

Relationships of the Cyclodorippoidea Ortmann: evidence from spermatozoal ultrastructure in the genera *Xeinostoma*, *Tymolus* and *Cymonomus* (Crustacea, Decapoda)

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Summary

The spermatozoa of two genera and species of Cyclodorippoidea, *Xeinostoma richeri* (Xeinostominae) and *Tymolus* sp. (Cyclodorippinae), and one species of *Cymonomus* sp. (Cymonomidae) are found to constitute a distinctive cyclodorippoid sperm-type characterized by (1) sperm anteroposteriorly depressed, mean ratio of length to width 0.54–0.63; (2) operculum extending to the lateral limits of the acrosome (autapomorphy of cyclodorippoids) and centrally perforate or (*Cymonomus* sp.) thinner; (3) contents of acrosome vesicle with two major horizontal zones, as in homolids and dynomenids, including a dense lower (posterior) zone; (4) perforatorium very wide (0.3 width of acrosome), anteriorly rounded, not capitate, lacking radiate projections; (5) acrosomal capsule with external projections over its posterior half; (6) slender dense filaments extending into the perforatorium from its walls, their bases associated with corrugations of its basal wall; (7) nucleus, cupping the acrosome and cytoplasm, with well-developed posterior median process; (8) nuclear arms lacking microtubules; (9) cytoplasm, a narrow postacrosomal band extending anteriorly as far as the operculum, associated with a few degenerate mitochondria. The noncapitate form of the perforatorium differs from the capitate condition in dromiids, the related dynomenids, homolids and the raninoid *Lyreidus*. The cyclodorippoid sperm resembles homolid and raninoid sperm in possessing a posterior nuclear process (questionably apomorphic) and resembles homolid sperm in the horizontal zonation of the acrosome with a dense lower zone. Features which resemble the sperm of raninoids are: the periacrosomal flange (*Xeinostoma richeri*) and smaller evaginations of the acrosome membrane (or capsule?) (*X. richeri*, less distinctly *Cymonomus* sp. and *Tymolus* sp.) reminiscent of the single acrosomal flange of *Ranina* and *Raninoides* sperm and the multiple keels of the *Lyreidus* sperm; and corrugations of the wall of the perforatorial chamber, as in raninoids though with significant differences. A dynomenid similarity (homoplasy?) is the discontinuous flange-like peripheral continuation of the lower zone of the acrosome contents in *Cymonomus* sp.

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Introduction

The internal relationships and classification of brachyuran crabs, and particularly of the Podotremata, are the subject of controversy. Guinot (1977, 1978, 1979; Guinot et al., 1994) divides the Brachyura into three sections, mainly on the basis of the location of the male and female pores: the Podotremata, the Heterotremata and the Thoracotremata. The Podotremata diagnosed by Guinot (1977, 1978, 1979) by the coxal positions of male and female pores and isolation of the spermathecae (Tavares and Secretan, 1993) from the oviducts, in combination with external fertilization, contain not only the Dromioidea and Homolodromioidea, both comprising the restricted subsection Dromiacea, but also the Archaeobrachyura, consisting of the Homoloidea, Raninoidea, and Cyclodorippoidea (formerly Tymoloidea; see Tavares, 1991). Monophyly of the Archaeobrachyura has been questioned (Guinot, 1978; Jamieson, 1991), but recent investigation of the sperm of the raninoid *Lyreidus brevifrons* Sakai, 1937, has revealed ultrastructural features which appear to support relationship of this raninoid with the Homolidae (Jamieson et al., 1994). It has been suggested by Guinot (1978, 1979) that the Podotremata may be the sister-taxon of the higher crabs (Heterotremata and Thoracotremata). Heterotremes and thoracotremes share a synapomorphy in the sternal location of the female pores and development of the spermatheca as a sternal vulva on sternite 6 concomitant with internal fertilization. The Thoracotremata are further apomorphic in the constant sternal location of the male pores.

Although Guinot (1977, 1978, 1979) allied the Dromiidae and Homolidae with the Raninidae in the Podotremata, it has been claimed that nucleotide sequences of 18S ribosomal RNA support the exclusion of the Dromiidae from the Brachyura (homolids and cyclodorippoids were not investigated) and inclusion of the Raninidae in the Brachyura (Spears and Abele, 1988; Abele, 1991; Spears et al., 1993). In the latter work the Dromiidae appear paraphyletic; *Hypoconcha* is the sister-taxon of the Anomura (*Clibanarius*) while *Dromia* is at the base of the raninid-heterotreme assemblage.

Within the Podotremata, the Cyclodorippoidea are, with the Latreillidae, the group that includes the smallest crabs known, averaging about 5 mm in carapace length. They inhabit the deep basins of the major oceans and are presently known by 68 species in 17 genera: 12 in the Cyclodorippidae and 5 in the Cymonomidae. Prior to the work of Bouvier (1897), *Cyclodorippe* and *Cymonomus*, the type genera of the Cyclodorippidae and Cymonomidae, respectively, were usually considered to belong to a single family (either the Dorippidae or the Cyclodorippidae). Bouvier (1897) erected the Cymonomidae ("Cymonominae") for *Cymonomus* and retained *Cyclodorippe* in the Cyclodorippidae. Later, Gordon (1963) and Tavares (1993) improved the diagnoses of both families. Tavares (1992) recognized two subfamilies within the Cyclodorippidae: Cyclodorippinae Ortmann, 1892, and *Xeinostominae* Tavares, 1992.

In the present study we describe the spermatozoal ultrastructure of a species of each of three cyclodorippoid genera in an attempt to elucidate cyclodorippoid relationships. They are *Xeinostoma richeri* Tavares, 1993 (Cyclodorippidae, *Xeinostominae*) and two new unnamed species in the genera *Tymolus* (Cyclodorippidae, Cyclodorippinae) and *Cymonomus* (Cymonomidae), all collected off New Caledonia.

Materials and Methods

Specimens of *Xeinostoma richeri* (station CP651) and *Cymonomus* sp. (CP660) were collected by B. Richer de Forges during the Bathus 1 cruise on the RV "Alis" (March 1993), off the east coast of New Caledonia. Specimens of *Tymolus* sp. (CP741) were collected during the Bathus 2 cruise on the RV "Alis" (May 1993) off the west coast of New Caledonia.

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 for further processing. On receipt 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

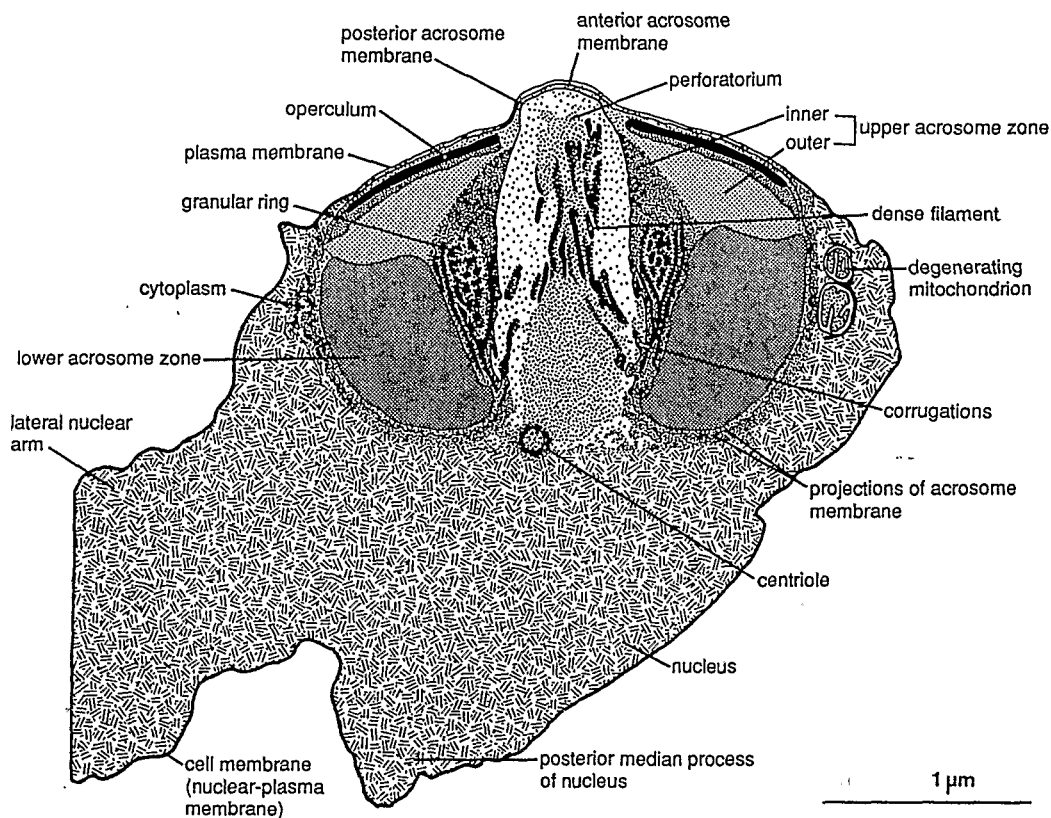


Fig. 3. *Tymolus* sp. (station CP741). Semi-diagrammatic vertical longitudinal section of the spermatozoon traced from a transmission electron micrograph.

Table 1. Dimensions of the acrosome in three cyclodorippoid species

	Mean width (μm)	Range in width (μm)	Mean length (μm)	Range in length (μm)	Mean ratio length:width
<i>Xeinostoma richeri</i>	3.5	3.2 - 4.1	1.9	1.7 - 2.1	0.54 (n=3)
<i>Cyonomus</i> sp.	4.1	3.5 - 4.6	2.2	2.0 - 2.5	0.56 (n=7)
<i>Tymolus</i> sp.	2.6	2.4 - 2.7	1.6	1.5 - 1.7	0.63 (n=4)

the perforatorium extends anteriorly from the opercular perforation (Fig. 6A) whereas in others it is contained below the level of the operculum (see Discussion).

The bulk of the contents of the acrosome vesicle forms an inflated ring surrounding the wide axial perforatorial chamber. The substance of the ring (Figs. 1, 4A-E, 2, 5A, 5B, 3, 6A, 6C, 7A-F) is subdivided into an upper, moderately large, electron-dense zone which has subdivisions described below, and a lower, undivided strongly electron-dense zone.

In *Cyonomus* sp. the upper zone is much thicker than the lower zone, but in *Tymolus* sp. the lower zone is the thicker of the two, while in *Xeinostoma* the upper and lower zones are approximately equal in thickness. In *Cyonomus* sp. the lower zone is approximately crescent shaped with the concavity anterior in longitudinal (vertical) section. That of *X. richeri* is similarly rounded posteriorly, but its anterior face comes to a low point, forming an obtuse angle, slightly lateral of its centre, as seen in longitudinal section. *Tymolus* sp. resembles *X. richeri* more

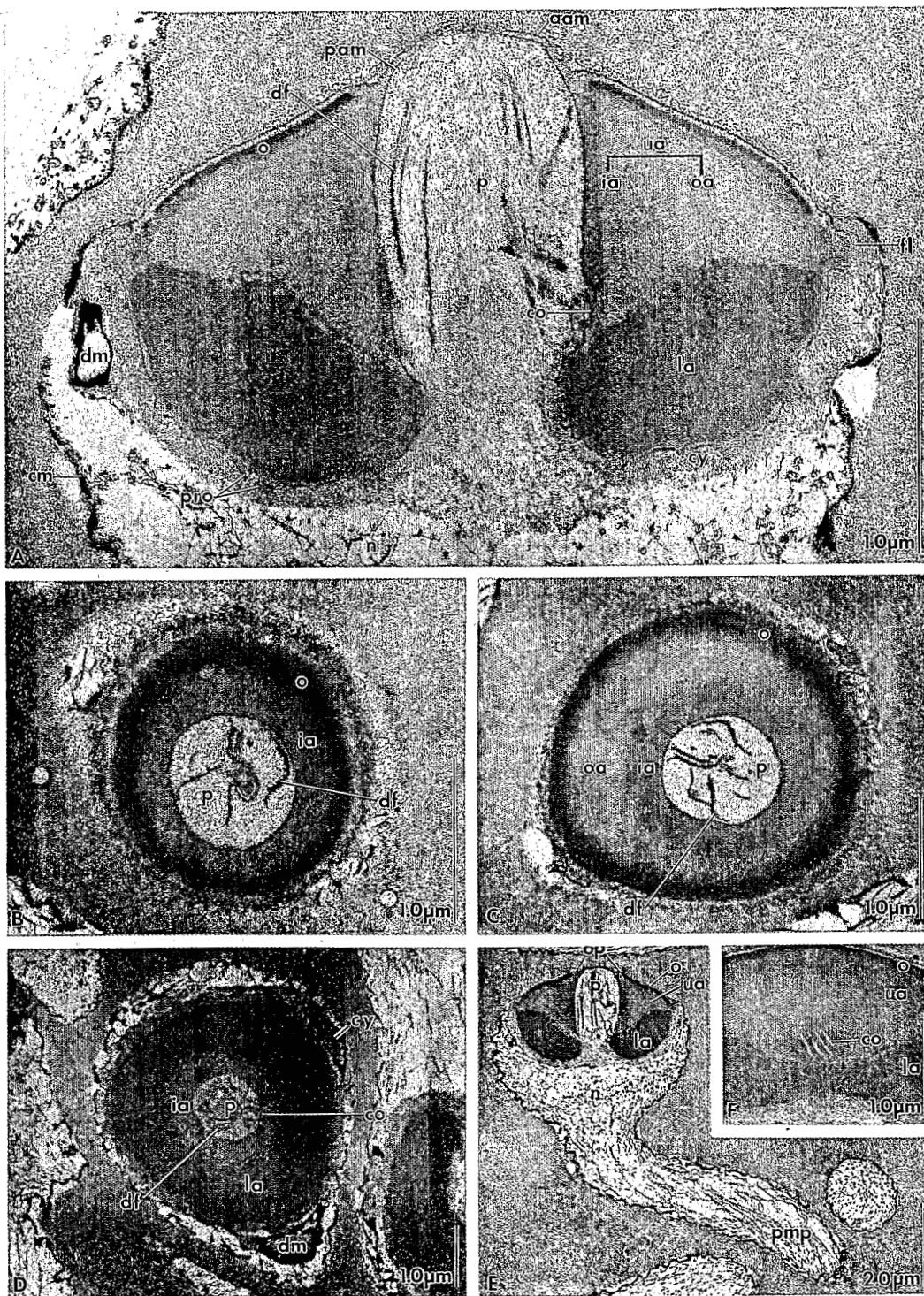


Fig. 4. *Xeinostoma richeri* (station CP651). Transmission electron micrographs. A. Vertical longitudinal section of a spermatozoon. B, C. Transverse sections through the opercular region, C being posterior to B. D. Transverse section through the dense lower acrosome zone, showing corrugations in wall of perforatorial chamber. E. Vertical longitudinal section of a spermatozoon, showing a well-developed posterior median process of the nucleus. F. Parasagittal section showing a group of corrugations of the wall of the perforatorial chamber. Abbreviations: a acrosome, aam anterior acrosome membrane, c centriole, cm cell membrane, co corrugations, cy cytoplasm, df dense filaments in perforatorium, dm degenerating mitochondrion, fl periacrosomal flange, gr granular ring, ia inner acrosomal zone, la lower acrosomal zone, n nucleus, na nuclear arm, o operculum, oa outer acrosomal zone, op apical perforation of operculum, p perforatorium, pam posterior acrosome membrane, pm plasma membrane, pmp posterior median process of nucleus, pro projections of acrosome membrane, ua upper acrosomal zone.

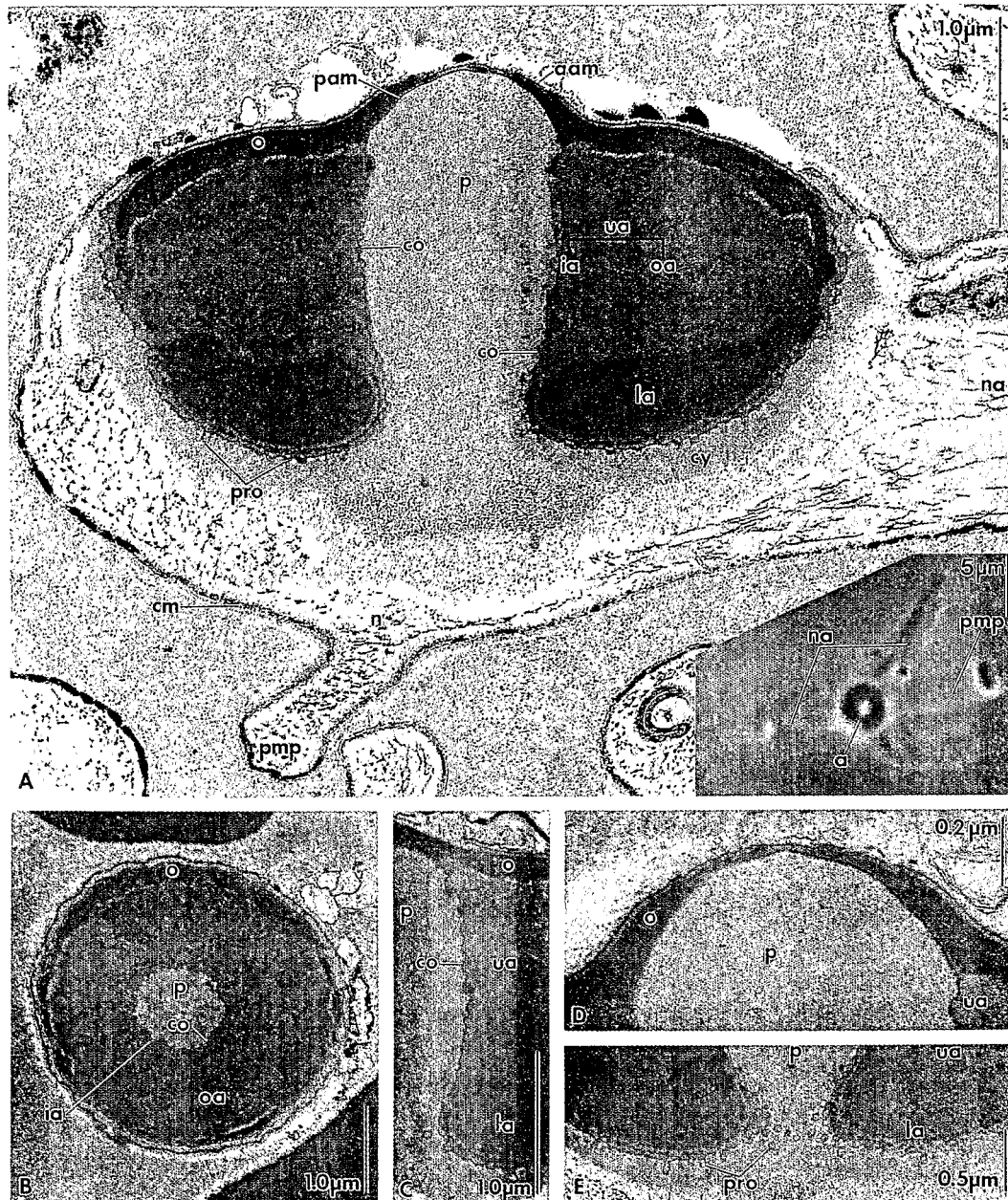


Fig. 5. *Cymonomus* sp. (station CP660). Transmission electron micrographs with, inset in A, a light micrograph of a spermatozoon. A. Vertical longitudinal sagittal section of a spermatozoon. B. Transverse section through the opercular region. C. Sagittal section through perforatorium showing corrugations of its walls. D. Sagittal section through apex of perforatorium, showing imperforate though centrally attenuated operculum. E. Parasagittal section of base of acrosome showing short finger-like or bulbous projections of the acrosome membrane in longitudinal and transverse section. (See Fig. 4 for abbreviations.)

closely than *Cymonomus* sp. in this respect, but the equivalent of the point of the lower dense zone forms a rounded right angle (Figs. 3, 6A, 6C). These zones are seen in transverse section in Figs. 4B-D, 5B, 7A-F.

The upper zone of the acrosome contents, constituting somewhat more than half of the height of the

acrosome in *X. richeri*, about two-thirds in *Cymonomus* sp., and less than one-half in *Tymolus* sp., is differently subdivided in the three species. In *X. richeri*, in longitudinal section, the upper zone is divided into an outer and inner zone by an oblique line running from the inner edge of the opercular perforation to the obtuse anterior peak of the dense

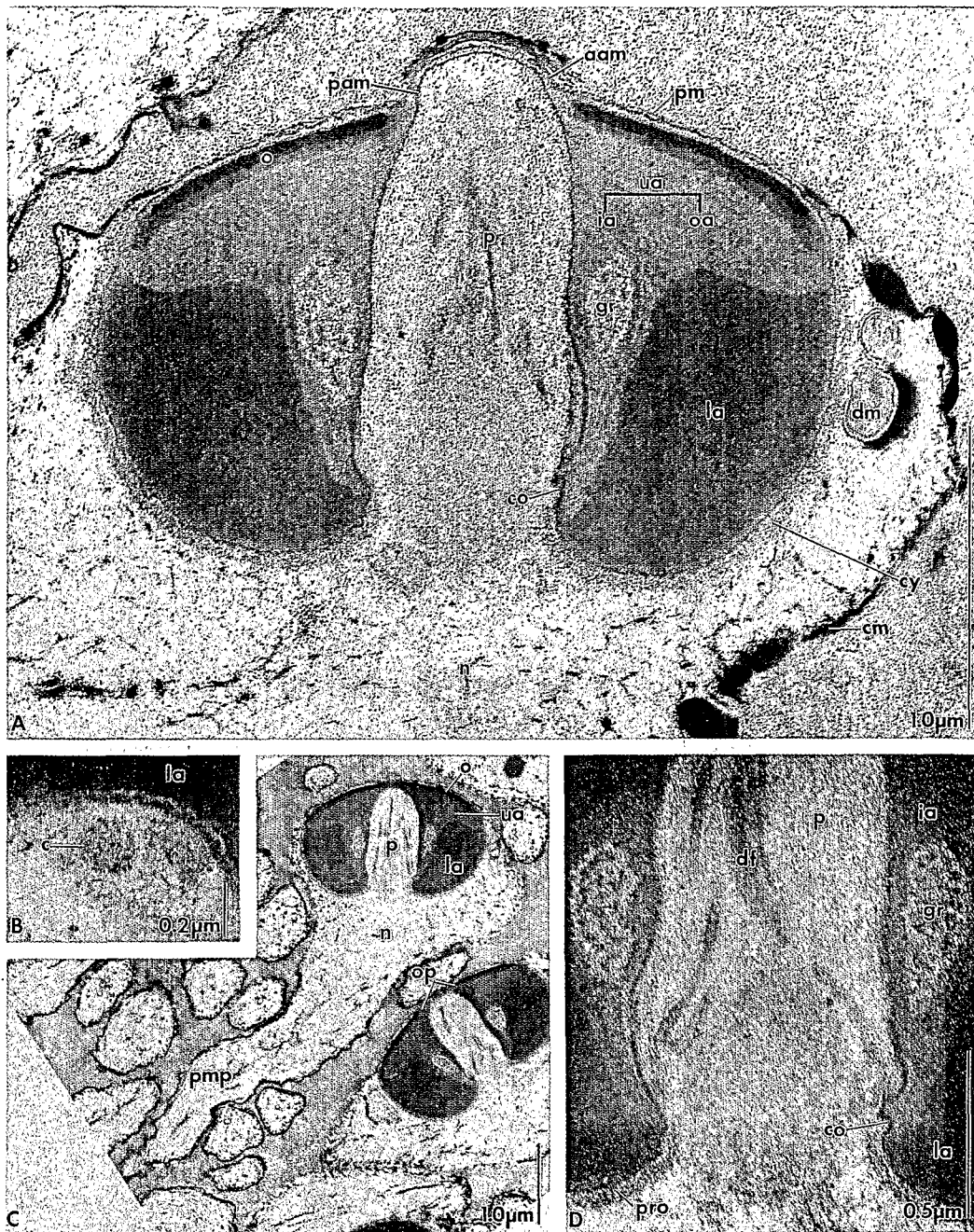


Fig. 6. *Tymolus* sp. (station CP741). Transmission electron micrographs. A. Vertical longitudinal sagittal section of a spermatozoon. B. Oblique section showing centriole at base of perforatorium. C. Longitudinal sections of two spermatozoa, one through the long posterior median process of the nucleus; both with perforatoria less protuberant than in A. D. Longitudinal section of the middle and basal region of the perforatorium and adjacent acrosome. (See Fig. 4 for abbreviations.)

lower zone. The outer zone is the palest, though still moderately dense, and is not further subdivided. The inner zone is more electron dense, though much less dense than the lower zone, and consists of two poorly distinguishable zones: an innermost zone, ensheathing the perforatorial chamber, and a triangular zone extending from the innermost zone to the peak

of the lower zone. The triangular zone is questionably equivalent in structure to the acrosomal ray zone of other brachyurans. In *Cymonomus* sp. the oblique subdivision of the upper zone is absent. The inner zone is again present, ensheathing the perforatorial chamber, but differs in basally extending laterally as a thin layer over the dense lower zone

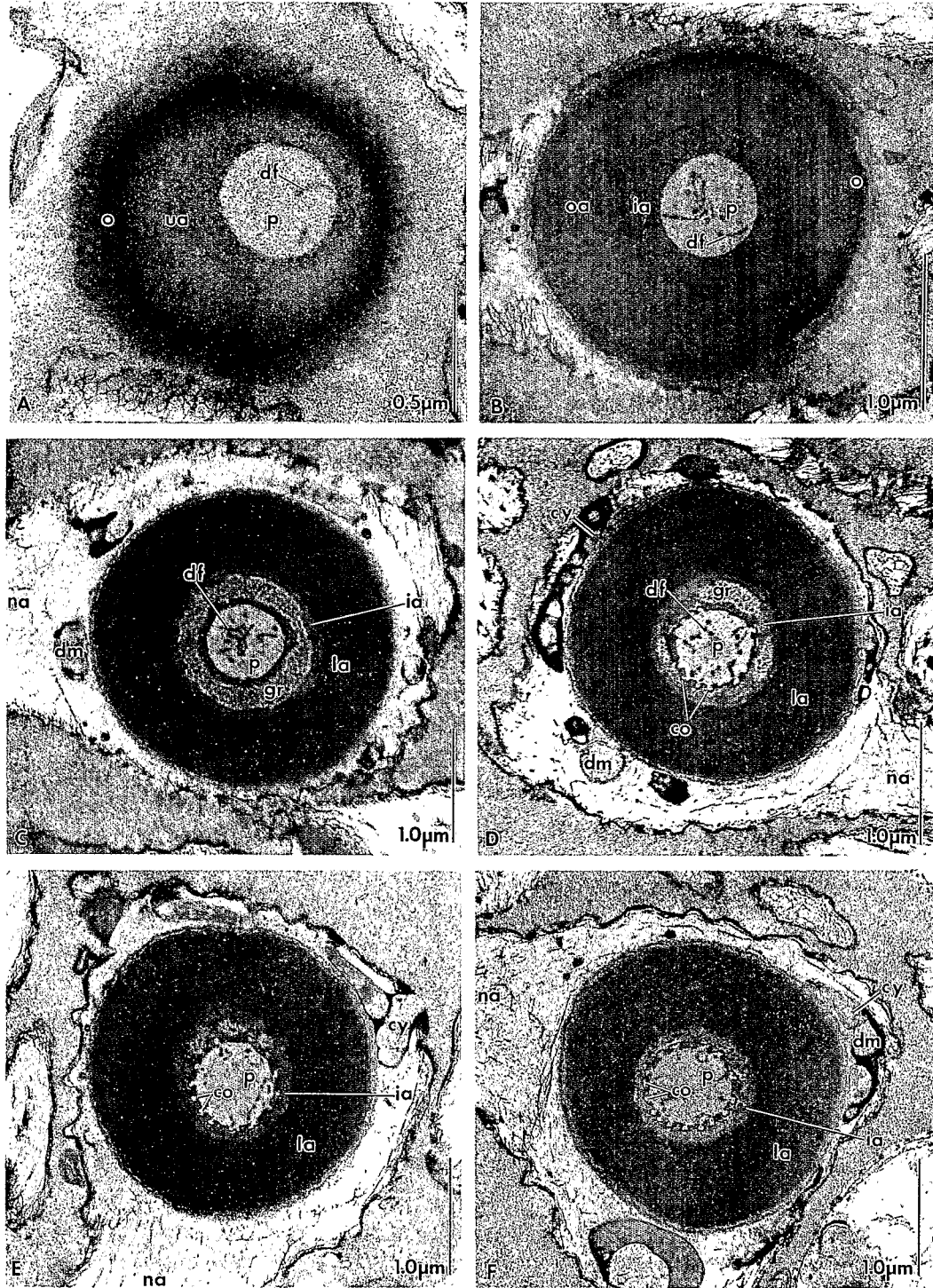


Fig. 7. *Tymolus* sp. (station CP741). Transmission electron micrographs. Successive anterior-posterior transverse sections through the acrosome. A. Through middle region of operculum. B. Through base of operculum. C. Through middle of granular ring. D and E. Through progressively more basal regions of granular ring, showing corrugations in wall of perforatorial chamber. F. Through base of perforatorium. (See Fig. 4 for abbreviations.)

(Figs. 2, 5A, 5C). No triangular zone or acrosomal ray structure is discernible. The outer edge of the lower zone is prolonged as a thin appendage, in longitudinal section, which apparently represents a discontinuous flange-like peripheral continuation around the lower zone (see Discussion). In *Tymolus* sp. the inner zone forms a broad barrel-shaped zone around the perforatorial chamber from the apex to near the base of the latter but is conspicuously different from the other two species in containing, from its equator to near its base, an oval zone (Figs. 6A, 6C, 6D), which in transverse section (Figs. 7C-E) is seen to form a ring. This zone is composed of large, often conjoined granules of stellate outline and is here termed the "granular zone" or "granular ring".

The operculum in *X. richeri* (Fig. 4A) and *Tymolus* sp. (Figs. 6A, 6C) is interrupted centrally by a wide perforation. This corresponds with the width of the perforatorial chamber which here almost abuts the apical acrosome membrane which in some sperm of *Tymolus* sp. (Fig. 6A) protrudes beyond the operculum. In *Cymonomus* sp., although the operculum is very thin at the anterior pole, it is not perforate (Figs. 5A, 5D). In *X. richeri* (Fig. 4A) and *Tymolus* sp. (Figs. 6A, 6C), the operculum is a thin, gently curving uniform line (also seen in transverse section in Figs. 4B, 4C, 7A); but in *Cymonomus* sp. (Fig. 5A) it is several times thicker and is uneven in thickness, being thinnest around the apical orifice. In all three species a thin, dense outer (anterior) layer can be distinguished from a less dense, thicker, inner (posterior) layer of the operculum, but no subopercular zone is differentiated. The lower layer extends further laterally than the dense layer. In *X. richeri* (Fig. 4A) the lower layer extends into a rounded evagination (representing a circum-acrosomal flange) of the acrosome membrane around which the upper limit of the cytoplasm extends and below which the upper limit of the nucleus abuts. In addition to this large evagination of the acrosome membrane, there are several smaller, somewhat irregular evaginations from its vicinity to the posterior limit of the acrosome. No periacrosomal flange occurs in the *Cymonomus* sp. and *Tymolus* sp., but some small evaginations are present. In some sperm of *Cymonomus* sp. these appear to form short finger-like or bulbous projections, some of which project into the base of the subacrosomal chamber (Fig. 5C, 5D). The external projections are less developed and less regular in *Tymolus* sp. (Figs. 6A, 6D).

The centre of the acrosome vesicle in the three cyclodorippoids is penetrated by a stout vertical column of paler material, which accounts for 0.3 of the width of the acrosome (Figs. 1-3). The column constitutes the subacrosomal chamber and its contents, the putative perforatorium. Its stalk is circular in cross section. The sides of the chamber and perforatorium are slightly curved outward or almost parallel but in *Tymolus* sp. a slight constriction is sometimes visible at the level of the granular ring. There is no capitate expansion.

In *X. richeri* several slender dense filaments are seen in longitudinal (Figs. 4A, 4E) or transverse (Figs. 4B-D) sections of the perforatorium, some of which are coiled on themselves near the summit of the perforatorium. These filaments appear, in some cases at least (Fig. 4A), to arise from the wall of the perforatorium near its base, which as a consequence may appear serrated or corrugated (Figs. 4A, 4D, 4F). In *Cymonomus* sp. the material of the perforatorium is moderately electron dense, though paler than any of the contents of the acrosome vesicle, and generally appears homogeneous (Figs. 5A, 5D) or may display a paler conical core which extends from its base as far as its widest subapical region. However, its bounding membrane sometimes appears fluted (Figs. 5A, 5D), and occasional dense filaments are seen in the perforatorial material (Fig. 2) which, although origin from the wall has not been demonstrated, are possibly homologous with the more conspicuous filaments seen in *X. richeri* and *Tymolus* sp.

In *X. richeri* and *Tymolus* sp. there are regular corrugations in the wall of the posterior half of the perforatorial chamber. In cross sections (Figs. 4D, 7D-F) these are seen as semi-circular to nearly circular evaginations of the acrosome membrane which lines the perforatorial chamber. They project into the inner third of the inner acrosome zone (Figs. 4D, 7D-F) but decrease in number until absent anteriorly. In *Tymolus* sp. at the level of the fullest development of the granular ring, there are few (Fig. 7D) or no corrugations (Fig. 7C). Long dense filaments which arise from the basal region of the perforatorium and extend to its apex arise from the uninvaginated membrane between the evaginations (longitudinal section, Fig. 6D; transverse section, Fig. 7F). In *Cymonomus* sp. much less developed shallow corrugations extend throughout the length of the perforatorial chamber (Figs. 5A-D).

Nucleus

The nucleus posteriorly cups the acrosome-cytoplasm portion of the sperm (Figs. 1–3). By light microscopy (e.g., *Cymonomus* sp., Fig. 5A, inset), the nucleus has three short lateral arms and one long posterior median process. By transmission electron microscopy it appears very irregular in form, sending out a few large processes laterally and posteriorly although these may not be apparent in a given longitudinal section. These processes include a posterior median process, which is possibly transient, and which may be several times the length of the body of the nucleus (Figs. 4E, 5A, 6C).

No microtubules are present in the arms or elsewhere in the sperm. The chromatin consists of fine, electron-dense diffusely arranged putative DNA fibrils in an electron pale matrix. The nucleus is bounded by a frequently interrupted electron-opaque layer, with the appearance of a thick perforate membrane which possibly incorporates chromatin. Outside this is a pale vesiculate layer which, in places in *X. richeri*, contains continuations of the inner fine chromatin fibres and therefore is not a simple plasma membrane nor merely a combination of nuclear and cytoplasmic membranes. We will, nevertheless, refer to the dense membrane and its overlying paler layer as the cell membrane. Anteriorly, the concavity of the nucleus is not separated by any membrane from the cytoplasm which underlies the nucleus (Figs. 4A, 5A, 6A).

Cytoplasm, centrioles and other organelles

In the three species a large mass of cytoplasm lies in the hiatus where the acrosome membrane or capsule invaginates at the posterior end of the acrosome to form the perforatorial chamber. It extends as a thick layer around the acrosome so far anteriorly as to shortly overlap the base of the operculum (Figs. 1–3; see also transverse sections, Figs. 4D, 5B, 7B–F). In *Tymolus* sp. (Figs. 6A, 7C, 7D) and *X. richeri* (Figs. 4A, 4D), degenerate mitochondria, some of which have residual cristae, are associated with the anterolateral aspect of the cytoplasm. They are partly surrounded by electron-opaque sheaths which resemble the putative chromatin adjacent to the nuclear periphery. In *Tymolus* sp. the mitochondria may be detached from the cytoplasm and lie in the chromatin (Fig. 6A). Masses projecting from the cytoplasm into the nucleus in *Cymonomus* sp. are less certainly identifiable as degenerate mitochondria. In all three species islands of degenerating

cytoplasmic products with convoluted membranes are present in the nucleus. Poorly defined, and possibly degenerating, centrioles have been identified in *Tymolus* sp. (Fig. 6B) and *X. richeri*.

Discussion

The spermatozoa of *X. richeri*, *Tymolus* sp. and *Cymonomus* sp. are very similar and constitute a distinctive cyclodorippoid sperm. This is definable by the following features in combination, though only the great width of the operculum is unique to cyclodorippoids: (1) sperm anteroposteriorly depressed, mean ratio of acrosomal length to width 0.54–0.63; (2) operculum extending to the lateral limits of the acrosome and centrally perforate or (*Cymonomus* sp.) thinner; (3) contents of acrosome vesicle with two major horizontal zones, including a dense lower (posterior) zone, as in homolids and dynomenids; (4) perforatorium very wide (0.3 width of acrosome), anteriorly rounded, not capitate, lacking radiate or other projections; (5) acrosomal capsule with external projections over its posterior half; (6) slender dense filaments extending into the perforatorium from its walls, their bases associated with corrugations of its basal wall; (7) nucleus cupping the acrosome and cytoplasm and with well-developed posterior median process; (8) nuclear arms lacking microtubules; (9) cytoplasm, a narrow postacrosomal band extending anteriorly as far as the operculum, associated with a few degenerate mitochondria. Projection of the tip of the perforatorium in *Tymolus* sp. anteriorly of the opercular perforation in some sperm results in a configuration which is extremely similar to that seen in homolid sperm (Guinot et al., 1993; Jamieson et al., 1993b). This condition, which is not seen in other sperm of the same individual, is here interpreted as representing full maturity of the sperm rather than commencement of the acrosome reaction as there is no evidence of the latter in surrounding sperm components.

A dynomenid similarity is seen in the discontinuous flange-like peripheral continuation of the lower zone of the acrosome contents, seen in *Paradynomene tuberculata* (see Jamieson et al., 1993a), giving some support to the view of Bouvier (1897) that the Dynomenidae gave rise to the Cyclodorippoidea (Bouvier's Cyclodorippinae). On the other hand, centrioles have been observed in the cytoplasm posterior to the acrosome in homolid sperm as in cyclodorippoids. Centrioles are unknown in dromiids

and raninids and are variable in occurrence in heterotremes (see Guinot et al., 1993). The presence of short centrioles is symplesiomorphic for brachyurans being seen in many other decapods.

The cyclodorippoid spermatozoon differs markedly from spermatozoa of the Heterotremata-Thoracotremata assemblage (see review by Jamieson, 1991) but agrees with the sperm of dromiids (Brown, 1966; Jamieson, 1990), dynomenids (Jamieson et al., 1993a), homolids (Guinot et al., 1993), and raninoids (Jamieson et al., 1994) in the anteroposteriorly depressed acrosome. The mean ratios of length to width of the acrosome of 0.54–0.63 overlap with mean ratios in raninoids which range from 0.53 in *Lyreidus brevifrons* Sakai, 1937, to 0.76 in *Ranina ranina* (Linné, 1758) (see Jamieson, 1989) and 0.68–0.72 in *Raninoides* sp. (Jamieson et al., 1994) and is greater than the 0.26 and 0.34 in the dromiids *Petalomera lateralis* Gray, 1831, now *Stindromia lateralis* (see McLay, 1993; Jamieson, 1990) and *Dromidiopsis edwardsi* Rathbun, 1919 (Jamieson et al., 1993) or 0.35 in the dynomenid *Paradynomene tuberculata* Sakai, 1963 (Jamieson et al., 1993a). Other species with mean length:width ratios lying within the lower limit for raninoids are the homolids *Homola* sp. (0.45–0.56) and *Paromola* sp. (0.42–0.57) (Guinot et al., 1993).

The proportions of the acrosome would not alone support monophyly of the cyclodorippoids, but the unique condition of the operculum — extending to the lateral limits of the acrosome — strongly endorses monophyly. The non-capitate form of the perforatorium differs from the capitate condition in dromiids, the related dynomenids, homolids and the raninoid *Lyreidus*. Although the capitate condition is clearly apomorphic for reptants and a non-capitate condition pleisomorphic, the non-capitate condition in cyclodorippoids may be a secondary reversal.

The cyclodorippoid sperm resembles homolid and raninoid sperm in possessing a posterior nuclear process (questionably apomorphic). It accords with homolid sperm described by Guinot et al. (1993) in the horizontal zonation of the acrosome, with a dense lower zone. Williamson (1976) suggested from the analysis of the larval development of *Cymonomus bathamae* Dell that the cyclodorippoids could have evolved from homolids. However, the absence of finger-like projections on the lower surface of the operculum into the perforatorium is a noteworthy difference from homolid sperm.

Raninoid features of cyclodorippoid sperm include the following. The periacrosomal flange (*Xein-*

ostoma) and smaller evaginations of the acrosome membrane (or capsule) (*Xeinostoma*, *Cymonomus*) are reminiscent of the acrosomal flange which is characteristic of *Ranina* (see Jamieson, 1989) and *Raninoides* sperm and the multiple keels of the *Lyreidus* sperm, all raninoids (Jamieson et al., 1994). The corrugations of the wall of the perforatorial chamber, though giving rise to filaments, bear some resemblance to the corrugations or septa diagnostic of raninoids, though it must be remembered that filaments also arise from the wall of the perforatorial chamber in most paguroids (Tudge, 1992). Raninoid corrugations differ in being formed by projections into the perforatorium while at least those in *Cymonomus* sp. are evaginations.

With regard to intergeneric relationships, the similarity of the thin, laminar operculum of *X. richeri* and that of *Tymolus* sp. (Cyclodorippidae) suggests that *Cymonomus* sp. (Cymonomidae), which has a thicker operculum, is less closely related to the other two species than they are to each other (unless the laminar operculum is pleisomorphic for cyclodorippoids), thus agreeing with the present classification on the basis of non-spermatozoal characters.

In conclusion, there is a distinctive cyclodorippoid sperm type which nevertheless shows ultrastructural affinities with dromioid, homolid and raninoid podotreme sperm but has strong resemblances to the sperm of the Homolidae and Raninoidea. The similarity of cyclodorippoid sperm to those of homolids and raninoids endorses placement of the Cyclodorippoidea, with the Homolidae and Raninoidea, in the Archaeobrachyura by Guinot (1978, 1979). Resemblance to heterotreme-thoracotreme sperm is low. Parsimony analysis to aid resolution of relationships in brachyuran groups, including the Cyclodorippoidea, will be attempted on acquisition of data from additional taxa.

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