SPERMATOLOGICAL EVIDENCE FOR THE TAXONOMIC STATUS OF TRAPEZIA (CRUSTACEA: BRACHYURA: HETEROTREMATA)

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Features of the spermatozoon of Trapezia which are general for heterotremes and endorse its inclusion in the Heterotremata are: extension of the subacrosomal chamber almost to the anterior apex of the sperm; division of the acrosome contents into inner and outer zones; presence of an acrosomal ray zone at the periphery of the inner acrosomal zone; and presence of a thickened ring where the acrosomal capsule surrounds the base of the subacrosomal chamber. A feature shared with 'higher' heterotremes is the restriction of cytoplasm to the periacrosomal region, the arms being nuclear only; and loss of a posterior median process, containing chromatin, which is present in raninids and majids. Additional features which Trapezia shares with the Xanthidae (exemplified by Xanthinae and Chlorodimae) and Panopeidae (exemplified by Eurytium) include the structure of the perforatorium, tapering anteriad, with a fibrous core; and extension of the chromatin around the operculum, leaving only a raised central area of this exposed. Peculiar features of xanthids (Xanthinae, Chlorodiinae) and panopaeids which separate them from all other heterotremes, including Trapezia, are the dense 'xanthid ring' around the base of the subacrosomal chamber and, in xanthids, the additional peripheral zone outside the outer acrosomal zone. Presence of a presumed derivative of the xanthid ring in thoracotremes indicates that the Xanthidae s. strict, and panopaeids are near the base of the Thoracotremata and absence of the ring in Trapezia suggests that it (in the Trapeziidae) is the plesiomorphic sister- or neighbouring-taxou of the xanthid-panopaeid assemblage. An apomorphy of Trapezia is restriction of the acrosome ray zone to an annulus around the anterior region of the perforatorium. Presence of the ring or its derivatives indicates that although the xanthids, panopaeids, and such thoracotremes form a monophyletic group, the Xanthoidea is a paraphyletic group, Crustacea, phylogeny, spermatozoa, ultrastructure, Trapezia, Pilodius, Eurythum, Mictyris.

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Trapezia Latreille, 1825, is a genus of heterotreme crabs, the species of which are obligate symbionts of corals (Abele & Felgenhauer, 1982). The 'trapézides' of A. Milne Edwards, 1862, were given subfamilial rank, as the Trapezinae, by Miers (1886) in the family Xanthidae of Macleay, 1838. This allocation of Trapezia was widely accepted. However, Guinot (1978) revived Ortmann's (1893) idea, subsequently abandoned, that a family Trapeziidae should be recognised. Within her Xanthoidea, Guinot (1978: 275) considered the Trapeziidae Miers to be a distinctive family equal in rank to the Xanthidae, and other xanthoid families (the Carpiliidae, Menippidae, Platyxanthidae, Pilumnidae, Panopeidae and Geryonidae), a view supported by specialists on the genus Trapezta (e.g. Clark & Galil, 1988).

Despite objections that classification on larval characters conflicts with that on adult characters (Gurney, 1938; Lebour, 1944), studies of larval development have been considered to confirm relationship of *Trapezia* with other xanthoid genera (Hyman, 1925; Wear, 1970; Rice, 1980; Martin, 1984). The classifications of Hyman (1925) and Wear (1970) suggested a special relationship of *Trapezia* to menippines and pilumnines (Menippidae and Pilumnidae sensu Guinot, 1978). Nevertheless, Guinot (unpublished) considers that the distinctive morphology of *Trapezia* may justify recognition of a distinct superfamily Trapezoidea.

The present study examines the ultrastructure of the spermatozoa of *Trapezia coerulea* with a view to providing evidence of its relationships. For comparative purposes, micrographs are included of the sperm of the xanthid *Pilodius areolatus* and the thoracotreme *Micryris longicarpus* (Mictyridae) and brief reference (in the Discussion) is made to the sperm of the panopaeid *Eurytium limosum* (Say) (Jamieson & Abele, unpublished). Published descriptions of xanthoid sperm are limited to a brief description for *Menippe mercenaria* (Menippinae) by Brown

(1966) in an unpublished doctoral thesis; a diagram of the sperm of Atergatis floridus (Linnacus) in a discussion of malacostracan phylogeny by Jamieson (1989c); detailed description of the sperm of Atergatis floridus (Xanthidae, Zosiminae), Etisus laevimanus Randall (Xanthidae, Efisinae), Liagore rubromaculata De Haan (Carpiliidae, incertae sedis) and Pilodius areolatus (H. Milne-Edwards) (Xanthidae, Chlorodiinae) by Jamieson (1989a); brief mention of Eurypanopeus depressus (Smith) and an SEM micrograph for Eurytium limosum (Say) (both Panopeidae) by Felgenhauer & Abele (1990) and a description for Geryon fenneri and G. quinquedens (Geryonidae), by Hinsch (1988). It is unfortunate that no descriptions of spermatozoal ultrastructure exist for Pilumnidae and that the brief description for Menippe mercenaria by Brown (1966) in an unpublished doctoral thesis does not give sufficient detail for purposes of comparison, in view of the supposed relationship of these to Trapezia.

MATERIAL AND METHODS

Species examined for sperm ultrastructure are: Trapezia coerulea Rüppell, from Heron Island, Great Barrier Reef; the xanthid Pilodius areolatus (H. Milne-Edwards), from One Tree Island, Great Barrier Reef; the panopaeid Eurytium limosum (Say) (see Discussion only) from the vicinity of Talahassee, Florida, USA; and the thoracotreme Mictyris longicarpus Latreille (Mictyridae), from Moreton Bay, Queensland, The specimen of Trapezia used has been lodged in the collections of the Queensland Museum.

Small portions of testes of were fixed in 3% glutaraldehyde in 0.1M phosphate buffer (pH 7.4), with 6% sucrose, at 4°C, washed in buffer, post-fixed for 80 min in similarly buffered 1% osmium tetroxide, washed in buffer, dehydrated through an ascending ethanol series, and infiltrated and embedded in Spurr's epoxyresin. Thin sections were cut with a diamond knife on an LKB 2128 UM IV ultrotome, collected on carbon stabilised colloidin-coated 200 mesh copper grids, and stained by the Daddow method: for 0.5 min in Reynolds' lead citrate, 1 min in 6% agueous uranyl acetate and a further 0.5 min in lead citrate, before rinsing in distilled water. Specimens were examined with a Hitachi 300 and a Jeol 100S transmission electron microscope operated at 80kV and 60kV respectively.

RESULTS AND COMPARATIVE REMARKS

The terminology adopted by Jamieson (1989a,b, 1991) will be employed in this account with the modification that the inner zone of the acrosome and the acrosome ray zone will be recognised as distinct layers, rather than being combined under the term inner dense zone. This modification of terminology will accommodate the condition in paguroid anomurans where the acrosome ray zone may form the widest layer of the acrosome. Although in Brachyura the acrosome ray zone is sometimes poorly delimited. from or forms part of an inner dense zone, the two layers will therefore be recognised as the 'inner acrosomal zone' and the 'acrosome ray zone'. To minimise repetition of data from Trapezia in the Discussion, some comparison with archaeobrachyuran and other heterotreme crabs will be made in the Results. Comparison with thoracotremes will chiefly be reserved to the Discussion.

GENERAL MORPHOLOGY

The spermatozoon of *Trapezia coerulea* is illustrated from transmission electron microscopy in a line drawing (Fig. 1) and in micrographs (Fig. 2). For comparison with a xanthid and a thoracotreme, these are illustrated by micrographs of the sperm of *Pilodius areolatus* (Fig. 3) and the thoracotreme *Micryris longicarpus* (Fig. 4).

The spermatozoon of Trapezia coerulea (Fig. 1) is spheroidal but slightly depressed anteroposteriorly and, like all decapod sperm, lacks a flagellum (Fig. 2B). This simple form is modified by the presence of broadly based lateral projections or 'arms'. From light micrographs, there are four arms, each with a length considerably surpassing the diameter of the sperm body. A plesiomorphic, chromatin-containing 'posterior median process', seen in Ranina and some majids, is absent. As is usual for brachyurans, the nucleus consists of diffuse, fibrous chromatin, and forms a cup surrounding the acrosome, a thin layer of cytoplasm intervening between nucleus and acrosome. The cytoplasm contains sparse mitochondria, some membranous (lamellar) structures of probable mitochondrial origin and, basal to the perforatorium, the two centrioles (Figs 2B,C,D).

ACROSOME

The subspheroidal core of the Trapezia spermatozoon consists entirely of the complex



FIG. 1. Trapezia coerulea. Diagrammatic representation of a longitudinal sagittal section of the spermatozoon.

acrosome. This is composed of a number of components identifiable with, and presumably homologous with, those described for other higher brachyuran sperm (Jamieson, 1989a,b, 1991).

The acrosome (Figs 2B,D) is invested by an acrosomal membrane underlain by an electron dense sheath, the 'capsule'. The length of the acrosome, from the apex of the operculum to the base of the thickened ring, is 2.4-2.9µm (mean of $3 = 2.6 \mu m$); the width is 2.6-3.0 μm (mean of 3 =2.8µm). The acrosomal membrane is separated by a very thin, pale layer, from the capsule and, like the capsule, is invaginated at the posterior pole to cover a columnar subacrosomal chamber (Fig. 2B), the contents of which are the perforatorium. The anterior tip of this chamber extends almost to the anterior apex of the sperm. As in most other crabs, this central, subacrosomal axis of the acrosome is surrounded by a wide electron dense sheath, the 'inner acrosomal zone' (Figs 2B, D). Unlike xanthoids for which sperm descriptions are sufficiently detailed (Pilodius areolatus, Fig. 3, Atergatis floridus, Etisus laevimanus and Liagore rubromaculata) there is no differentiation of the posterior part of the inner

acrosomal zone as an electron dense prominent annulus, the 'xanthid ring'.

As in xanthids of the Xanthinae and Chlorodiinae, but in this case in the absence of the xanthid ring, the inner acrosomal zone in *Trapezia* is surrounded by an 'acrosome ray zone' (Fig. 2A,B) seen also in other heterotremes and in paguroid anomurans (Jamieson, 1991). In xanthids (Fig. 3), the dorippid *Neodorippe*, and portunids, the acrosome ray zone extends for much of the length of the inner layer (being especially wide in portunids), but in *Trapezia* (Fig. 2A,B) it is limited to a slightly convex annulus restricted to, and embedded in, the anterior region of the inner acrosomal zone, from which it is poorly demarcated.

In Trapezia as in xanthids, portunids and other heterotremes, the inner acrosomal zone, with the ray zone, is in turn surrounded by a broad layer, the outer acrosomal zone (Figs 2B,D). In Trapezia, as in heterotremes excepting xanthids, this zone is the only additional concentric layer and continues to the capsule. In xanthids, in contrast, it is differentiated into an outer dense zone, next to the inner acrosomal zone and ray zone, and a further, peripheral zone (Fig. 3). The external





FIG. 3. Transmission electron micrograph of a longitudinal sagittal section of the spermatozoon of the xanthid *Pilodius areolatus*. Abbreviations: am = acrosome membrane; ar = acrosomal rays; ca = capsule; cm = cell membrane; ia = inner acrosomal zone; la = base of lateral arm; n = nucleus; o = operculum; oa = outer acrosomal zone; p = perforatorium; pc = vestigial periacrosomal cytoplasm; pmt = microtubules of perforatorium; so = subopercular zone; tr = thickened ring; xr = xanthid ring.

margin of the outer dense zone peculiar to xanthids is ragged and deeply dissected (*Atergatis* and *Pilodius*) or slightly crenulated (*Etisus*) or almost smooth (*Liagore*).

At the anterior pole of the *Trapezia* acrosome, as in all other brachyurans and paguroids with the doubtful exception of *Pagurus bernhardus* (see Chevaillier, 1968), there is a dense caplike structure, the operculum (Fig. 2B), 1.3-1.5 μ m wide (mean of 3 = 1.4 μ m). As in *Portunus*, the operculum is imperforate whereas in *Ranina* and the majid *Menaetheus monoceros* it is perforate (see Jamieson, 1991), although in some individual xanthid sperm it appears weakened apically (it is also perforate but is closed by an apical button in most of the investigated thoracotremes, Fig. 4A, see Discussion).

Below the operculum, as in many other crabs, a further, caplike structure of moderately electron dense material, the subopercular zone, separates the operculum and adjacent region of the capsule from the summit of the inner acrosomal zone and acrosome ray zone (Fig. 2B). In *Trapezia*, as in xanthids, the operculum extends laterally slightly beyond the acrosome ray zone. In contrast the operculum is limited in *Calappa* to the width of the ray zone while in portunids and dorippids it is more extensive as it also caps the outer acrosomal zone (see Jamieson, 1991).

At the opposite, posterior, pole the capsule is perforated by invagination of the acrosome membrane and capsule as a narrow orifice which opens into the columnar subacrosomal chamber. Unlike the *Ranina* sperm but like that of *Calappa*, portunids, *Neodorippe* and xanthids, a thickening of

FIG. 2. *Trapezia coerulea*. Transmission electron micrographs of the spermatozoon. A. Detail of acrosome ray zone. B. Longitudinal sagittal section. C. Detail of centriolar region. D. Transverse section shortly below the equator of the acrosome. E. Detail of the cytoplasmic layer in transverse section, showing mitochondria in various stages of degeneration. Abbreviations: am = acrosome membrane; ar = acrosomal rays; c = centriole(s); ca = capsule; cm = cell membrane; ia = inner acrosomal zone; ine = multilayered inner nuclear envelope; la = base of lateral arm; lm = contorted (lamellar) membranes; m = degenerating mitochondrion; n = nucleus; o = operculum; oa = outer acrosomal zone; p = perforatorium; pc = vestigial periacrosomal cytoplasm; pmt = microtubules of perforatorium; so = subopercular zone; tr = thickened ring.

the capsule forms a 'thickened ring' on each side of the subacrosomal invagination (Fig. 2B).

SUBACROSOMAL REGION

In Trapezia, as in xanthids and other heterotreme (and thoracotreme) Brachyura, the subacrosomal material consists of a highly differentiated stout perforatorium that extends from the posterior perforation in the capsule to the vicinity of the operculum at the apex of the acrosome (Fig. 2B). The perforatorium in Trapezia is a stout cylinder, slightly tapering anteriad, with a bluntly pointed tip and a posterior stalk constricted at the thickened ring. This form, together with differentiation of the perforatorium into a central dense fibrous core, is indistinguishable from that stated to be distinctive of xanthids (see Pilodius, Fig. 3) by Jamieson (1989a). In cross section, the perforatorium is seen to contain, as in xanthids and portunids (Jamieson, 1991) many circular profiles resembling microtubules though differing from typical microtubules in varying in size and in sometimes being irregular in section (Fig. 2D).

CYTOPLASM

A thin layer of spermatozoal cytoplasm surrounds the acrosomal capsule. As in portunids, dorippids and xanthids the cytoplasm does not extend into the arms. In majids, in contrast, the cytoplasm extends into the lateral arms together with contained microtubules which are not discernible in the other heterotremes mentioned. In Trapezia the cytoplasm is enlarged anterolaterally on one side of the capsule and contains several subspheroidal and apparently degenerating mitochondria with sparse cristae (Figs 2D,E). The degree of representation of mitochondria is variable in other heterotremes, usually being negligible, though it is similar to that in Trapezia in the thoracotreme Macrophthalmus crassipes and the archaeobrachyuran Ranina ranina (see Jamieson, 1991). The postacrosomal cytoplasm, typical of brachyurans and well developed in Trapezia, contains two centrioles (Figs 2B,C), a plesiomorphic condition seen in majids, parthenopids, calappids, portunids, dorippids and Macrophthalmus but absent in xanthids (Fig. 3) and, usually, in thoracotremes (see Jamieson, 1991).

Contorted membranes are present among the mitochondria of the dilated region of the cytoplasm and in extensions of the cytoplasm into the chromatin (Fig. 1, 2B). These membranes are the equivalent of the sometimes better developed lamellar structure seen in other brachyuran sperm. In *Trapezia* some of the membranes are continuous with the multilaminar prenuclear membrane (see below) and also appear to be continuous with membranes of disintegrating mitochondria. It seems possible, therefore, that the multilaminar membrane is at least partly derived from mitochondrial membranes.

NUCLEUS

In Trapezia, as in xanthids, and other brachyurans, the nuclear material is located in the lateral arms and their branches (Fig. 2B) and in the cup-shaped structure around both the acrosome and its cytoplasmic sheath. The chromatin extends around the operculum, leaving only the raised central area of this exposed (Fig. 2B), as in xanthids, whereas in portunids and Neodorippe the operculum is not covered. The envelope between the chromatin and the basal cytoplasm is unusually well developed in Trapezia and is represented by a dense double membrane bounding the cytoplasm (the nature of which is obscure as it cannot be the plasma membrane). Posterior to this membrane, bounding the anterior face of the nucleus, a series of six or more dense membranes (inner nuclear membrane in Fig. 2B), make up a multilaminar membrane. In xanthids and Portunus, for instance, the nuclear envelope though retained is disrupted and is not multilaminar. Nevertheless, the multilaminar membrane in Trapezia is incomplete, as it ends anteriorly at the lamellar structures. The external, basal surface of the cell, is bounded by a dense membrane, which may represent fused nuclear and plasma membranes, here termed the cell membrane (Fig. 2B). The general chromatin consists of electron dense filaments in a pale matrix, as in most brachyurans, but is less densely packed than in xanthids (see Discussion).

FIG. 4. Mictyris longicarpus, a mictyrid thoracotreme. A. Transmission electron micrograph of a longitudinal sagittal section of the spermatozoon. B. Transverse section to show the 'onion ring' lamellation of the acrosome. Abbreviations: ab = apical button of operculum; ba = branches of lateral arms; cl = concentric 'onion ring' lamellation; ia = inner acrosomal zone; n = nucleus; o = operculum; oa = outer acrosomal zone; p = perforatorium; pc = vestigial perfactorsomal cytoplasm; pmt = microtubules of perforatorium; so = subopercular zone; tr = thickened ring; xrm = putative modification of xanthid ring.





FIG. 5. Tentative phylogeny of the Brachyura based on apparent trends in the evolution of spermatozoal ultrastructure (modified from Jamieson, 1991). The chart of taxonomic features of location of gonopores is after Guinot (1978). The basal position of the Dromiidae, below the Paguroidea, which was tentatively suggested as an alternative to a brachyuran relationship by Jamieson (1991), is supported by evidence from rRNA (Spears et al., in preparation, cited in Abele, 1991). The position of the Potamonautidae is based on description of the sperm of *Potamonautes* by Jamieson (1993).

DISCUSSION

We may now consider the relationships of *Trapezia* as indicated by spermatozoal ultrastructure. These are tentatively indicated in Figure 5 within the context of a phylogeny of the Brachyura based on apparent trends in spermatozoal evolution.

The following are features of the spermatozoon of Trapezia that are general for heterotremes: extension of the subacrosomal chamber almost to anterior apex of the sperm whereas it reaches only to the approximate equator of the acrosome in the archaeobrachyuran Raninu: division of the acrosome contents into inner and outer zones; presence of an acrosomal ray zone at the periphery of the inner acrosomal zone; presence of a thickened ring where the capsule surrounds the base of the subacrosomal chamber; and absence of thoracotreme features mentioned below. A feature shared with 'higher' heterotremes is the restriction of cytoplasm to the periacrosomal region; unlike majids, for instance, it does not extend into the arms. The sperm of Trapezia thus confirms its heterotreme status and endorses separation from thoracotremes (Guinot, 1977, 1978) on the basis of the arrangement of the genital pores.

Features of the spermatozoon of Trapezia that are shared with the Xanthidae (compare Figs 2B &3), at least as exemplified by investigated Xanthinae and Chlorodiinae, and the Panopeidae, exemplified by Eurstium limosum, include all of the above general heterotreme features but also the following apparently apomorphic xanthid features: the structure of the perforatorium, tapering anteriad, with a fibrous core; and extension of the chromatin around the operculum, leaving only the raised central area of this exposed, the latter feature less developed in Eurytium than in the xanthids. These features are of questionable significance and could possibly arise homoplasically. Nevertheless, the form of the perforatorium is shared only with xanthids and Eurytium and, bearing in mind differences in sperm structure from the latter family outlined below, is not inconsistent with recognising relationship of Trapegia with xanthids though in a separate family.

Peculiar features of xanthids (Xanthinae, Chlorodiinae) (Jamieson, 1989a, and this study) and panopaeids (Jamieson & Abele, unpublished) which separate them from all other investigated heterotremes are the dense 'xanthid ring' around the base of the subacrosomal chamber and, in xanthids only, the additional peripheral zone outside the outer acrosomal zone (Fig. 3). A presumed derivative of the xanthid ring occurs in thoracotremes (see Mictyris, Fig. 4A) and this fact suggests that the Xanthidae are an advanced heterotreme group near the base of the Thoracotremata (see Jamieson, 1991). Presence of the ring or its derivatives indicates that although the xanthids and such thoracotremes form a monophyletic group, the Xanthoidea, as it is currently understood, is a paraphyletic group. The absence of the ring in Trapezia may parsimoniously be taken to be plesiomorphic rather than due to loss because loss would involve one extra evolutionary step. This, with the xanthid-like perforatorium and undoubted somatic similarities of Trapezia and xanthids, suggests that Trapezia is the plesiomorphic sister- taxon or, at least a neighbouring taxon, of the xanthid-panopaeid assemblage in so far as they are represented spermatologically by xanthines, chlorodiines and panopacids. In Geryon the ring is also absent (Jamieson, 1991, from micrographs by Hinsch, 1988). The condition in other xanthoids is unknown.

Whereas the sperm of *Trapezia* shows clear heterotreme features, it lacks thoracotreme features, well exemplified by *Micryris* (Fig. 4A,B), which include the perforate operculum with apical button (excepting *Macrophthalmus*); absence of the acrosome ray zone; absence of the thick-ened ring; and presence of concentric 'onion ring' lamellation of the outer acrosome zone (excepting *Uca*).

In conclusion, spermatologically Trapezia confirms its heterotreme position, shows features (especially the form of the perforatorium) linking it with xanthids and panopaeids, but warrants separate familial status in lacking the xanthid ring. It remains to be seen whether examination of sperm ultrastructure in further xanthoids will confirm this conclusion.

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