bilateral (autapomorphy); (15) corrugations of the wall of the perforatorial chamber absent; (16) centrioles apparently absent; (17) posterior median process of the nucleus absent; (18) thickened ring (typical of Eubrachyura) absent; (19) concentric lamellae (typical of Thoracotremata) in the outer acrosome zone absent; (20) capsular chambers absent; and (21) capsular flange absent, unlike *Ranina ranina* and *Raninoides* sp. Spermatologically *Sphaerodromia lamellata* appears closer to the dynomenid *Dynomene tanensis* than it is to the mutually paraphyletic *Dromidiopsis edwardsi* and *Stimdromia lateralis*. The spermatozoon of *Homolodromia kai* (Homolodromiidae) shares a striking putative synapomorphy with *Paradynomene tuberculata*: a flange-like lateral extension of the lower acrosome zone; both species appear to lie within a dromiid clade. Neither the Dromiidae nor the Dynomenidae appear monophyletic spermatologically. The spermatozoal evidence is discussed in the light of a brief review of nonspermatozoal morphology. General morphology and spermatozoal ultrastructure both strongly endorse monophyly of the Dromiacea.

The Podotremata sensu Guinot (1977, 1978) contain the Dromiacea and Archaeobrachyura. The Dromiacea consist of the Dromioidea and Homolodromioidea. The Archaeobrachyura contain the Homoloidea (containing the three families Homolidae, Latreilliidae, and Poupiniidae), Raninoidea, and Cyclodorippoidea (=Tymoloidea). In other classifications, the superfamily Homoloidea is often associated with or placed in the Dromiacea (see review by Guinot and Richer de Forges, 1995). In some contrast with the classification of Guinot, nucleotide sequences of 18S ribosomal RNA support the exclusion of a mono- or polyphyletic Dromiidae from the Brachyura, and their association with Anomura, but support inclusion of the Raninidae in the Brachyura (Spears and Abele, 1988; Abele, 1991; Spears *et al.*, 1992); homolids were not considered in the molecular analyses.

Podotreme and wider Brachyuran phylogeny was investigated by parsimony analysis by Jamieson (1994) and Jamieson *et al.* (1995), using spermatozoal characters and a combination of these with nonspermatozoal morphological characters. It was found that the Dromiacea as constituted by Guinot for the Dromiidae, Dynomenidae, and Homolodromiidae (Guinot, 1978, 1995) formed a monophyletic group in both analyses. However, neither the constituent Dromiidae nor the Dynomenidae was found to be monophyletic spermatologically. It was concluded that there is distinctive dromiacean spermatozoal ground plan, but that sperm structure does not distinguish the constituent families Dromiidae, Homolodromiidae, and Dynomenidae. The nonspermatozoal characters which separate the three families were indicated.

In the previous analyses (Jamieson, 1994;

Jamieson *et al.*, 1995), brief definitions of the spermatozoa of *Homolodromia kai* Guinot (Homolodromiidae) and *Dynomene tanensis* Yokoya, as *D.* aff. *devaneyi* Takeda (Dynomenidae), were included. In the present account, more detailed descriptions are given of the spermatozoa of these species, and those of *Sphaerodromia lamellata* Crosnier (Dromiidae) are described for the first time. Spermatozoal evidence for monophyly of the Dromiacea, but paraphyly of the Dromiidae and Dynomenidae, is further considered in the light of evidence from general, nonspermatozoal morphology.

Materials and Methods

Mature male specimens of *Homolodromia kai*, *Sphaerodromia lamellata*, and *Dynomene tanensis*, were collected by Dr. B. Richer de Forges during the BATHUS 3 Cruise (Stations CC848, CP813, and CP805, respectively) east of New Caledonia between 22 November and 2 December 1993.

The male reproductive material (usually both testes, including the ducts of the vasa deferentia) was removed from fresh crab specimens and immediately fixed in cold glutaraldehyde for a minimum of 2 h at 4°C, then posted to Brisbane at ambient temperature, where the remainder of the fixation and embedding process for transmission electron microscopy (TEM) was carried out. For TEM, the gonad tissue was processed in the Zoology Department, The University of Queensland, by the standard fixation procedure (outlined below) for TEM. This was carried out in a Lynx -el. Microscopy Tissue Processor (Australian Biomedical Corporation, Ltd., Mount Waverley, Victoria, Australia), after the initial glutaraldehyde fixation and first phosphate buffer wash. Portions of the testis (approximately 1 mm^3) were fixed in 3% glutaraldehyde in 0.2 M phosphate buffer (pH 7.2), with 1–3% sucrose added, for a minimum of 2 h at 4°C. They were washed in phosphate buffer (3 washes in 15 min), postfixed in phosphate-buffered 1% osmium tetroxide for 80 min; similarly washed in buffer and dehydrated through ascending concentrations of ethanol (40–100%). After being infiltrated and embedded in Spurr's epoxy resin, thin sections (500–800 Å thick) were cut on an LKB 2128 UM IV microtome with a diamond knife. Sections were placed on carbon-stabilized colloidin-coated 200-μm mesh copper grids and stained (according to Daddow, 1986) in Reynold's lead citrate for 30 s, rinsed in distilled water, then 6% aqueous uranyl acetate for 1 min, Reynold's lead citrate again for 30 s, and a final rinse in distilled water. Micrographs were taken on a Hitachi H-300 transmission electron microscope at 80 kV and a JEOL 100-S transmission electron microscope at 60 kV.

Spermatozoal Ultrastructure

Homolodromia kai

General.—A spermatozoon of *Homolodromia kai* is illustrated semidiagrammatically in Fig. 1 and in TEMs in Fig. 2A–E. Glutaraldehyde-fixed spermatozoa appear almost spherical, reflecting the shape of the nucleus. However, by TEM, and probably in life, the nucleus often appears very irregular in shape (Fig. 2A, B), being drawn out laterally and asymmetrically (Fig. 2A) or being almost symmetrical beneath the acrosome which it then may exceed in anterior-posterior extent (Fig. 2B). A symmetrically fixed spermatozoon is 4.8 μm wide and 5.4 μm in anterior-posterior thickness. Almost the entire width of a large anterior portion of the spermatozoon (Figs. 1, 2A, B) consists of the anteroposteriorly depressed acrosome. The acrosome is covered, with the exception of its anterior opercular pole, by a thin layer of nuclear material. It is wider in one vertical plane than the other, and, while having the form of a thick discus in the greater width (Fig. 2A), has anterolateral "shoulders," owing to depression of the surface around its apex, in the plane at right angles (Fig. 2B).

The nucleus is electron pale, but is laced with innumerable slender, dense chromatin fibers. A very small amount of cytoplasm, chiefly apparent by the presence of degenerating mitochondria, adheres to the posterolateral aspects of the acrosome and sends short extensions into the nucleus.

The longitudinal axis of the acrosome of *Homolodromia kai* is occupied by a capitate perforatorium with a slender stalk which approximately equals the "head" (apical expansion) in length. The head is wider in one diameter than in that at right angles (Fig. 2A, B). There is no division of the head into radial rays.

A low dome-shaped or low conical, 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, dromiids, dynomenids, homolids, raninids, and more advanced crabs. It is covered by the general acrosome membrane and the plasma membrane of the sperm cell.

It appears that nuclear arms are absent, as determined by TEMs of a transversely sectioned spermatozoon and by light microscopy of glutaraldehyde-fixed sperm.

Acrosome.—The anterior surface of the acrosome is gently domed over the operculum (Figs. 1, 2A, B), which occupies about two-thirds of its greater width (Fig. 2A). The

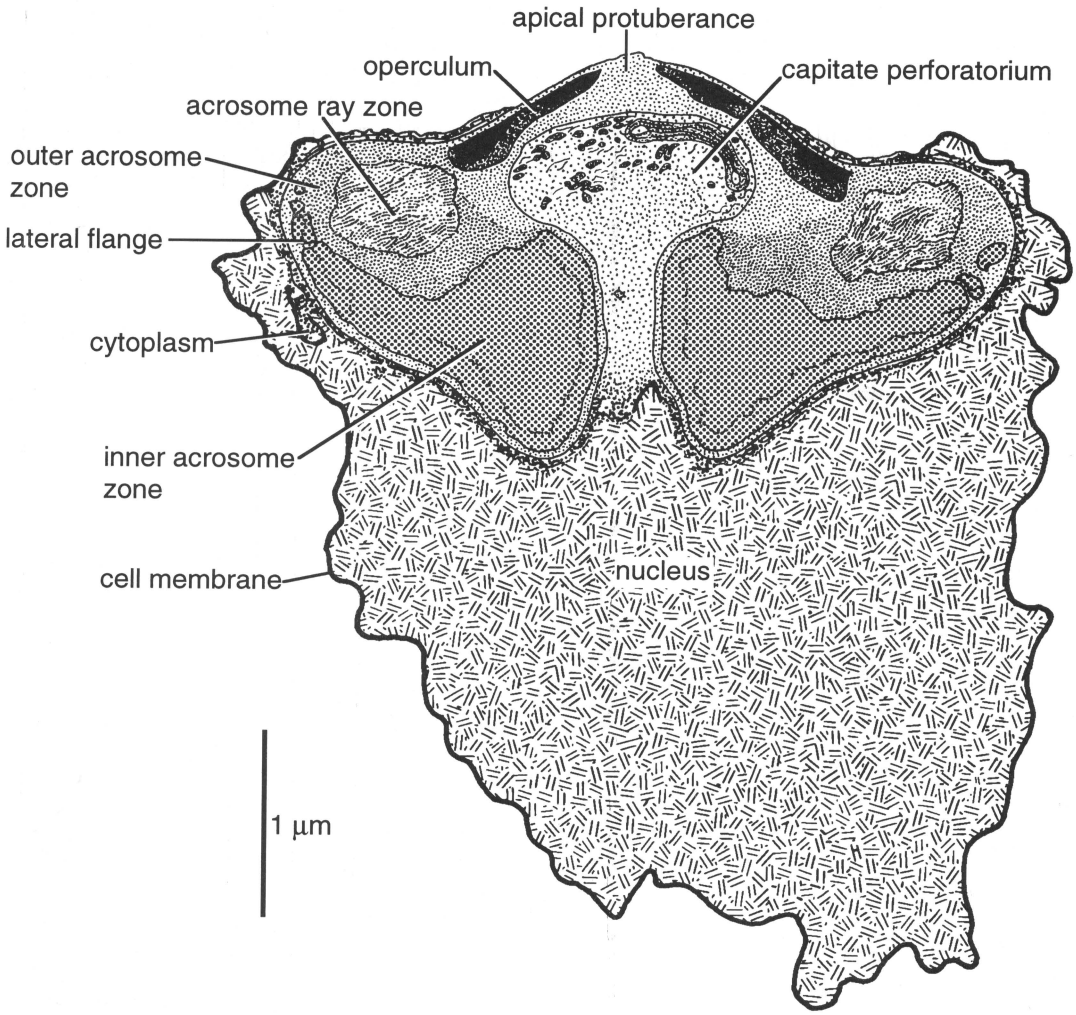


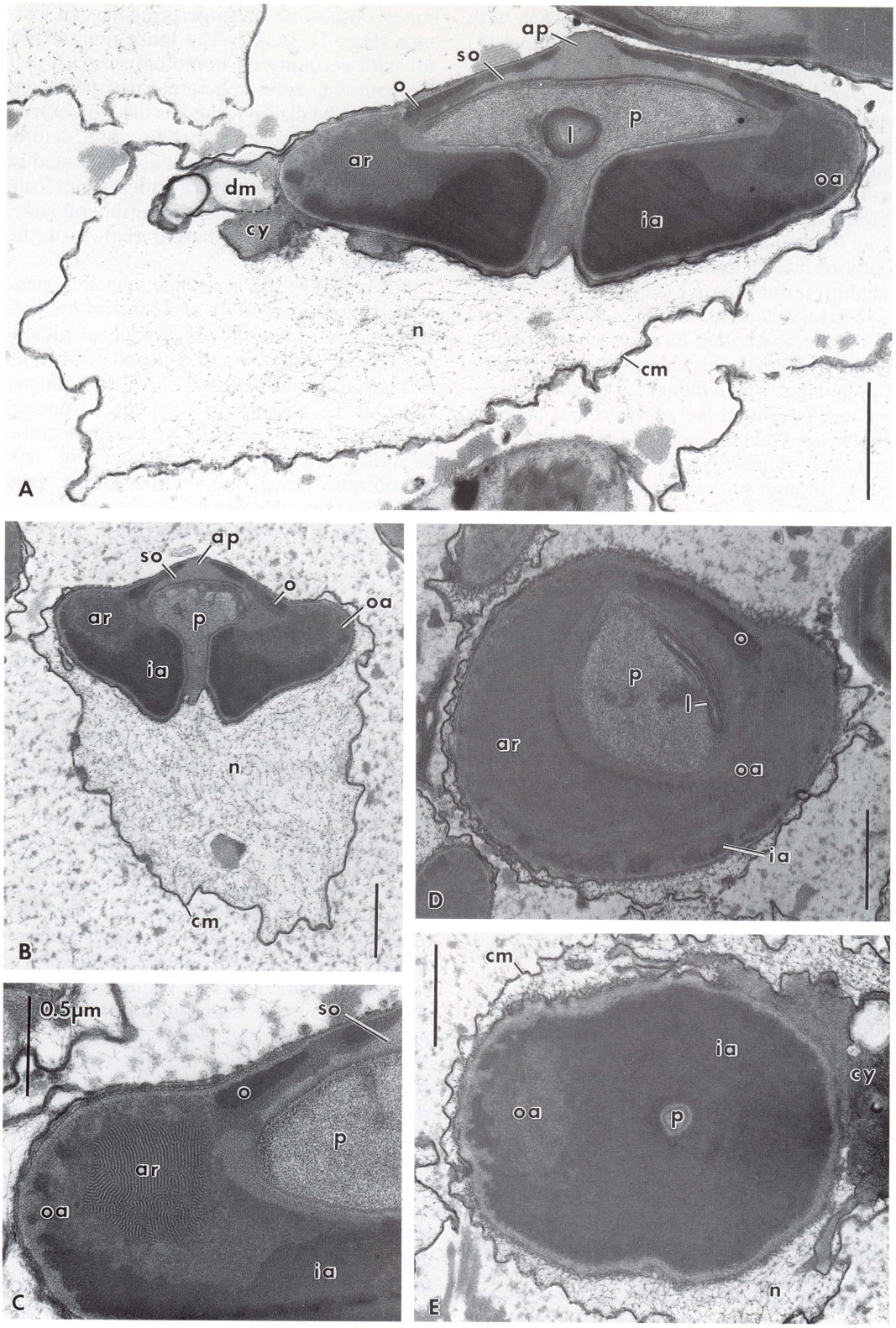
Fig. 1. *Homolodromia kai*. Semidiagrammatic representation of a spermatozoon traced from a transmission electron micrograph.

greater diameter of the acrosome vesicle, seen in sagittal longitudinal section, is approximately 5.1 µm (Fig. 2A) and its lesser diameter is 4.2 µm (Fig. 2B); its anterior-posterior thickness is 2.2 µm (Fig. 2A, B), giving a ratio length : width = 0.43. The vesicle is bounded by a unit acrosomal membrane around its entire periphery, including the lining of the perforatorial chamber (Fig. 2A–C). A separate layer identified as the "capsule" in many brachyuran sperm is not apparent.

The contents of the acrosome vesicle, peripheral to the axial perforatorium (described below), show a zonation (Figs. 1, 2A–E) which is more conspicuously horizontal than concentric. Six zones or regions are dis-

→

Fig. 2. *Homolodromia kai*. Transmission electron micrographs. A, Midvertical longitudinal section of entire spermatozoon in the wide axis of the capitate perforatorium; B, Same, in the short axis of the perforatorium; C, Detail of the lateral portion of a midvertical section; D, Transverse section of acrosome through the fingerprint zone; E, Transverse section chiefly through the inner acrosome zone. Abbreviations: ap, apical protuberance; ar, fingerprint zone (questionably homologous with acrosome ray zone of Heterotremata); cm, cell membrane; cy, cytoplasm; dm, degenerating mitochondrion; ia, inner acrosome zone; l, lamellae in perforatorium; n, nucleus; o, operculum; oa, outer acrosome zone; p, perforatorium; pa, anterolateral pale zone of acrosome; so, subopercular zone. Scale bars = 1 µm unless otherwise indicated.


ap
so
o
l
p
ar
dm
cy
oa
ia
n
cm
A
so
ap
o
oa
ar
p
ia
n
cm
B
0.5µm
so
o
p
ar
oa
ia
C
o
p
l
ar
oa
ia
D
cm
ia
cy
oa
p
n
E

cernible in the acrosome contents, each with its own peculiar features. These include: (1) The operculum is 3.5 μm in its greater diameter (Fig. 2A), and 2.2 μm wide in its lesser diameter (Fig. 2B), and appears in vertical section as a dome-shaped or low conical, moderately electron-dense plate. The anterior layer of this plate (about half its total thickness) forms a strongly electron-dense zone thickened at its outer rim and with one or more interruptions on each side. The operculum is interrupted centrally by a hiatus. (2) Moderately dense material protrudes from below the operculum through the perforation as an approximately hemispheroidal plug. The layer, of which the protuberance is an extension, is termed the subopercular zone, as in *Paradynomene tuberculata* Sakai (see Jamieson, Guinot, and Richer de Forges, 1993), though homology with a zone of the same name in other brachyurans is uncertain (Jamieson, Guinot, and Richer de Forges, 1993). The subopercular zone directly overlies the capitate expansion of the perforatorium. The four remaining zones of the acrosome vesicle include: (3) The inner acrosome zone, surrounding the stalk of the perforatorium. This has exactly the appearance of the same zone in *Paradynomene tuberculata*. It occupies approximately the posterior half of the acrosome, extending from the periphery of the stalk of the perforatorium, from which it is separated by a narrow pale layer bounded centrally by the membrane which encloses the stalk, to the posterolateral wall of the acrosome. Its anterior-posterior extent is greatest near the perforatorium and its decreases more peripherally to a platelike form for more than half of its transverse extent. Its outer edge in longitudinal section of the sperm is often accompanied by small apparently detached portions of the same composition. These portions presumably represent irregularities of the edge or flange of this zone, as was determined from cross sections for *P. tuberculata*. As in the latter species, the lateral flange (Fig. 2A, C), and at least an anterior layer of the thickened central portion, show wide cross striations. Anterior to the inner acrosome zone, but separated from it by a diffuse zone, which may be the equivalent of the unnamed round zone described for *P. tuberculata*, lies (4) a region, as in *P. tuberculata*, of parallel dense lines separated by pale lines (tubules?), giving in longitudinal sagittal section a tortuous honey comb-like or fingerprint-like appearance (Figs 1, 2A–C). The latter region cannot with certainty by homologized with that acrosome ray zone in heterotreme sperm and may better be distinguished as the "fingerprint zone." (5) An outer acrosome zone, lateral to the fingerprint zone, has been indicated in Figs 1, 2A–E, but is possibly not distinct from (6) an electron-pale zone, the peripheral zone, which fills the anterolateral region of the acrosome.

The center of the acrosome vesicle is penetrated by a moderately slender vertical column of dense material which widens apically so as to attain the form of a closed mushroom in sagittal section (Figs. 1, 2A, B), consistent with its possessing a capitate structure, the whole being the putative perforatorium. Its stalk is circular in cross section (Fig. 2E). An oblique transverse section of the head (Fig. 2D) confirms that it is longer in one diameter than in that at right angles. The long axis of the head measures 3.1 μm (Fig. 2A), while the shorter axis is 1.3 μm (Fig. 2B), a ratio of about 2.6:1. The perforatorial head contains lamellar structures (Figs. 1, 2A, D).

Nucleus.—The nucleus, when symmetrically fixed (Figs. 1, 2B), forms approximately two-thirds of the length of the spermatozoon, being at least twice as long in total anterior-posterior extent as the acrosome, which is embedded in its anterior aspect. The acrosome is thinly invested by nuclear material up to the level of the base of the operculum, though falling somewhat short of the latter. The nuclear contents consist of a pale matrix containing a reticulum of fine putative DNA fibrils (Fig. 2A, B, E). The nucleus is in direct contact with the cell membrane and a discrete nuclear membrane is not visible. However, the cell membrane surrounding the nucleus appears to be too thick and dense to be a simple unit membrane and presumably consists of two apposed membranes, the nuclear envelope and the plasma membrane. A dense but occasionally interrupted inner nuclear membrane separates the nucleus from the cytoplasm (Fig. 2E). The plasma membrane continues apically over the surface of the acrosome to which it is closely adherent, without the intervention of cytoplasm (Fig. 2C). No nuclear processes or arms are observable.

Centrioles.—Centrioles have not been observed. Their absence cannot be assumed, but

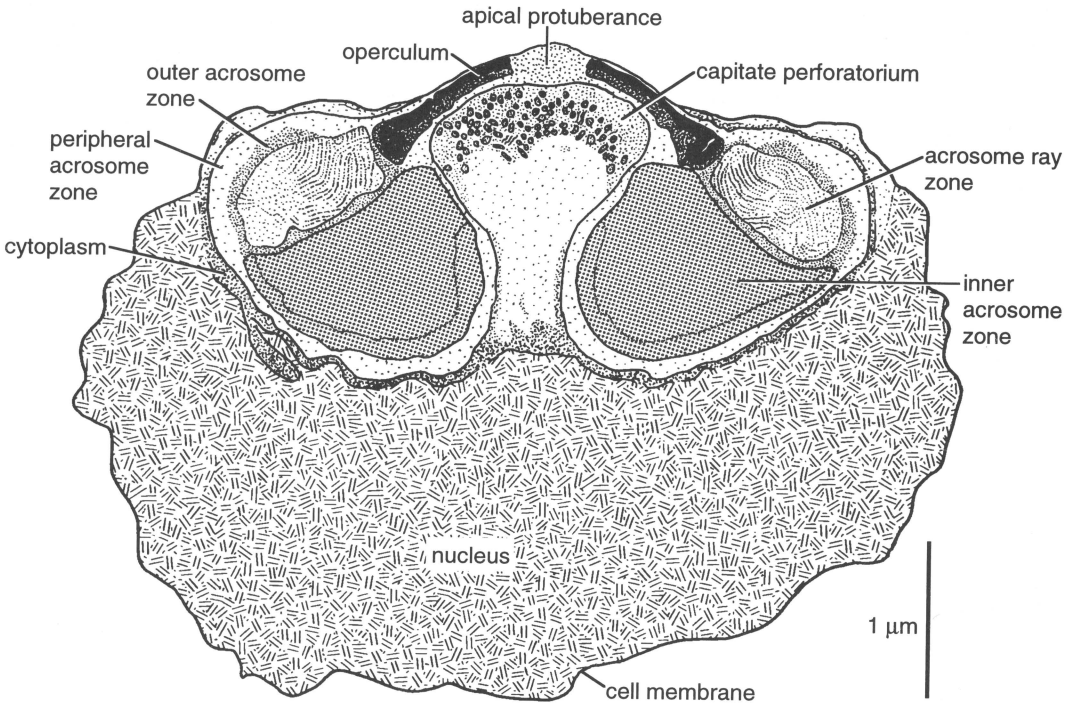


Fig. 3. *Sphaerodromia lamellata*. Semidiagrammatic representation of a spermatozoon traced from a transmission electron micrograph.

the absence of a substantial amount of cytoplasm at the base of the perforatorial stalk, where centrioles, if present, are normally situated in brachyurans, suggests that centrioles may be absent from the mature sperm of *Homolodromia kai*.

Sphaerodromia lamellata

General.—A spermatozoon of *Sphaerodromia lamellata* is illustrated diagrammatically in Fig. 3 and in TEMs in Fig. 4A, B. Glutaraldehyde-fixed spermatozoa have the form of a thick ellipse; there are no obvious arms but two nuclear vertices are apparent on opposite sides of the acrosome in dorsal view in some, but not all, sperm. By TEM (Fig. 4A), the spermatozoon is 7.0 μm wide and 4.0 μm in anterior-posterior thickness. The anterior portion of the spermatozoon (Fig. 4A, B) consists of the anteroposteriorly depressed acrosome. The acrosome is covered, with the exception of its anterior, opercular pole, by a thin layer of nuclear material. It is wider in one vertical plane than the other. It has the form of a thick, posteriorly slightly concave, ellipse in the greater width (Fig. 4A). Anterolateral "shoulders," which are not as pronounced as in *Homolodromia kai*, are seen in the plane at right angles owing to the domelike protuberance of the opercular region (Fig. 4B).

The nucleus is electron pale, but is laced with innumerable slender, dense chromatin fibers. A very small amount of cytoplasm, chiefly apparent by the presence of degenerating mitochondria, adheres to the posterolateral aspects of the acrosome (Fig. 4A, B). A posteriorly protruding region at the posterior end of the perforatorium is probably also to be considered cytoplasmic (Fig. 4B).

The longitudinal axis of the acrosome of *Sphaerodromia lamellata* is occupied by a capitate perforatorium with a moderately broad stalk which is somewhat shorter than the "head" (apical expansion) in length. The head is wider in one diameter than in that at right angles (Fig. 4A, B) and, unlike *Homolodromia kai*, this is true also of the stalk. As in all nonhomolids, there is no division of the head into radial rays.

An operculum is present, as in *Homolodromia kai*, and consists of a low dome-shaped or low conical, dense layer, with a narrow apical interruption, which covers the anterior limit of the perforatorium and extends laterally over much of the anterior aspect of the acrosome vesicle.

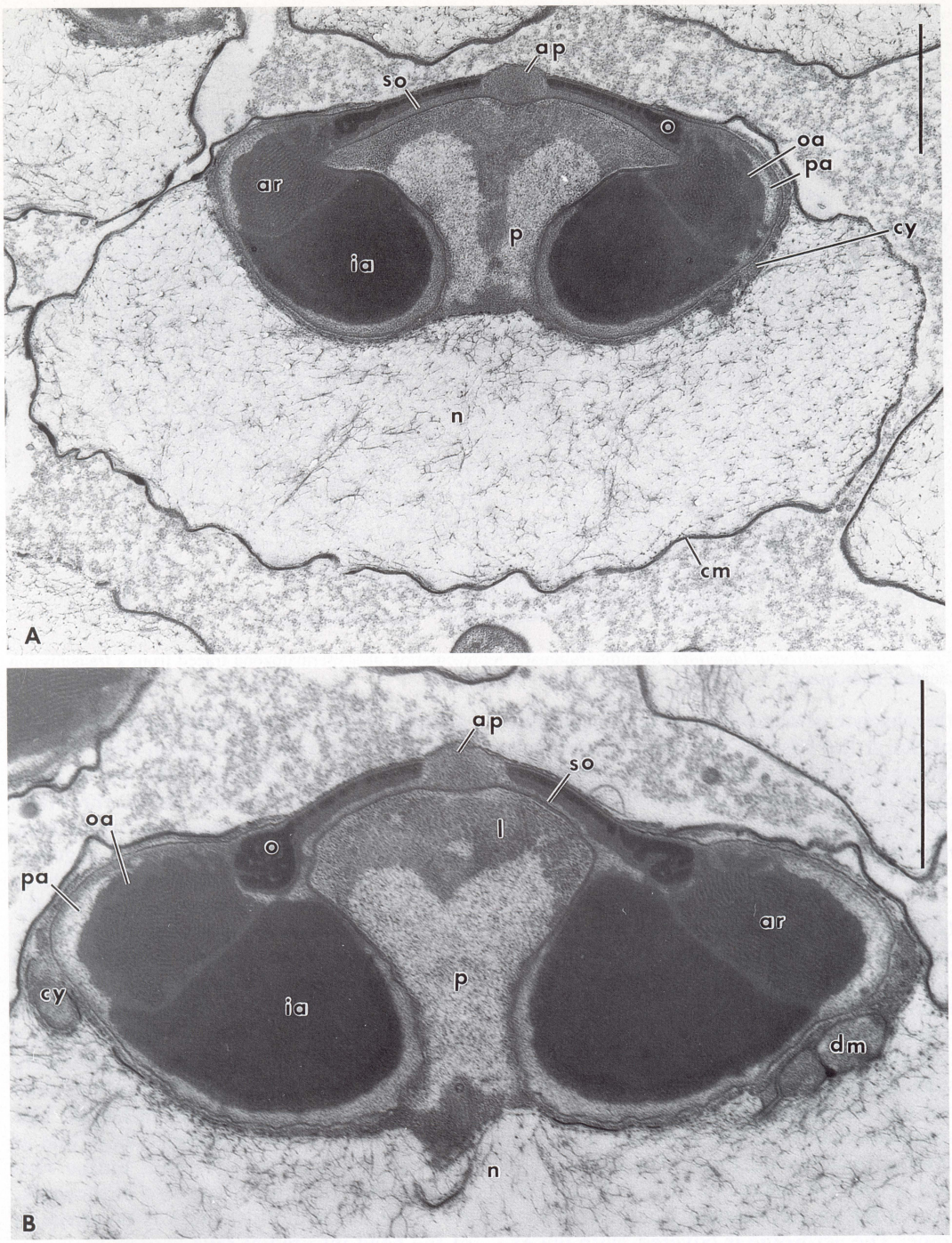


Fig. 4. *Sphaerodromia lamellata*. Transmission electron micrographs. A, Midvertical longitudinal section of entire spermatozoon in the wide axis of the capitate perforatorium; B, Same, in the short axis of the perforatorium. Abbreviations as in Fig. 2.

Acrosome.—The anterior surface of the acrosome forms a dome over the operculum (Fig. 4A, B), which occupies about half of its width (Fig. 4B). The dome is strongly protuberant in the plane of the lesser diameter of the perforatorium (Fig. 4B), moderately so in the diameter at right angles (Fig. 4A). Unlike *Homolodromia kai*, the diameter of the acrosome

vesicle is the same in the two planes at right angles, with a mean of 4.6 μm, SD = 0.11; its mean anterior-posterior length is 2.1 μm, SD = 0.11 (Fig. 4A, B), giving a ratio length : width = 0.45 (N = 7). The vesicle is bounded by the acrosomal membrane around its entire periphery, including the lining of the perforatorial chamber (Fig. 4A, B). A separate layer identified as the "capsule" is not apparent.

The contents of the acrosome vesicle, peripheral to the axial perforatorium (described below), show a zonation (Fig. 4A, B) which may, somewhat arbitrarily, be considered intermediate between horizontal (as in *Homolodromia kai*) and concentric (as in Heterotremata sensu lato). Apart from this intermediate condition, zonation of the acrosome resembles that of *H. kai*, but there are some noteworthy differences. Six zones or regions may be arbitrarily recognized. These include: (1) The operculum, which is 2.7 μm in its greater diameter (Fig. 4A), and 2.5 μm wide in its lesser diameter (Fig. 4B). Its form is as described for *H. kai*, with the exceptions that, at least in its lesser diameter (Fig. 4B), its lateral rim, including its electron-dense anterior layer, is strongly thickened and that the dense layer is more or less broken up into beads (Fig. 4A, B). It is interrupted centrally by a hiatus. (2) Moderately dense material protrudes from below the operculum through the perforation as an approximately hemispheroidal plug as in *H. kai*. The four remaining zones of the acrosome vesicle include: (3) The inner acrosome zone, surrounding the stalk of the perforatorium. This differs from that in *H. kai* in being more bulky and in having only a rudiment of the flangelike lateral expansion, and their peripheral irregularities, seen in that species. Striations of this zone, seen in *H. kai*, have not been observed, but its periphery, except anterolaterally, is differentiated as a denser zone. Unlike *H. kai*, there is only a very narrow pale zone separating the inner acrosome zone from zone (4) which, as in the latter species, is a fingerprint zone, which cannot with certainty be homologized with the acrosome ray zone of heterotreme sperm. This zone is embedded in pale material continuous with the narrow strip which separates it from the inner acrosome zone. The outer region of this pale zone constitutes (5), the outer acrosome zone. Finally (6), a pale peripheral zone, fills the anterolateral region of the acrosome, as in *H. kai*, but differs from that in the latter species in being clearly distinct from the outer acrosome zone (Fig. 4A, B).

The center of the acrosome vesicle is penetrated by a capitate perforatorium (Fig. 4A, B). The stalk of this is stouter than in *Homolodromia kai* and is not circular in cross section, but is wider in the wide diameter of the head. The long axis of the head measures 2.9 μm (Fig. 4A), while the shorter axis is 1.5 μm (Fig. 4B), a ratio of about 1.9:1. The perforatorial head lacks the lamellar structures seen in that of *H. kai*, but has differentiated anterior and axial dense material. Its anterior outline is that of a cupid's bow. As in *H. kai*, the lateral edges of the head are sharp in the long diameter but rounded in the short diameter.

Nucleus.—The nucleus, with diffuse DNA, is less bulky than in *Homolodromia kai*, the major part, behind the acrosome, forming about one-half of the length of the spermatozoon. The acrosome is thinly invested by nuclear material which differs in overlapping the rim of the operculum. The cell membrane presumably consists of two apposed membranes, the nuclear envelope and the plasma membrane, and a dense but occasionally interrupted inner nuclear membrane separates the nucleus from the cytoplasm (Fig. 4A, B). The plasma membrane continues apically over the surface of the acrosome to which it is closely adherent, without the intervention of cytoplasm (Fig. 4A, B).

Centrioles.—Centrioles have not been observed, but their occurrence cannot be ruled out.

Dynomene tanensis

General.—A spermatozoon of *Dynomene tanensis* is illustrated semidiagrammatically in Fig. 5 and in TEMs in Fig. 6A, B and Fig. 7A–E. Glutaraldehyde-fixed spermatozoa (Fig. 6A, B) have the form of a thick ellipse; two nuclear vertices are apparent on opposite sides of the acrosome in dorsal view in some, but not all, sperm and are here interpreted as arms. By TEM (Figs. 5, 6A, B), the spermatozoon is 4.7 μm wide and 3.2 μm in anterior-posterior thickness. Considerably more than the anterior portion of the spermatozoon (Figs. 5, 6B) consists of the anteroposteriorly depressed acrosome. The acrosome is covered, with the exception of its anterior opercular pole, by a thin layer of nuclear material. The acrosome, unlike the contained

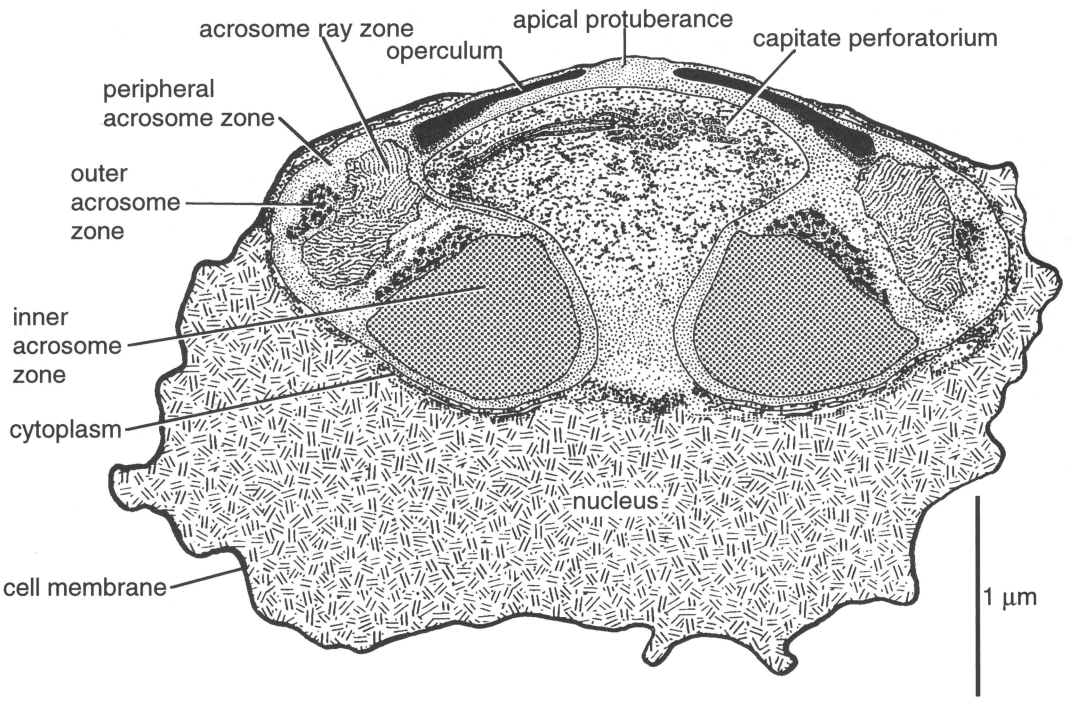


Fig. 5. *Dynomene tanensis*. Semidiagrammatic representation of a spermatozoon traced from a transmission electron micrograph.

perforatorium, is approximately isodiametric, having a mean diameter of approximately 3.6 μm, SD = 0.22, with a mean length of 1.9 μm, SD = 0.16 (N = 7). The anterior surface over its entire diameter (Figs. 5, 6A, B) describes a broad arc, lacking the lateral shoulder seen in *Sphaerodromia lamellata* and, especially, *Homolodromia kai*.

The nucleus is electron pale, but is laced with innumerable slender, dense chromatin fibers. The cytoplasm is even more reduced than in *Sphaerodromia lamellata* and *Homolodromia kai*, being represented only by a minute residue posterior to the base of the perforatorium, which is unusual for the Brachyura in containing no evident vestiges of mitochondria (Fig. 5, 6A, B).

The longitudinal axis of the acrosome of *Dynomene tanensis* is occupied by a capitate perforatorium with a broad stalk which is about equal in length to the "head" (apical expansion) from which it is not abruptly demarcated. The head is wider in one diameter than in that at right angles (Fig. 6A, B) and, unlike *Homolodromia kai*, this appears to be true of the stalk (Figs. 6A, B, 7E).

The operculum consists of a dome-shaped or low conical, dense layer, with a narrow apical interruption, which covers the anterior limit of the perforatorium. It forms a lower, less convex dome than in *Homolodromia kai* and *Sphaerodromia lamellata*. It extends over about 0.6 of the anterior aspect of the acrosome vesicle.

Acrosome.—The anterior-posterior thickness of the acrosome is 1.7–2.0 μm (Fig. 6A, B), giving a ratio length : width = 0.47–0.52 (N = 2). The vesicle is bounded by the acrosomal membrane around its entire periphery, including the lining of the perforatorial chamber (Figs. 5, 6A, B). A separate layer identified as the "capsule" is not apparent.

The contents of the acrosome vesicle, peripheral to the axial perforatorium (described below), show a zonation (Fig. 6A, B) which may, as in *Sphaerodromia lamellata*, be considered intermediate between horizontal and concentric. Six zones or regions may be arbitrarily recognized. These include: (1) At its base, the operculum is 2.2 μm in both the long and the short diameters of the head of the perforatorium. However, it appears bilaterally compressed when observed in transverse section (Fig. 6B). Its form is as described for *Homolodromia kai*, with the ex-

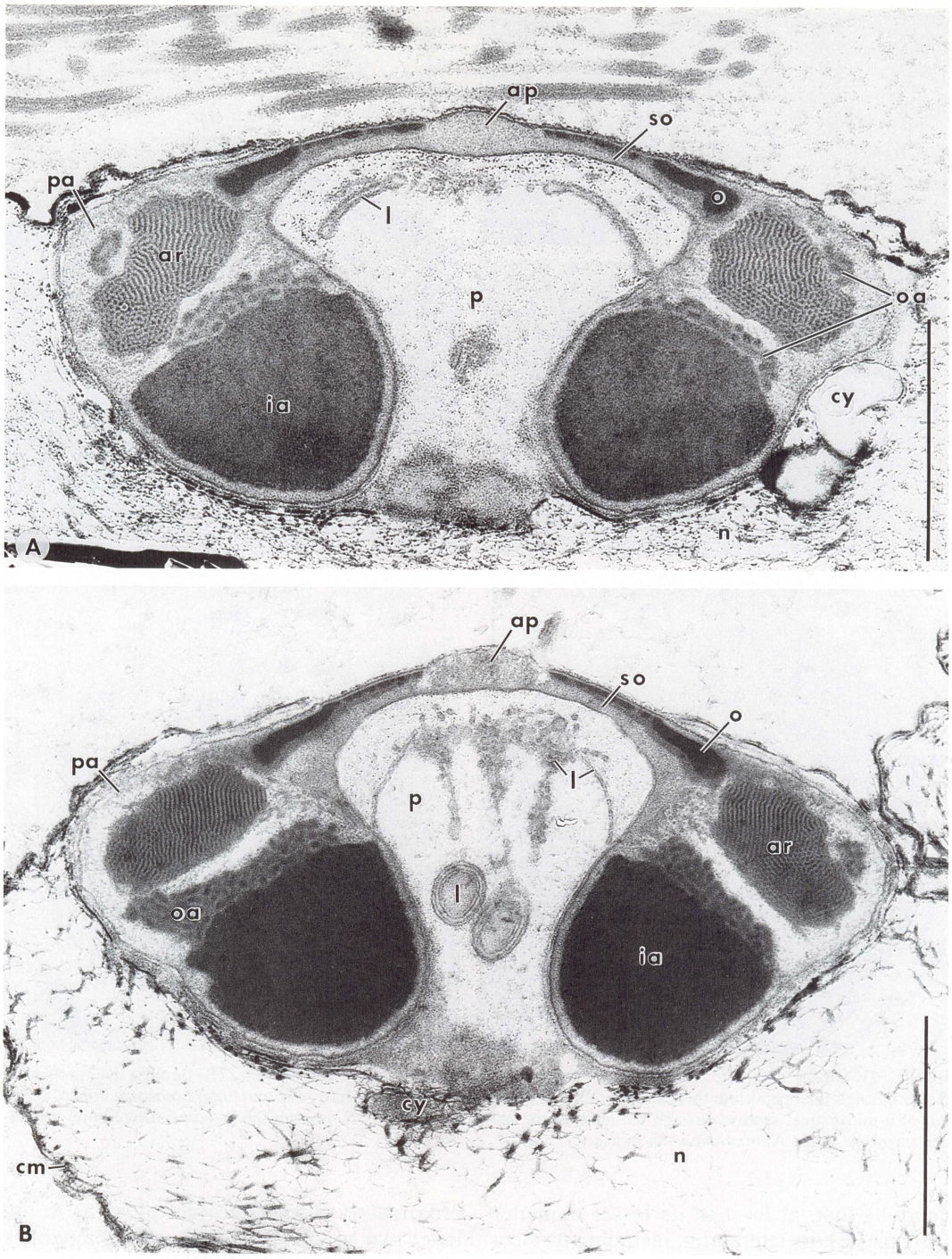


Fig. 6. *Dynomene tanensis*. Transmission electron micrographs. A, Midvertical longitudinal section of entire spermatozoon in the wide axis of the capitate perforatorium; B, Same, in the short axis of the perforatorium. Abbreviations as in Fig. 2.

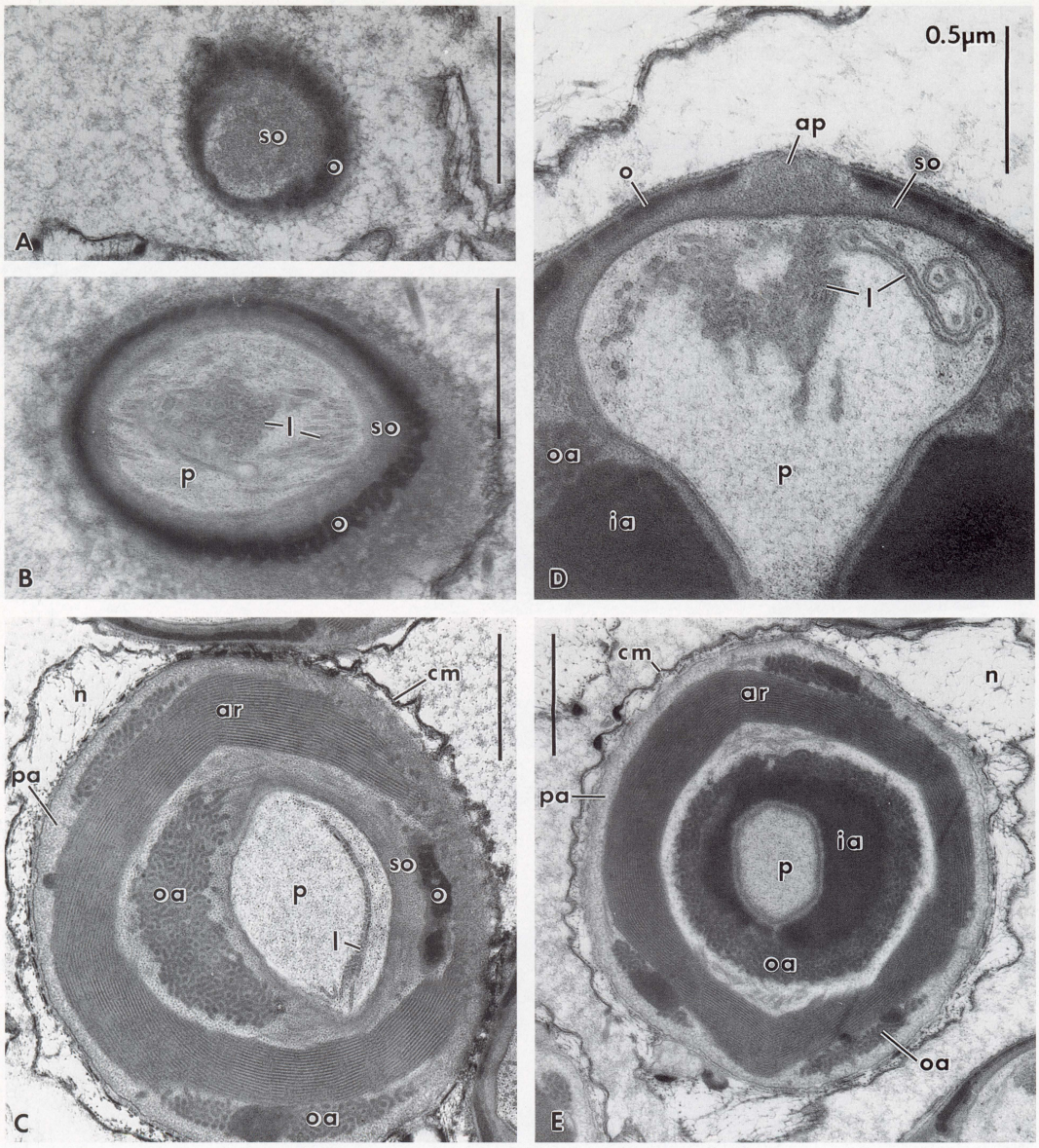


Fig. 7. *Dynomene tanensis*. Transmission electron micrographs. A, Transverse section (TS) through the operculum; B, TS through the operculum more basally; C, TS through the fingerprint-like zone and outer acrosome zone; D, Detail of a midvertical section through the head of the perforatorium; E, TS through the fingerprint-like zone and inner acrosome zone. Abbreviations as in Fig. 2.

ceptions that, at least in its lesser diameter (Fig. 6A, B), its lateral rim, including its electron-dense anterior layer, is strongly thickened, though not as strongly as in *S. lamellata*. The dense layer is broken up to an extent intermediate between these two species (Figs. 6A, B, 7D). As in all podotremes, it is interrupted centrally by a hiatus. (2) Moderately dense material protrudes from below the operculum through the perforation as an approximately hemispheroidal plug, as in the latter two species. The four remaining zones of the acrosome vesicle include: (3) The inner acrosome zone, surrounding the stalk of the perforatorium. This differs from that in *H. kai*, and conforms with that of *S. lamellata* in being more bulky and hardly wider anteroposteriorly than laterally. It differs from the other two species in lacking even a rudiment of the flangelike lateral expansion or pe-

Table 1. Comparison of dromiacean spermatozoa.

	Stimdromia lateralis. Jamieson (1990)	*Dromidiopsis edwardsi.* Jamieson *et al.* (1993)	*Sphaerodromia lamellata.* This study.	*Dynomene tanensis.* This study.	*Paradynomene tuberculata.* Jamieson *et al.* (1994)	*Homolodromia kai.* This study.
Acrosome length/width	0.3	0.3	0.5	0.5	0.3	0.4
Acrosome zonation	horizontal, podotreme synapomorphy	intermediate between horizontal and concentric	intermediate between horizontal and concentric	horizontal	horizontal	horizontal
Opercular perforation	perforate, opens in all	podotreme synapomorphy				
Subopercular protuberance	well developed, in all	dromiacean synapomorphy				
Acrosome ray zone	fingerprint-like, in all	dromiacean synapomorphy				
Anterolateral pale zone	present, in all	dromiacean synapomorphy				
Flangelike lower zone	absent	absent	absent	absent	present	present
Head of perforatorium	bilateral, in all	dromiacean or possibly podotreme synapomorphy as also seen in *Latreillia* (see Jamieson, 1994)				
Lateral arms	absent	three	two	two	absent	absent
Centrioles	absent	absent	?	absent	?	absent
Postmedian process	absent	absent	absent	absent	absent	?
Capsular projections	present	absent	absent	absent	absent	absent

ripheral irregularities. Striations of this zone, seen in *H. kai*, are absent, and, unlike *S. lamellata*, its periphery is not notably differentiated as a denser zone. A difference from the other two species, seen also in *Paradynomene tuberculata*, is a zone (zone 3a, labeled outer acrosome zone in Figs. 6A, B, 7C–E), which consists of large dense granules in a paler matrix, separating the inner acrosome zone from zone (4). Zone 4, as in *H. kai*, *S. lamellata*, and *P. tuberculata*, is a fingerprint zone (questionable acrosome ray zone). This fingerprint zone, seen in cross section of the acrosome (Fig. 7C), consists of a cingulus of parallel striae. Material identical with that of zone 3a may be present laterally to the fingerprint zone (Fig. 6A, B) and, with zone 3a, is apparently homologous with zone (5), the outer acrosome zone in the other species. Finally (6), a pale peripheral zone, fills the anterolateral region of the acrosome, as in other podotremes, but differs, as does that of *S. lamellata*, from that in *H. kai* in being clearly distinct from the outer acrosome zone (Figs. 5, 6A, B).

As in all dynomenids and dromiids investigated, the center of the acrosome vesicle is penetrated by a capitate perforatorium (Figs. 5, 6A, B, 7B–E). The stalk of this is stouter than in *Homolodromia kai* and is not circular in cross section, but is wider in the wide diameter of the head. The long axis of the head measures 1.8 μm (Fig. 6A), while the shorter axis is 1.4 μm (Fig. 6B), a ratio of about 1.2:1; however, shortly below its greatest width the ratio is 1.3:1 (Fig. 7C). The perforatorial head (Figs. 6A, B, 7D) contains lamellar structures as seen in that of *H. kai*, but also diffuse dense material as in *Sphaerodromia lamellata*. Its anterior outline is that of a cupid's bow. It is not as sharply pointed laterally, in its widest diameter, as it is in *H. kai* and *S. lamellata*.

Nucleus.—The nucleus, once more with diffuse DNA, is less bulky than in *Homolodromia kai*, and has a slightly lesser volume relative to the acrosome than in *Sphaerodromia lamellata*, forming less than one-half of the length of the spermatozoon (Figs. 5, 6B). The acrosome is thinly invested by nuclear material which, as in *S. lamellata*, overlaps the rim of the operculum. A dense, but occasionally interrupted, inner nuclear membrane separates the nucleus from the cytoplasm (Fig. 6A, B).

Centrioles.—Centrioles have not been definitely observed, but the organization of cytoplasm at the posterior end of the perforatorium (Fig. 6A) suggests the presence of two centrioles.

Discussion

Spermatozoa

Known Dromiacean spermatozoa are compared in Table 1 and further comparison with

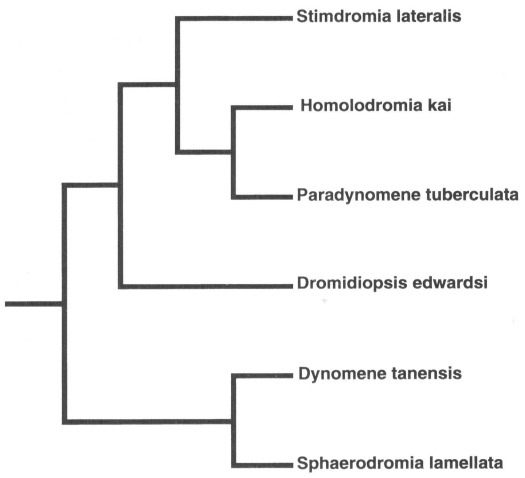


Fig. 8. Tentative phylogeny of the six Dromiacea investigated for sperm ultrastructure. In view of the small sample, the phylogram can only be regarded as heuristic for the paraphyly of the Dromiidae and Dynomenidae which it demonstrates.

other Brachyura is made below. An extension of the cladistic analysis of Jamieson *et al.* (1995) to include *Sphaerodromia lamellata* suggests the relationships shown in Fig. 8 for the six Dromiacea in which sperm ultrastructure has been studied (Jamieson, 1990; Jamieson, Tudge, and Scheltinga, 1993; Jamieson, Guinot, and Richer de Forges, 1993).

Spermatozoal synapomorphies of a monophyletic Dromiacea, endorsed here for *Sphaerodromia lamellata*, are depression of the acrosome, well-developed protrusion of subopercular material through the perforate operculum (a lesser protrusion occurs in homolids), and development of an anterolateral pale zone of the acrosome. The fingerprint-like zone of the acrosome, questionably homologous with the heterotreme acrosome ray zone, may be a further synapomorphy.

Although the Dromiacea form a monophylum, neither the constituent Dromiidae nor the Dynomenidae appear monophyletic spermatologically, as also shown in cladistic analysis (Jamieson, 1994; Jamieson *et al.*, 1995; Fig. 8). Thus, there is a distinctive dromiacean spermatozoal ground plan, but sperm structure does not distinguish the constituent families Dromiidae, Homolodromiidae, and Dynomenidae.

Constant features of Dromiacea which have been investigated to date (*Dromidiopsis edwardsi* Rathbun, *Stimdromia lateralis* (Gray), *Sphaerodromia lamellata, Homolodromia kai, Dynomene tanensis*, and *Paradynomene tuberculata*) are as follows: (1) operculum perforate, but lacking the apical button which occurs in thoracotremes; (2) opercular projections into the subopercular material, diagnostic of homolids, absent; (3) operculum discontinuous with the capsule, continuity being diagnostic of raninoids; (4) operculum moderately thick, not extremely thin as in the cyclodorippoids *Tymolus* and *Xeinostoma* (see Jamieson, 1994; Jamieson *et al.*, 1995); (5) operculum not extremely wide, contrasting with the great width in cyclodorippoids; (6) periopercular rim absent; (7) accessory opercular ring absent, being present in some eubrachyurans; (8) subopercular protuberance through operculum well developed (synapomorphy), weak development occurring in homolids; (9) true acrosome ray zone absent but fingerprint-like zone present; (10) outer acrosome zone border with the peripheral zone not ragged, the latter being characteristic of some xanthoids; (11) anterolateral pale zone of acrosome contents present (autapomorphy); (12) xanthid ring absent; (13) subacrosomal chamber or perforatorium extending preequatorially (only in *Ranina ranina* (L.) is it postequatorial); (14) head of perforatorium bilateral (autapomorphy); (15) corrugations of the wall of the perforatorial chamber absent, these being present in some anomurans, raninoids, and some eubrachyurans; (16) centrioles apparently absent (questionably so in *Sphaerodromia*), though present in at least homolids, some anomurans and eubrachyurans; (17) posterior median process of the nucleus absent, whereas it is present in at least some homolids, cyclodorippoids, and raninoids; (18) thickened ring (typical of Eubrachyura) absent; (19) concentric lamellae (typical of Thoracotremata) in the outer acrosome zone absent; (20) capsular chambers absent (known only in *Ranina ranina* and *Raninoides* sp.); and (21) capsular flange (known only in *Ranina ranina* and *Raninoides* sp.) absent.

Homolodromia kai.—The spermatozoon of *Homolodromia kai* (Homolodromiidae) displays a mixture of dromiid and dynomenid spermatozoal features. It resembles that of *Paradynomene tuberculata*, as described by Jamieson, Guinot, and Richer de Forges (1993), more closely than that of any other podotreme or brachyuran sperm investigated.

These two species have a striking putative

synapomorphy: a flangelike lateral extension of the lower acrosome zone. In the purely spermatozoal cladistic analysis (Jamieson *et al.*, 1995), *Homolodromia* was distinguished from *Paradynomene* only by its slightly more depressed acrosome. It is noteworthy, in view of the origin of *Homolodromia* in the phylograms between *Paradynomene* and *Dynomene*, with or without intervention of dromiids, that Guinot (1978) stated that in some regard it is the dynomenids which seem closer to the Homolodromiidae than do the Dromiidae.

On morphological grounds, the Homolodromiidae is placed in a monotypic superfamily Homolodromioidea, within the Dromiacea, by Guinot (1978, 1995). She listed a long series of characters in support of the contention that the Homolodromioidea represent the most primitive members of the Podotremata. Scholtz and Richter (1995) also supported the primitive status of the Homolodromiidae, but went so far as to regard homolodromiids as the sister group of all other Brachyura. However, they have since returned homolodromiids to the Dromiacea (oral statement in the 2nd European Crustacean Conference, Liège, 1996) in which they were placed by Guinot.

It is difficult to evaluate the relatively advanced position that *Homolodromia* appears to occupy, in terms of spermatozoal ultrastructure, relative to other dromiaceans, as indicated by cladistic analysis (Jamieson *et al.*, 1995; present study) in view of its apparently plesiomorphic status in morphological taxonomy (see below). From a spermatological standpoint, reconsideration of the validity and relationships of the families Dromiidae, Homolodromiidae, and Dynomenidae seems necessary, but it must be stressed that spermatozoal ultrastructure unequivocally supports monophyly of the Dromiacea.

Sphaerodromia lamellata.—The Dromiidae (see McLay, 1993) are elusive of definition spermatologically, as indicated above (see also Jamieson, 1994), being a paraphyletic group in both cladistic analyses (Jamieson *et al.*, 1995).

On the grounds of spermatozoal ultrastructure, *Sphaerodromia lamellata* appears less close to the dromiid *Stimdromia lateralis* than are *Dynomene tanensis, Paradynomene tuberculata*, and *Homolodromia kai*, among the dromiaceans investigated, the latter two species appearing closest to each other. *Sphaerodromia lamellata* has no spermatozoal characters that are shared with all Dromiacea investigated, as listed above, except for the presence of two nuclear vertices which are also seen in *D. tanensis*.

Dynomene tanensis.—The sperm of *Dynomene tanensis* differs from that of *Homolodromia kai* in that the ratio of length to width of the acrosome is 0.5 as compared with 0.4 in *H. kai*. Its acrosome lacks the lateral shoulder seen in *Sphaerodromia lamellata* and, especially, in *H. kai*. The cytoplasm is even more reduced than in *S. lamellata* and *H. kai*, being represented only by a minute residue posterior to the base of the perforatorium containing no evident vestiges of mitochondria. The operculum forms a lower, less convex dome than in *H. kai* and *S. lamellata*; otherwise it resembles that of *H. kai*, with the exception that its lateral rim is strongly thickened, though not as strongly so as in *S. lamellata*, and the dense layer is broken up to an extent intermediate between these two species. The inner acrosome zone differs from that in *H. kai*, and conforms with that of *S. lamellata*, in being more bulky and hardly wider anteroposteriorly than laterally. It differs from the other two species in lacking even a rudiment of the flangelike lateral expansion or peripheral irregularities. Striations of this zone, seen in *H. kai*, are absent and, unlike *S. lamellata*, its periphery is not notably differentiated as a denser zone. The stalk of the perforatorium is stouter than in *H. kai* and is not circular in cross section, but is wider in the wide diameter of the head. The perforatorial head contains lamellar structures as seen in that of *H. kai*, but also diffuse dense material as in *S. lamellata*. Its anterior outline is not as sharply pointed laterally, in its widest diameter, as it is in *H. kai* and *S. lamellata*. The nucleus is less bulky than in *H. kai*, and has a slightly lesser volume relative to the acrosome than in *S. lamellata*, forming less than one-half of the length of the spermatozoon.

The suggestion from spermatozoal ultrastructure of paraphyly of the Dynomenidae, as in the case of the Dromiidae, does not necessarily refute definition of these families on the grounds of nonspermatozoal morphology (e.g., McLay, 1993; Guinot, 1995), but warrants further consideration of their mono-

phyly, which, in the case of the Dromiidae, has previously been challenged by molecular data (Spears and Abele, 1988; Abele, 1991; Spears *et al.*, 1992).

Morphological Taxonomy

In view of the fact that spermatozoal ultrastructure, while endorsing the unity of the Dromiacea, does not support recognition of the Dromiidae, Dynomenidae, and probably the Homolodromiidae as separate families, it will be appropriate to consider the comparative morphology of the three families in some depth.

Dromiacean Synapomorphies.—In the Podotremata, many exclusive characters are shared by the Homolodromiidae, Dromiidae, and Dynomenidae and endorse recognition of a monophyletic Dromiacea. Two in particular, the very long hollow stylet of the second sexual male pleopod, longer than the first pleopod, and the very small spermathecal aperture (Guinot, 1995) are related to reproduction. In Dromiacea, the loss of the tail fan present in Macrura and Anomura constitutes the essential brachyuran apomorphy and, as such, is a dromiacean symplesiomorphy. Dromiaceans are also plesiomorphic in the retention in both sexes of a pair of appendages (vestiges of uropods) on abdominal segment 6 relative to other podotremes (i.e., Archaeobrachyura: Homoloidea, Cyclodorippoidea, Raninoidea) in which pleopods have been lost from segment 6 as in the Heterotremata-Thoracotremata assemblage. The appendages of segment 6 in dromiaceans occur as dorsal uropods (all Dynomenidae, Dromiidae with few exceptions) or as exclusively ventral lobiform uropods (all Homolodromiidae). A further dromiacean character appears to be the urinary article of the antenna, with an acicle, but this requires confirmation in the dynomenid genus *Acanthodromia* A. Milne Edwards. We may add, as an additional dromiacean character, the presence of sternocoxal depressions on the thoracic sternum (cf. Guinot, 1995), but this condition is also found in Homolidae and Poupiniidae.

Distinctive Features of the Homolodromiidae.—In her revision of the family Homolodromiidae, where the total number of species grouped in two genera was increased from 9 to 20, Guinot (1995) recognized it as monophyletic. The genus *Homolodromia* shows a greater number of plesiomorphic characters (arrangement of the cephalic structures, vestigial pleopods on segments 3–5 in the male, abdominal pleura well developed) than *Dicranodromia* A. Milne Edwards.

The characters of the Homolodromiidae are as follows: (1) plates of the endophragmal skeleton connected by anastomoses only; (2) sternites 1–3 in a plane above that of the following sternites (shared with the Dromiidae); (3) no ventral folding of the carapace; (4) no lateral or pleural line; (5) always with a wide branchiostegite which is soft and differently colored, as a dehiscence zone; (6) absence of a complete orbital fossa; (7) the arrangement of the eyes and cephalic appendages, not in the same plane (Pichod-Viale, 1966); (8) the pediform third maxillipeds; (9) abdominal pleura often well developed in the male and, to a lesser extent, in the female; (10) the long telson in the male; (11) often, presence of vestigial pleopods on somites 3–5 in the male; (12) never with dorsal uropods, and presence of lobiform uropods which are exclusively inserted on the ventral surface of abdominal segment 6 and never dorsally visible; (13) gills very numerous and intermediate between the tricho- and phyllobranchiate types; and (14) in the male, the coxa of pereiopod 5 continuing without suture into a long, calcified, and immovable penial tube.

Features of Dromiidae Shared with Homolodromiidae.—In his revision of the Dromiidae, McLay (1993) did not mention possible paraphyly of the family, but evoked the complex evolutionary relationships among the 100 species distributed in about 30 genera. Although most dromiid genera appear to belong to the same clade, the inclusion of some of them (e.g., *Hypoconcha* Guérin Méneville, *Conchoecetes* Stimpson) requires further justification.

Characters shared by the Homolodromiidae and Dromiidae are: (1) thoracic sternum tilted at the level of somites 7 and 8; (2) sternites 1–3 at a higher level than the following sternites; and (3) both P4 and P5 reduced, subdorsal, with a distal subcheliform apparatus.

Features Shared by Dromiidae and Dynomenidae.—The characters shared by Dromiidae (taking into account that dromiids are diverse) and Dynomenidae that support their reunion in the Dromioidea are as follows: (1)

endophragmal skeleton fused, never with simple anastomoses; (2) generally, a ventral folding of the carapace; (3) presence of a lateral or pleural line (in some rare dromiids, there is a soft branchiostegite as in homolodromiids, see below); (4) the brachyuran arrangement of the eyes and cephalic appendages, e.g., in the same plane; (5) presence of an orbital fossa; (6) the brachygnath condition of the buccal frame, with more operculiform third maxillipeds; (7) abdominal pleura never well developed (except some dromiid genera, such as forms commensal in ascidians, cf. Guinot, 1995: 186, see below); (8) generally, dorsal uropods well developed and dorsally visible (exceptionally ventral in some rare dromiids, see below); and (9) gills reduced in number and very far from the trichobranchiate type.

Differences Between Dynomenidae and Dromiidae.—Many differences, albeit some of them inconstant, distinguish Dynomenidae from Dromiidae. In dynomenids, the disposition is as follows: (1) thoracic sternum wider, tilted only at the level of somite 8 (in dromiids, the sternum tilted at the level of somites 7 and 8, and corresponding arthrodial cavities not aligned) and with the anterior part forming a shield; (2) P4 similar to P3 in size and shape; (3) only P5 reduced, almost rectilinear, intercalated between the body and P4, and sometimes with a small chelate ending; (4) in the male of all the species examined of *Dynomene* and in *Paradynomene*, the constant presence of vestigial, sometimes bifid, pleopods on somites 3–5 (also, however, present in some primitive dromiid genera, see below); (5) the constant arrangement of the uropods, always as large plates which are dorsally visible (there are, however, some instances of lateral or even ventrally intercalated uropodal plates in dromiids, see below); and (6) in male dynomenids, the coxa of P5 more or less triangular or elongate, in continuation with a calcified tube, so that the whole coxa is transformed, whereas in most dromiids, so far as is known, the coxa of P5 is completely separated from a long, soft, mobile penial tube.

In dynomenids, camouflaging by the last legs, P5, is not possible, since they are very short and inserted laterally (Guinot *et al.*, 1995). In contrast, carrying behavior utilizing subcheliform P4 and P5 is the rule in dromiids, except in more advanced forms.

All the Dynomenidae examined show also vestigial, sometimes bifid, pleopods on abdominal somites 3–5 and have an abdomen which is always relatively wide, but with no evident pleura. The gill formula and arrangement is not yet well known, the genus *Acanthodromia* having phyllobranchiate gills in contrast with the other Dynomenidae (McLay, in correspondence).

In the Dromiidae, only the most primitive members have pleopodal remnants in the male, and abdominal pleura are rare. The loss of camouflage is evident in advanced forms, where the last pairs of legs are very small. The character state of the branchiostegite and of the uropods in an exceptional ventral position needs further study.

Plesiomorphic structures, such as remnants of pleopods on somites 3–5 in the male and the abdominal pleura are present in Homolodromiidae in all species of the genus *Homolodromia* and only in primitive species of *Dicranodromia*, a genus which has acquired the brachyuran cephalic arrangement.

Sphaerodromia has been considered as the most primitive dromiid genus, particularly in its gill formula, in the presence of vestigial pleopods on the male abdomen, and in the structure of the propodal and dactyl spines of pereiopods 2 and 3. We here emphasize the fact that in *Sphaerodromia* the narrow thoracic sternum, the male abdomen without pleura, the two reduced last pairs of pereiopods 4 and 5 are dromiid features, but that the anterior region is dynomenid and the ventral surface in the anterior part of the carapace resembles *Paradynomene*. In the male of *Sphaerodromia*, the coxa of P5 does not bear a long, soft, mobile penial tube as in most Dromiidae and is intermediate between the dynomenid and homolodromiid state. The presence of an exopod, of variable length, on the second sexual male pleopod characterizes *Sphaerodromia* and a few other dromiids, but all dynomenids (plesiomorphy). In contrast, *Stimdromia lateralis* represents the most advanced dromiid genus.

The exceptional (more plesiomorphic?) dromiids noted for characters (3), (7), and (9) in the list of shared features of the Dromiidae and Dynomenidae above, and for characters (4) and (5) in the list of differences, suggest that consideration may have to be given to the possibility that it is only the (more apomorphic?) majority of the Dromi-

idae (including the type genus) which are monophyletic with the Dynomenidae and Homolodromiidae, and that the Dromiidae is a paraphyletic taxon. These findings are in accordance with spermatozoal ultrastructure as summarized in Fig. 8.

The ambiguous morphological features of *Sphaerodromia*, some of which resemble those of dynomenids more closely than they do dromiids, are complemented by the characters of the spermatozoa which connect *Sphaerodromia* more closely to *Dynomene* than to *Stimdromia*. Most of the morphological similarities are here considered plesiomorphic features, but the spermatozoal similarities which contribute to the phylogram are, by definition, apomorphic.

The close spermatological connection between *Homolodromia* and *Paradynomene* is difficult to explain, the homolodromiid and dynomenid families being clearly distinct from a morphological point of view.

The present spermatozoal study and the morphological review indicate that the status of the three dromiacean families requires reevaluation.

Acknowledgements

The authors cordially thank Dr. C. L. McLay for identification of the dynomenid and for discussions. We also thank Mrs. L. Y. Daddow and Mr. D. Scheltinga (Zoology Department, The University of Queensland) for technical assistance with the electron microscopy. This research was supported by Australian Research Council funding to BGMJ.

Literature Cited

Abele, L. G. 1991. Comparison of morphological and molecular phylogeny of the Decapoda.—Memoirs of the Queensland Museum 31: 101–108.

Daddow, L. 1986. An abbreviated method of the double lead stain technique.—Journal of Submicroscopic Cytology 18 (1986): 221–224.

Guinot, D. 1977. Propositions pour une nouvelle classification des crustacés décapodes brachyoures. —Compte Rendu Hebdomadaire des Séances de l'Académie des Sciences, Paris D 285: 1049–1052.

——— 1978. Principes d'une classification évolutive des crustacés décapodes brachyoures.—Bulletin Biologique de la France et de la Belgique 112: 211–292.

——— 1995. Crustacea Decapoda Brachyura: révision des Homolodromiidae Alcock, 1900.—*In*: A. Crosnier, ed. Résultats des Campagnes MUSORSTOM, Volume 13. Mémoires du Muséum national d'Histoire naturelle, Paris 163: 155–282.

———, and B. Richer de Forges. 1995. Crustacea Decapoda Brachyura: révision des Homolidae de Haan, 1839.—*In:* A. Crosnier, ed. Résultats des Campagnes MUSORSTOM, Volume 13. Mémoires du Muséum national d'Histoire naturelle, Paris 163: 283–517.

———, D. Doumenc, and C. Chintiroglou. 1995. A review of the carrying behaviour in brachyuran crabs, with additional information on the symbioses with sea anemones.—Raffles Bulletin of Zoology 43: 377–416.

Jamieson, B. G. M. 1990. The ultrastructure of the spermatozoa of *Petalomera lateralis* (Gray) (Crustacea, Brachyura, Dromiacea) and its phylogenetic significance.—Invertebrate Reproduction and Development 17: 39–45.

———. 1994. Phylogeny of the Brachyura with particular reference to the Podotremata: evidence from a review of spermatozoal ultrastructure.—Philosophical Transactions of the Royal Society B 345 (1994): 373–393.

———, D. Guinot, and B. Richer de Forges. 1993. The ultrastructure of the spermatozoon of *Paradynomene tuberculata* Sakai, 1963 (Crustacea, Brachyura, Dynomenidae): synapomorphies with dromiid sperm.—Helgoländer Meeresuntersuchungen 47: 311–322.

———, ———, and ———. 1995. Phylogeny of the Brachyura: evidence from spermatozoal ultrastructure (Crustacea, Decapoda).—*In:* B. G. M. Jamieson, J. Ausio, and J.-L. Justine, eds., Advances in spermatozoal phylogeny and taxonomy. Vol. 166, pp. 265–283. Mémoires du Muséum national d'Histoire naturelle, Paris, France.

———, C. C. Tudge, and D. M. Scheltinga. 1993. The ultrastructure of the spermatozoon of *Dromidiopsis edwardsi* Rathbun, 1919 (Crustacea: Brachyura: Dromiidae): confirmation of a dromiid sperm type.—Australian Journal of Zoology 41: 537–548.

McLay, C. L. 1993. Crustacea Decapoda: the sponge crabs (Dromiidae) of New Caledonia and the Philippines with a review of the genera.—*In:* A. Crosnier, ed., Résultats des Campagnes MUSORSTROM, Vol. 10, pp. 111–251. Mémoires du Muséum national d'Histoire naturelle, Paris.

Pichod-Viale, D. 1966. L'exuviation céphalique au cours de la mue des Crustacés Décapodes.—Vie et Milieu 17: 1235–1271.

Scholtz, G., and S. Richter. 1995. Phylogenetic systematics of the reptantian Decapoda (Crustacea, Malacostraca).—Zoological Journal of the Linnean Society 113: 289–328.

Spears, T., and L. G. Abele. 1988. Molecular phylogeny of brachyuran crustaceans based on 18S rRNA nucleotide sequences.—American Zoologist 28: 2A. (Abstract.)

———, ———, and W. Kim. 1992. The monophyly of brachyuran crabs: a phylogenetic study based on 18S rRNA.—Systematic Biology 41: 446–461.

Received: 2 April 1997.
Accepted: 15 May 1997.

Addresses: (DG) Laboratoire de Zoologie (Arthropodes), Muséum National d'Histoire Naturelle, 51 rue Buffon, Paris, Cedex 05, France; (BGMJ) Zoology Department, University of Queensland, Brisbane, Queensland, Australia 4072; (BRF) ORSTOM, B. P. A5, Nouméa Cedex, New Caledonia; (CCT) Crustacean Laboratory, Museum of Victoria, 71 Victoria Crescent, Abbotsford, Australia 3067. (e-mail: b.jamieson@mailbox.uq.oz.au)