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SPERMATOPHORE AND SPERMATOZOAL MORPHOLOGY IN THE PORCELLANIDAE. II. THE GENERA *PETROLISTHES* AND *POLYONYX* (DECAPODA: ANOMURA)

C. C. Tudge and B. G. M. Jamieson

ABSTRACT

The porcellanid genera *Petrolisthes* and *Polyonyx* are shown to have differing spermatozoal morphology reflecting an apparently natural division of the family previously suggested on adult and larval somatic morphology. Species investigated in the genus *Petrolisthes* have spermatozoa with a globular nucleus and autapomorphic opercular ridge and tubular ring structure within the acrosomal vesicle. Spermatozoa of *Polyonyx transversus* (Haswell) have a long "taillike" nucleus penetrated throughout by a central microtubular core. This latter spermatozoal morphology is shared with other members investigated in the "*Porcellana*-group," (*Aliaporcellana* and *Pisidia*). All the Porcellanidae investigated share a suite of spermatozoal characters that unite them (superior acrosomal vesicle; broad, centrally perforate operculum; 4 or more external microtubular arms; perforatorial chamber wall folded into corrugations or septa; dense perforatorial cone; posterior perforatorial ring and divided inner acrosome zone). A unique spermatophore morphology, consisting of a tubular extension of the anterior end of the ampulla, is described for representatives in the genus *Petrolisthes*.

The members of the Porcellanidae Haworth, 1825, can be readily divided into two groups on the basis of adult somatic morphology (Haig, 1965) and larval morphology (Sankolli, 1965; Gore, 1971; Van Dover *et al.*, 1982). The genus *Petrolisthes* is always placed in a separate division (herein referred to as the "*Petrolisthes*-group") from other porcellanid genera, such as *Porcellana, Pisidia,* and *Polyonyx* (herein referred to as the "*Porcellana*-group"). Recent research (Tudge, 1995a; present study) into the spermatophore and spermatozoal morphology of the family appears to support this basic dichotomy.

Retzius (1909) described and illustrated, at the light microscope level, the spermatophore and spermatozoal morphology of the porcellanid crab *Pisidia longicornis* (Linnaeus, 1767) (as *Porcellana longicornis*). A light microscope description of the spermatophore structure and dehiscence action of the spermatophore of *Pisidia longicornis* (again as *Porcellana longicornis*) was also provided by Mouchet (1931) in her monographic work on the spermatophores of anomuran and brachyuran decapods. Brown (1966) used a single light micrograph to show the morphology of the spermatophore of an unidentified species of *Petrolisthes,* and further illustrated the ultrastructure of the spermatozoa of the same species in a series of electron micrographs. In his review of crustacean spermatozoa, Jamieson (1991) presented a transmission electron micrograph of *Petrolisthes lamarckii* (Leach, 1820) to illustrate examples of anomuran spermatozoa. Tudge and Jamieson (in press) describe and illustrate the spermatophore and spermatozoal ultrastructure of the porcellanids *Aliaporcellana suluensis* (Dana, 1852) and *Pisidia longicornis.*

In the present paper, a detailed, illustrated description of the spermatophore morphology and spermatozoal ultrastructure of the porcellanid, *Petrolisthes lamarckii* is presented for the first time. For comparison, the spermatozoal ultrastructure of *Polyonyx transversus* (*Porcellana*-group) is also described and illustrated, but, at present, there is no information available on the form of the spermatophore in this species.

MATERIALS AND METHODS

Specimens of *Petrolisthes armatus* (Gibbes, 1850) were collected from the Florida coast, Gulf of Mexico, U.S.A. (30°N, 84°W) in November 1990 by staff of the laboratory of Prof. L. Abele, Florida State University, and by the senior author from a similar location in November 1995. *Petrolisthes lamarckii* (Leach, 1820) was collected by the authors from Heron Island, Great Barrier Reef, Queensland, Australia (23°27′S, 151°55′E) in December 1988. *Petrolisthes* sp. was collected by Dr. B. Richer de Forges (ORSTOM) from New Caledonia, Southwest Pacific in September 1993. *Polyonyx transversus* (Haswell, 1882) was collected by the authors from Dunwich, North Stradbroke Is-

land, Queensland, Australia (27°30′S, 153°24′E) in August 1991.

The male reproductive material (testes including the ducts of the vasa deferentia) was removed from freshly pithed crab specimens and immediately fixed in cold glutaraldehyde for transmission electron microscopy (TEM). Live spermatozoa and spermatophores were also smeared on microscope slides and viewed and photographed by light microscopy. Specimens which were collected on our behalf by colleagues were fixed in cold glutaraldehyde for a minimum of 2 h at 4°C, then shipped at ambient temperature to Brisbane, Australia, where the remainder of the fixation and embedding process was carried out. The gonads of *Petrolisthes armatus* were sent to us in resin blocks after fixation and processing in the laboratory of Prof. Abele.

Light Microscopy.—For light microscopy, fresh or glutaraldehyde-fixed sperm and spermatophores were viewed and photographed under an Olympus BH2 Nomarski interference-contrast microscope. Micrographs were taken with an attached Olympus OM-2 camera.

Transmission Electron Microscopy.—For all specimens processed in the Zoology Department, University of Queensland, the standard fixation procedure (outlined below) for TEM 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 rinse.

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 1 h at 4°C. They were rinsed in phosphate buffer (3 rinses in 15 min), postfixed in phosphate buffered 1% osmium tetroxide for 80 min; similarly rinsed in buffer and dehydrated through ascending concentrations of ethanol (40–100%). After being infiltrated and embedded in Spurr's epoxy resin (Spurr, 1969), thin sections (500–800 Å thick) were cut on a 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 (Reynolds, 1963) 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.

Results

Petrolisthes armatus, Petrolisthes lamarckii, and *Petrolisthes* sp.

Spermatophore Morphology.—All three species studied have the same spermatophore morphology with minor size differences. The spermatophore is composed of an elongate ampulla, which has a swollen posterior region and a thin apical tubular projection, and is attached basally to a short broad stalk and pedestal (Fig. 1A, B). The entire spermatophore is 340 μm long in *Petrolisthes* sp. and 325 μm long in *P. la-*

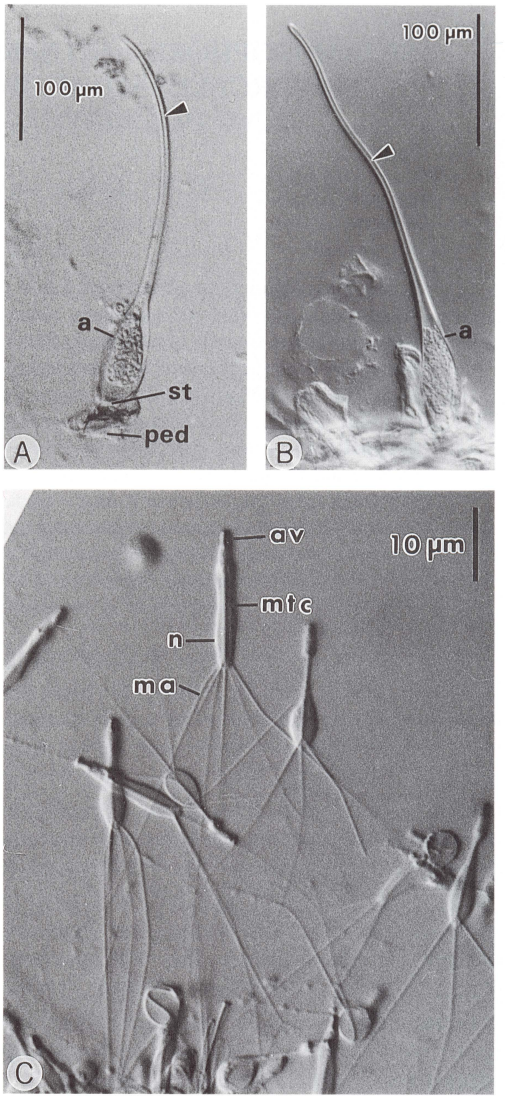

Fig. 1. A, B. Light micrographs of spermatophores of (A) *Petrolisthes lamarckii* and (B) *Petrolisthes* sp. C. Light micrograph of spermatozoa of *Polyonyx transversus.* (Note that several of the spermatozoa shown are slightly immature and still have swollen regions of uncondensed nucleus.) Abbreviations for Figs. 1, 3–5: a = ampulla; av = acrosomal vesicle; ce = centriole; cy = cytoplasm; dpc = dense perforatorial cone; exl = extra-opercular layers; ia = inner acrosome zone; m = mitochondrion; ma = microtubular arm; ms = membrane system; mt = microtubules; mtc = microtubular core; n = nucleus; o = operculum; oa = outer acrosome zone; or = opercular ridge; p = perforatorial chamber; pa = peripheral acrosome zone; ped = pedestal; ppr = posterior perforatorial ring; ps = perforatorial septum; so = subopercular zone; st = stalk; tu = tubular ring; arrowhead indicates tubular projection of ampulla.

marckii, with ampullar dimensions being 325 μm long × 30 μm wide (at the widest point) and 300 μm long × 36 μm wide, respectively. The posterior bulbous region is 80 μm long in *P. lamarckii* and 70 μm long in *Petrolisthes* sp. The sperm cells occur in the bulbous area of the ampulla and a thin lumen is still present in the anterior projection, making a tubular structure (Fig. 1A, B). The anterior tube does not appear to open externally at the tip and no spermatozoa were seen in the lumen of the projection. It is not known if a raised or thickened ridge, seen in many anomuran crabs, occurs around the ampulla of the spermatophore in this genus.

Spermatozoal Morphology.—At the light microscope level, the spermatozoa of all three species of *Petrolisthes* appear very similar, but TEM was carried out only on *Petrolisthes armatus* and *P. lamarckii.* The fixation of the gonad tissue of *P. armatus* was not of consistent quality to allow a large number of micrographs, but the presence of all of the spermatozoal features diagnostic for this genus was confirmed.

The spermatozoa are composed of a cylindrical to ovoid acrosomal vesicle attached posteriorly to a globular nucleus, via a small necklike region of cytoplasm (Figs. 2, 3B, C). The acrosomal vesicle (approximately 2.1 μm long × 1.2 μm wide) is capped by a domed operculum and penetrated posteriorly by a perforatorial chamber. Four long microtubular arms extend laterally from the cytoplasmic region. The entire sperm cells are generally 5 μm in length (refer to Figs. 2–4 throughout).

Acrosome.—The ovoid acrosomal vesicle of *Petrolisthes armatus* and *P. lamarckii* is capped at its anterior end by an electron-dense, perforate operculum. The operculum forms a high dome with a small opening at its apex, is thickest at its posterior rim, and possesses a laterally directed thickened ridge on the external posterior surface (Figs. 3A–C, 4A–E). A region with the appearance of closely apposed membranes lies external to the operculum, but under the plasma membrane. These stacked membranes are here termed extra-opercular layers (Figs. 3A, 4A–F). Directly beneath the operculum and applied to its posterior surface is the subopercular zone. This zone is finely granular, homogeneous, of moderate electron density, and is thickest directly posterior to the perforation in the operculum (Figs. 3A, B, 4A, B). The inner acrosome zone occupies the center of the acrosomal vesicle, except for the interruption of the perforatorial chamber, and contains several morphologically distinct regions (Figs. 3A, B, 4A–F). Its innermost region thinly envelopes the perforatorial chamber and extends anteriorly as a thin central projection which meets the subopercular zone. It is finely granular and moderately electron dense and is laterally surrounded by an apically perforated, thin cone of electron-dense material, for most of its length. This dense perforatorial cone extends from the subopercular zone posteriorly to a position approximately two-thirds of the way down the perforatorial chamber; with its widest internal diameter being at its posteriormost edge (Figs. 3A, B, 4A–F). Another cone-shaped region which is very similar in appearance to the extra-opercular layers lies external to the anterior portion of the dense perforatorial cone. It is composed of moderately electron-dense material arranged in a series of parallel, membranelike layers. This region of the inner acrosome zone extends from the subopercular zone posteriorly to a position level with the midpoint of the acrosomal vesicle. At the posterior limit of this layered cone, a small electron-dense tubular ring occurs. In longitudinal section, this tubular ring appears to be composed of a bundle of electron-lucent tubules concentrically orientated around the perforatorial chamber and the surrounding dense perforatorial cone (Fig. 3A, B). A broad ring, the last region of the diverse inner acrosome zone, projects posteriorly from the tubular ring and surrounds the base of the perforatorial chamber. This area, here termed the posterior perforatorial ring, is finely granular, homogeneous, and more electron dense than adjacent zones. The posterior perforatorial ring lies adjacent to the perforatorial chamber wall near the posterior (basal) region of the chamber (Figs. 3A, B, 4F–H). Lateral to, and external to, the five regions of the inner acrosome zone is the outer acrosome zone, and, most exterior, the peripheral acrosome zone. The outer acrosome zone extends from the subopercular zone posteriorly to the constricted basal

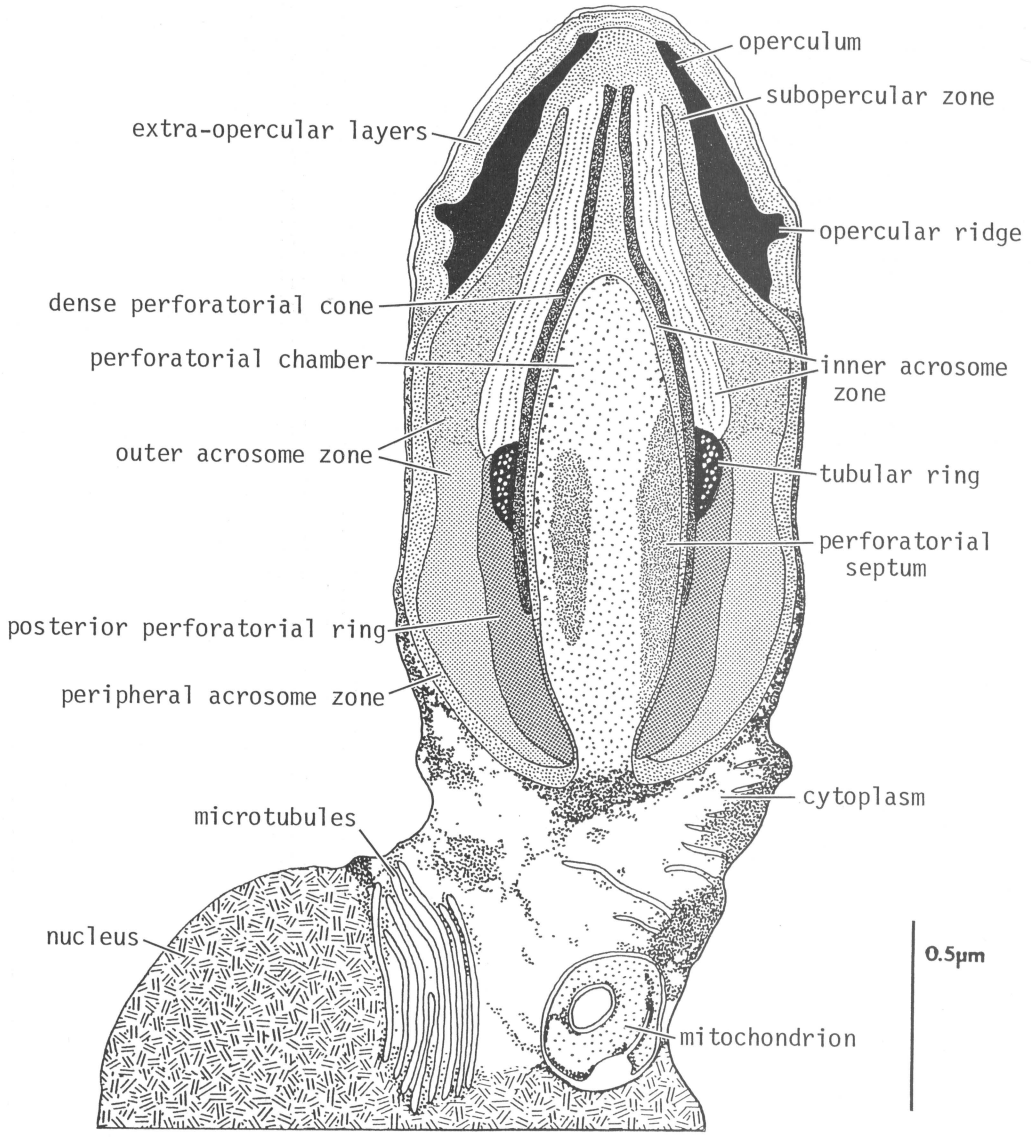

Fig. 2. *Petrolisthes lamarckii.* Semidiagrammatic longitudinal section of an acrosomal vesicle of a spermatozoon, traced from a micrograph. Scale bar = 0.5 µm.

opening of the perforatorial chamber. It forms a hollow cylinder composed of two distinct areas, separated at the midpoint of the acrosomal vesicle. Both regions are coarsely granular, subtly heterogeneous, and less electron dense than the inner acrosome zone. The point of division between the two zones forms an obvious boundary at the level of the tubular ring (Fig. 3A, B). The thin peripheral acrosome zone envelopes the combined internal zones and extends around the acrosome boundary, from

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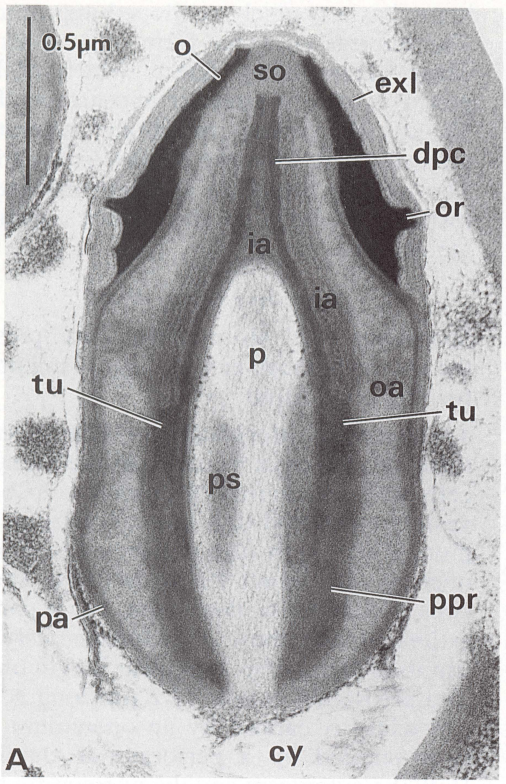
Fig. 3. *Petrolisthes lamarckii.* A–E. Transmission electron micrographs of spermatozoa. A, Longitudinal section (LS) of acrosomal vesicle of a spermatozoon. B, LS of a spermatozoon. C, Low power micrograph of many spermatozoa cut in various planes. D, Transverse section (TS) of nucleus showing four bundles of microtubules. E, Oblique section of cytoplasmic region. Abbreviations as in Fig. 1. Scale bars = 1 µm, except where indicated.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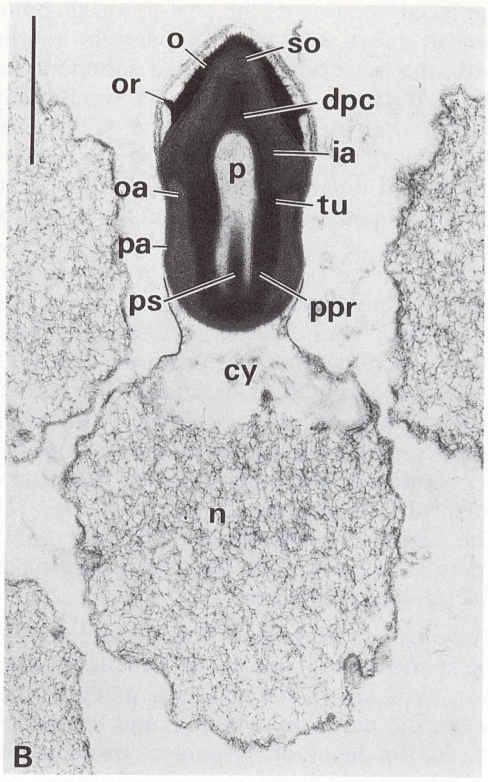
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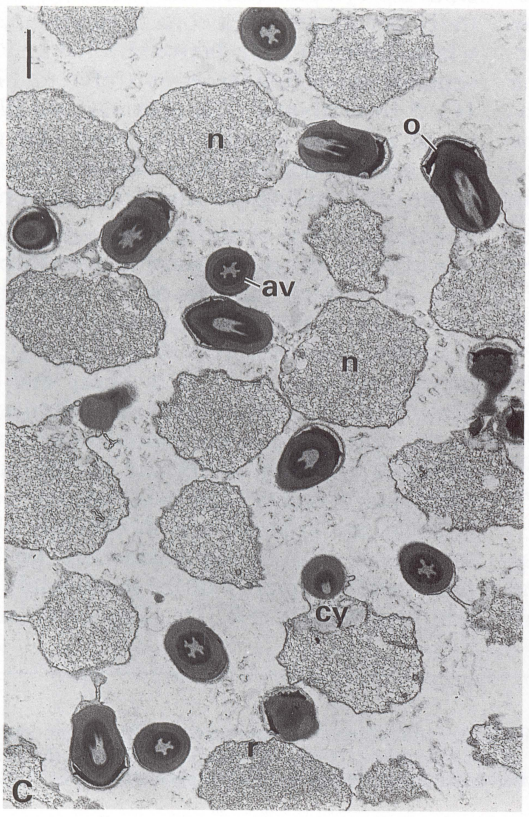
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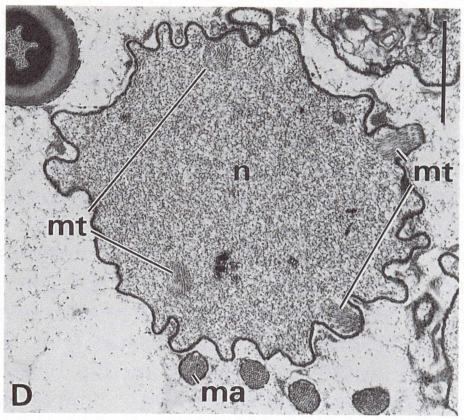
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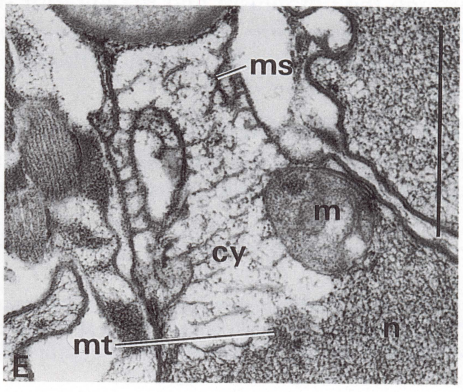
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the basal opening of the perforatorial chamber, to meet with, and apparently merge with, the posterior edge of the subopercular zone. It forms a conspicuous moderately electron-dense peripheral band (Figs. 3A, B, 4G, H).

The columnar perforatorial chamber posteriorly penetrates the acrosomal vesicle for two-thirds of its length and ends bluntly, level with the posterior rim of the operculum. The perforatorial chamber is widest at its equator (Figs. 3A–C, 4C–H). In transverse section, the perforatorial chamber wall is convoluted or extended to form robust septa (generally between 4 and 8 in number) for most of its length, except the very anteriormost region where the chamber profile is circular (Figs. 3A–C, 4C–H). The chamber contents appear as a finely granular, almost fibrillar, network in an electron-lucent matrix.

Cytoplasmic Region.—The cytoplasm in the sperm cell of species of *Petrolisthes* occurs as a small electron-lucent region between the acrosomal vesicle and the nucleus. A thin layer of cytoplasm projects anteriorly to envelope the posteriormost region of the acrosomal vesicle. The cytoplasm directly below the open perforatorial chamber appears continuous with the chamber contents and may show some condensation at this point (Fig. 3A). Very few organelles can be distinguished except for some membranes, occasionally arranged in a horizontal "ladderlike" pattern (Fig. 3E), and some loose bundles of microtubules and mitochondria. The mitochondria are scarce and often appear degenerate, owing to the absence of visible cristae (Fig. 3E). The microtubular bundles are the bases of the four microtubular arms which pass through the cytoplasm and the anterior part of the nucleus (Fig. 3D, E). No centrioles were observed in the sperm cells of *Petrolisthes.*

Nucleus.—The nucleus is subspheroidal and is attached to the base of the acrosomal vesicle and cytoplasm. The nuclear membrane has a coarsely scalloped appearance. The nuclear contents form a network of dense anastomising fibers, which at low power assume a granular appearance (Fig. 3B–D). No distinct membrane separating the cytoplasm from the nucleus is apparent. The nuclear boundary is thickened and is assumed to be a combined nucleoplasma membrane.

Polyonyx transversus

Spermatophore Morphology.—At present the spermatophore morphology is unknown for this porcellanid species.

Spermatozoal Morphology.—The spermatozoa of *Polyonyx transversus* are elongate cells with an anterior, cylindrical acrosomal vesicle connected to a thin cytoplasmic region, which is in turn connected to a long nucleus. The exact length of these sperm cells is difficult to determine, but it can be estimated that they are approximately 20 μm long (acrosome + nuclear length only). The acrosomal vesicle (2.2 μm long × 0.9 μm wide) is capped by an operculum and is penetrated by a perforatorial chamber. Both the cytoplasm and the nucleus are centrally penetrated by a core of microtubules which splits to form between three and six separate microtubular arms (refer to Figs. 1C, 5 throughout). The spermatozoa illustrated may be slightly immature and this may account for the large amount of cytoplasm surrounding the microtubular core.

Acrosome.—The cylindrical acrosomal vesicle of *Polyonyx transversus* is apically capped by a thin, electron-dense operculum which also extends posterolaterally to form a shallow, inverted cup (Fig. 5A, D). Although not illustrated, it is likely that the operculum is centrally perforate. Subjacent to the operculum is the subopercular zone, which is centrally perforated by the inner acrosome contents. The subopercular zone contents are granular and moderately electron dense and extend posteriorly for approximately a quarter of the acrosomal vesicle length (Fig. 5A, D). The inner acro-

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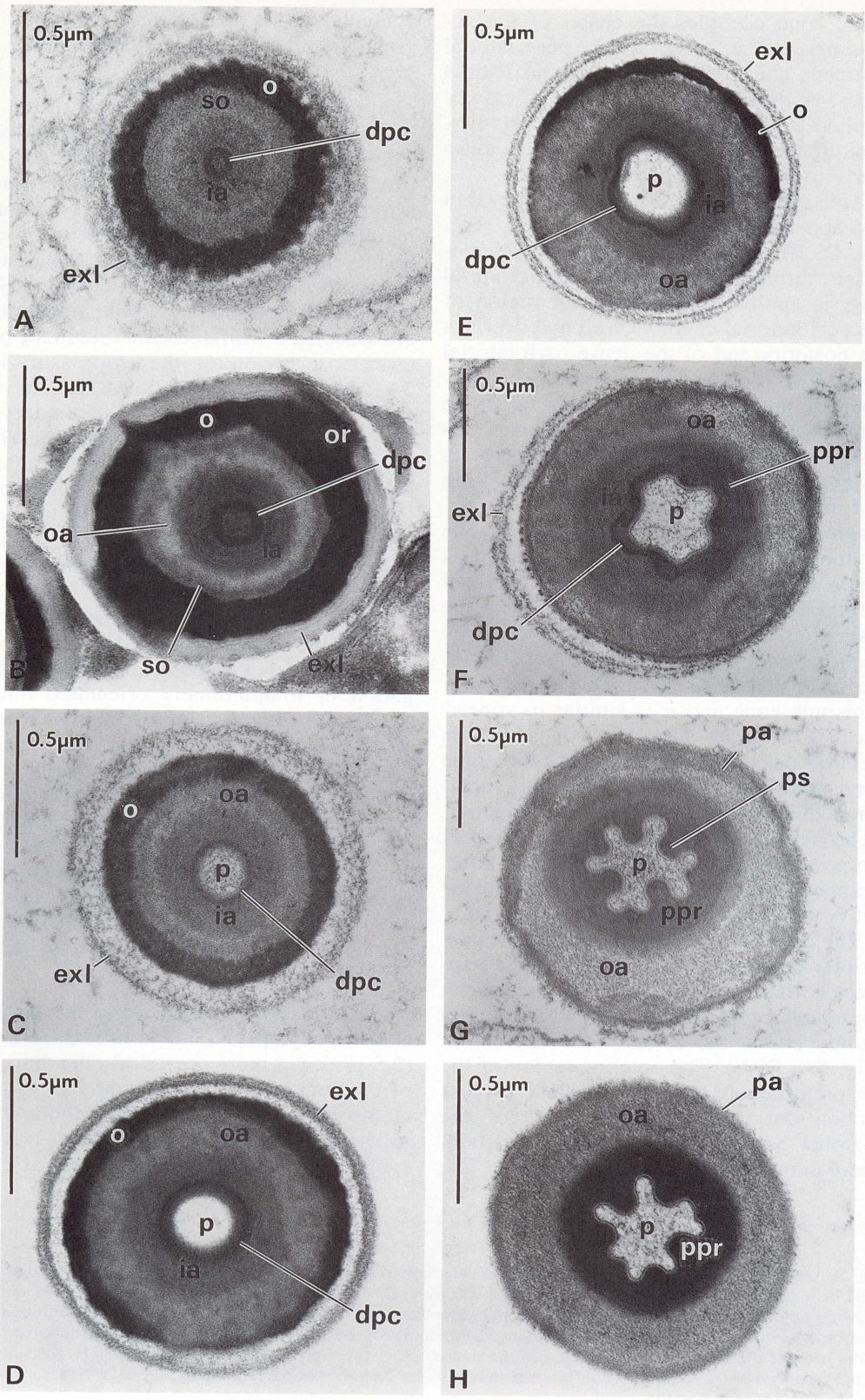
Fig. 4. *Petrolisthes lamarckii.* A–H. Transmission electron micrographs of spermatozoa. Transverse sections (TSs) through acrosomal vesicle (A, B) at the level of the operculum, (C–E) the anterior portion of the perforatorial chamber, and (F–H) the posterior portion of the perforatorial chamber. Abbreviations as in Fig. 1. Scale bars = 1 μm, except where indicated.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some zone occupies the center of the acrosomal vesicle, except for the perforatorial chamber, and is divisible into three distinct areas. A dense core of material is closely applied to the upper two-thirds of the perforatorial chamber wall and projects anteriorly to nearly the opercular region.

This dense perforatorial cone is very thin and appears to have a perforate apex (Fig. 5A, D, E). An electron-dense ring of material, termed the posterior perforatorial ring, is applied to the posterior region of the perforatorial chamber wall and overlaps the posterior end of the dense perforatorial cone. This dense ring is heterogeneously granular and sometimes appears reticulate (Fig. 5A). The third area of the inner acrosome zone envelopes the dense perforatorial cone and posterior perforatorial ring and extends for the entire length of the acrosomal vesicle. This thin, cylindrical zone is finely granular, homogeneous, and less electron dense than the two zones contained (Fig. 5A). A zone which extends from the operculum to the base of the perforatorial chamber as a thin cylinder lies external to the inner acrosome zone. This is the outer acrosome zone and it is similar in appearance to the inner acrosome zone, but less electron dense. A thin peripheral acrosome zone surrounds the inner and outer acrosome zones and extends from the constricted base of the perforatorial chamber to meet the posterior edge of the subopercular zone. It appears continuous with this latter zone but is more electron dense (Figs. 5A, E).

The columnar perforatorial chamber posteriorly penetrates the acrosomal vesicle for greater than two-thirds of its length. It maintains a consistent width and terminates bluntly below the level of the operculum (Fig. 5A, D, E). The anterior region of the perforatorial chamber is circular in cross section but posteriorly the walls of the chamber become convoluted to form faint undulations, but no septa (Fig. 5E). The contents of the perforatorial chamber are granular and moderately electron dense.

Cytoplasmic Region.—The cytoplasmic region envelopes the posterior end of the acrosomal vesicle and extends posteriorly. The cytoplasm is approximately 2.0–2.5 μm wide and may extend to 3.0–3.5 μm in length. A series of parallel, horizontal membranes which are attached to the cell membrane (possibly only in the immature spermatozoa) are situated anterolaterally in the cytoplasm. These ladderlike membranes are associated with mitochondria in the posteriormost region of the cytoplasm (Fig. 5A). Many large, sometimes cristate, mitochondria are visible at the boundary of the cytoplasm and the nuclear material (Fig. 5A, F). No distinct membrane separates the cytoplasm from the nucleus. A pair of centrioles is apparent in the cytoplasm directly below the open end of the perforatorial chamber; they mark the anteriormost end of a large bundle of microtubules (Fig. 5B). This microtubular core extends posteriorly through the center of the cytoplasm and the nucleus, and is composed of a tight aggregation of longitudinally orientated microtubules. The core is circular in cross section with a diameter of 0.9 μm in the cytoplasmic region which reduces to 0.6 μm in the nucleus (Fig. 5A, F, G). The microtubular core splits into smaller bundles of microtubules (4 or 5?) at the posterior end of the nucleus (Figs. 1C, 5C, H) and each emerges from the nucleus as an individual microtubular arm (approximately 0.2 μm in width). The arms may be up to 50 μm in length (Fig. 1C).

Nuclear Material.—Anteriorly the nucleus abuts the cytoplasm and is of similar width (2.5 μm), but more posteriorly the diameter of the nucleus decreases slightly to 1.4 μm at the point where the microtubular core splits. The nuclear material forms a long cylinder surrounding the microtubular core.

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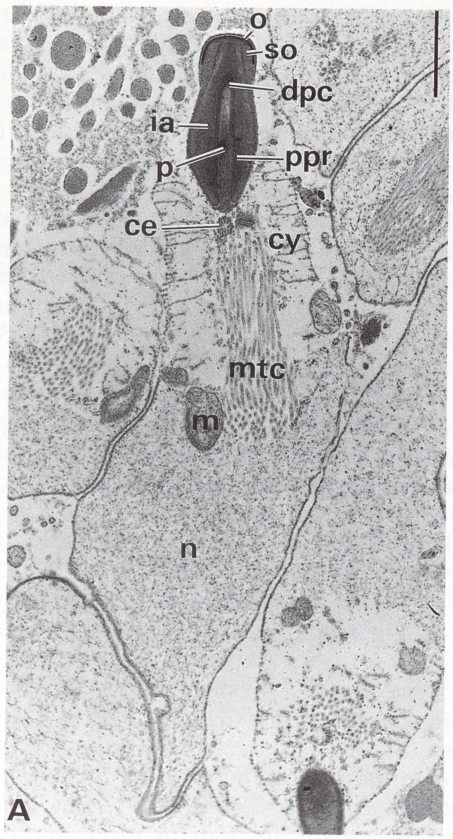
Fig. 5. *Polyonyx transversus.* A–H. Transmission electron micrographs of spermatozoa. A, Longitudinal section (LS) of a spermatozoon. B, Detail of pair of centrioles. C, Oblique LS through posterior region of nucleus showing splitting of microtubular core into microtubular arms. D–H, Transverse sections (TSs) through (D) acrosomal vesicle at the level of the operculum, (E) midpoint of the acrosomal vesicle, (F) through spermatozoon at the level of the mitochondrial region, (G) the microtubular core surrounded by nucleus, and (H) the splitting of the microtubular core into several internal microtubular bundles. Abbreviations as in Fig. 1. Scale bars = 1 μm, except where indicated.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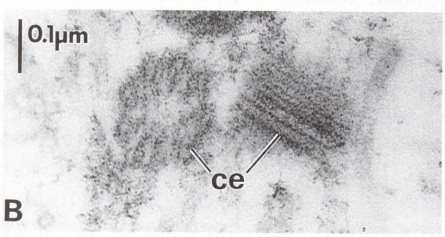
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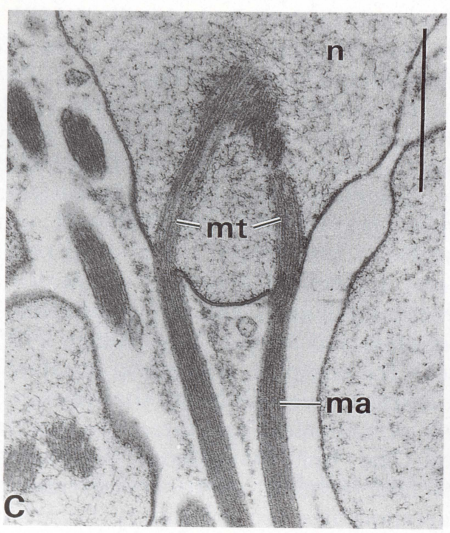
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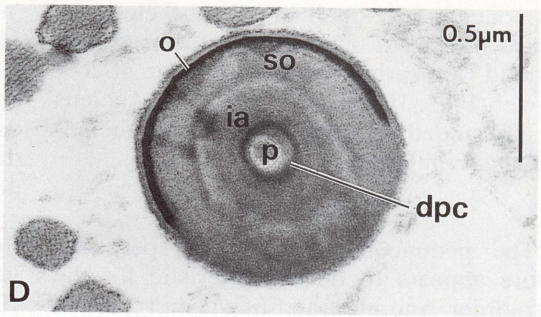
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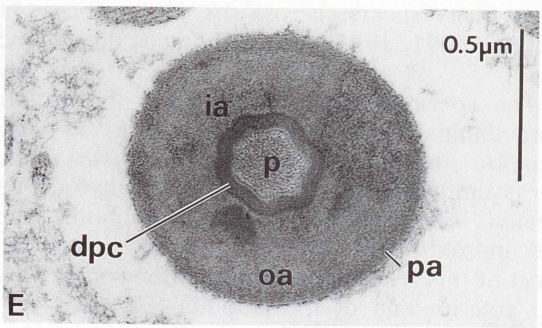
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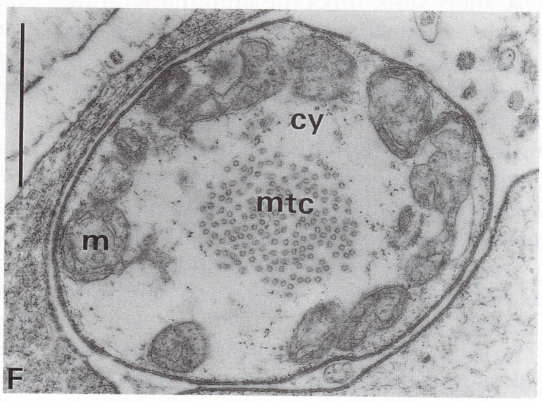
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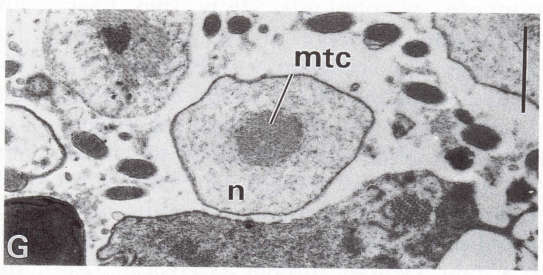
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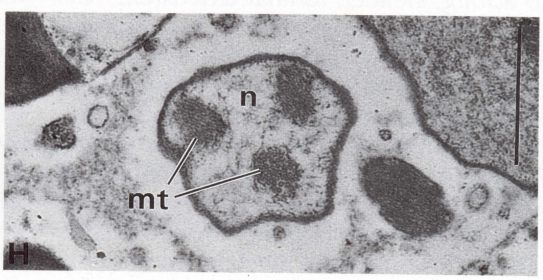
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Its contents are small bundles of electron-dense fibers in an electron-lucent background, appearing almost granular at low power (Figs. 1C, 5A, C, G, H). The nucleus is surrounded by a thick, combined nucleoplasma membrane.

Discussion

The pedunculate or stalked spermatophore appears to be characteristic for the infraorder Anomura and has been recorded from many species across the 13 families (Tudge, 1991, 1995a, and references therein).

The spermatophore morphology of the porcellanids *Petrolisthes armatus, P. lamarckii,* and the unidentified *Petrolisthes* sp. is unique among the anomurans investigated. The pedunculate spermatophores are approximately 300–350 μm long, but most of this length is a tubular extension of the anterior end of the ampulla (Fig. 1A, B). A short stalk links the ampulla with the extensive pedestal. The spermatozoa are concentrated in the posterior, bulbous region of the ampulla and the anterior extension, though appearing hollow, is devoid of spermatozoa. This unique anteriorly directed tubular extension of the spermatophore has been recorded only in members of the genus *Petrolisthes* (see Brown, 1966; present study) within the Porcellanidae investigated (Tudge, 1995a; Tudge and Jamieson, in press).

The four representatives of the Porcellanidae, which have been investigated for spermatophore morphology, show two basic spermatophore forms. In *Aliaporcellana* (see Tudge and Jamieson, in press) and *Pisidia* (see Mouchet, 1931; Tudge and Jamieson, in press) the pedunculate spermatophores are small and spherical to ovoid, while in the three species of *Petrolisthes* (see Brown, 1966; present study) the anterior end of the ampullae has been drawn out into a long, slender, tubular extension. This dichotomy of the porcellanids investigated, based on spermatophore shape, is endorsed by external somatic characters (Haig, 1965) and larval characters (Sankolli, 1965; Gore, 1971; Van Dover *et al.,* 1982). Mouchet (1931) showed that the spermatophores of *Pisidia longicornis* possess a lateral ridge where the ampulla splits to release the spermatozoa. Transmission electron microscopy of the spermatophore of *Aliaporcellana suluensis* (see Tudge and Jamieson, in press) reveals that this species also possesses a lateral ridge and that it is ultrastructurally complex. The presence of a lateral ridge on the ampulla of the spermatophore in the genus *Petrolisthes* has not been proven.

All members of the Porcellanidae investigated show a particular suite of acrosomal vesicle characters which unites them (Brown, 1966; Jamieson, 1991; Tudge and Jamieson, in press, present study). (1) The acrosomal vesicle is superior in relation to the cytoplasm (which generally forms a thin, necklike region). This condition is approached by some galatheids, but generally in the remainder of the Anomura the posterior portion of the acrosomal vesicle is embedded into the cytoplasm, which in turn is embedded in the nucleus (Tudge, 1995a, b). (2) The acrosomal vesicle is capped by a broad, perforate operculum. Within the remainder of the Anomura investigated, a perforate operculum occurs only in the diogenid hermit crab *Cancellus* sp. (3) It is often difficult to ascertain the exact number of external microtubular arms in the spermatozoa of these porcellanids, but it appears that there are four or more microtubular arms in each species. The number of microtubular arms in the mature spermatozoa of representatives from the Paguroidea and Galatheoidea (with the exception of the above-mentioned Porcellanidae) is always three (Tudge, 1995a, b). (4) The posterior portion of the wall of the perforatorial chamber in the spermatozoa of the porcellanids investigated is variously folded to form low corrugations to broad septa. The genera *Aliaporcellana, Pisidia,* and *Polyonyx* have small, subtle corrugations (Tudge and Jamieson, in press; present study), while obvious, thick septa are found in the two species of *Petrolisthes* investigated. Similar perforatorial chamber-wall ornamentation (homoplasy?) are observed in several species of *Pagurus,* a species of *Porcellanopagurus,* and the galatheids *Allogalathea* and *Munida* (see Tudge, 1995a, b). (5) The complex, concentric zonation of the acrosomal vesicle in the spermatozoa of these porcellanids has three distinct features. The first two (dense perforatorial cone and posterior perforatorial ring) are autapomorphies for the family Porcellani-

dae, while the third (divided inner acrosome zone) is a synapomorphy, shared with members of the family Galatheidae.

A major difference in the overall sperm cell morphology divides the members of the Porcellanidae. The globular nuclear form in species of *Petrolisthes* (Fig. 3B, C) clearly differentiates this genus from the other genera which have an elongate sperm cell (Figs. 1C, 5A–H). Both *Petrolisthes armatus* and *P. lamarckii* exhibit unique acrosomal characters which, with the globular nuclear shape, separate them from the other three porcellanid genera. These acrosomal characters are a conspicuous opercular ridge and a tubular ring which encircles the perforatorial chamber at its midpoint. Neither of the structures has been recorded from any other anomuran studied for spermatozoal morphology. *Aliaporcellana, Pisidia,* and *Polyonyx* have an elongate spermatozoal morphology characterized by the possession of a central core of microtubules which splits, posteriorly, to form several microtubular arms. The microtubular core extends the entire length of the sperm cell, from the necklike region of cytoplasm below the acrosomal vesicle to the posteriormost end of the nucleus. The cytoplasm and nucleus surround the microtubular core and form little more than a veneer for most of its length. Subtle differences in acrosomal vesicle shape, dimension, and zonation differentiate the spermatozoa of these three porcellanid genera.

The basic division in sperm cell morphology (elongate nucleus with microtubular core in contrast to a globular nucleus) seen in the genera of the Porcellanidae endorses previous dichotomies of the family suggested from adult somatic morphology (Haig, 1965) and larval somatic morphology (Sankolli, 1965; Gore, 1971; Van Dover *et al.,* 1982). In the above-mentioned papers, the genera *Petrolisthes* and *Pachycheles* (sometimes with *Petrocheles* and *Megalobrachium*) are in a separate division or group (*Petrolisthes*-group) from *Porcellana, Pisidia, Polyonyx* (*Aliaporcellana* was previously assigned to this latter genus by Haig (1965)), and several other genera such as *Raphidopus, Porcellanella,* and *Euceramus* (*Porcellana*-group). Investigations into the spermatophore and spermatozoal morphology in these additional genera (plus further species from the genera already studied) will help to promote or refute the apparently natural division of this anomuran family.

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