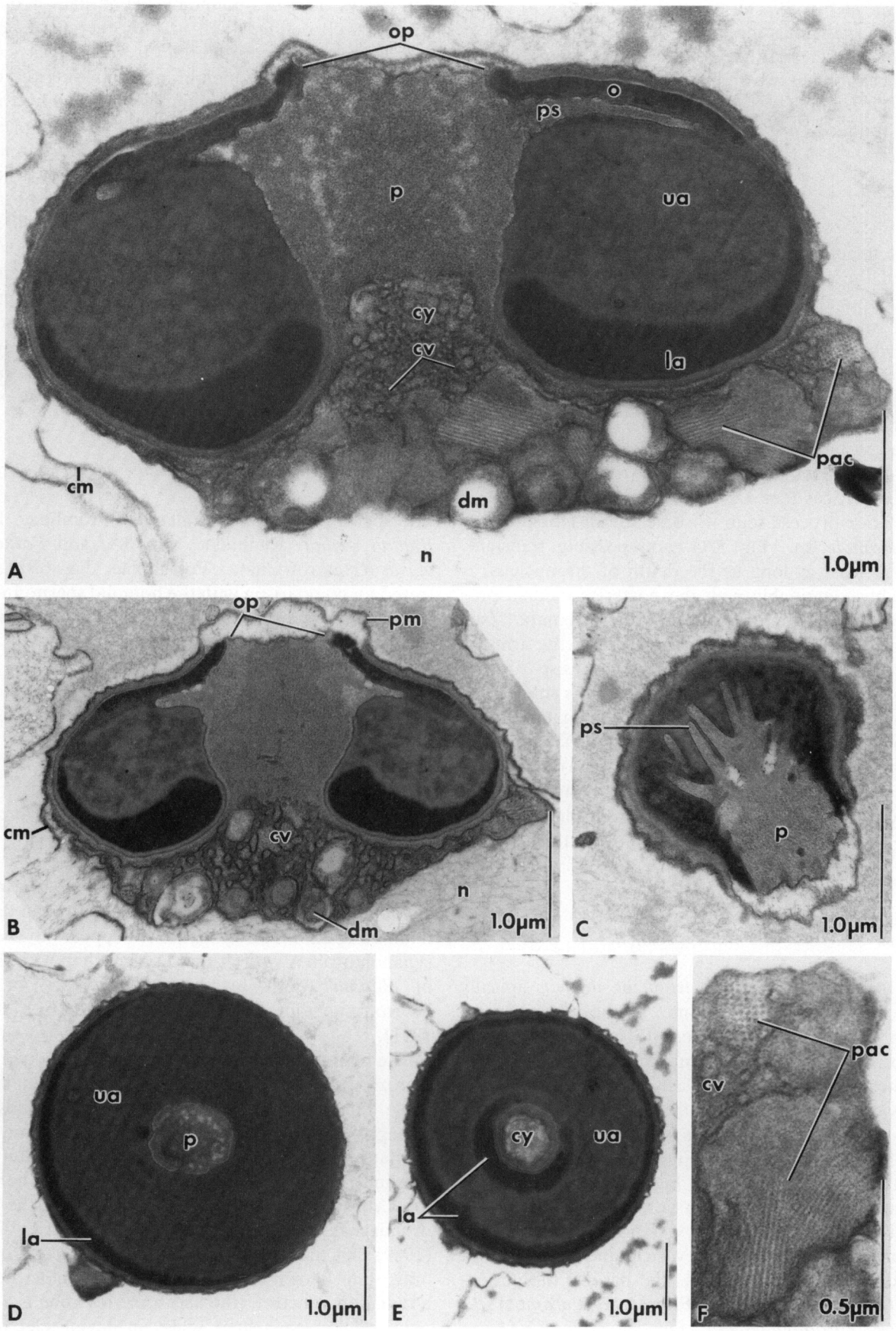

Fig. 3. Transmission electron micrographs of spermatozoa of *Paromola* sp.—*A*, *B*. Sagittal longitudinal sections.—*C*. Very oblique section showing radial spikes of head of perforatorium.—*D*. TS acrosome through base of perforatorium.—*E*. Through anterior extension of cytoplasm.—*F*. Detail of paracrystalline material in transformed mitochondria.

The radial spikes are supported by fibrous cores, radiating from the central core of the perforarium, shown for *Homola* sp. in Fig. 2C, in which there appears to be 12 spikes. The radial arrangement, as seen in transverse sections of the head of the perforatorium, is not entirely regular, occasionally two spikes arise from the same base (Figs 2B–D, *Homola* sp.; Fig. 3C, oblique, *Paromola* sp.; Fig. 4C, oblique, *Paromola petterdi*).

Nucleus

The nucleus posteriorly cups the acrosome–cytoplasm portion of the sperm (Figs 1, 2A, 3A, B, 4A, B, 5A). Its thickness is about one-third to one-half of that of the acrosome and it extends anteriorly as far as the equator of the acrosome. It is very irregular in form, sending out a few large processes laterally and posteriorly or these may not be apparent in a given longitudinal section. However, a cross-section of the nucleus at its junction with the postacrosomal cytoplasmic region (Fig. 2G, *Homola* sp.), shows the nucleus as a triradiate structure, with three vertices (see Discussion).

A posterior process seen in some sperm (for instance one of *Homola* sp., Fig. 5A), and possibly transient, which is at least as long as the depth of the nucleus, is questionably identifiable with the posterior median process of the Anomura–lower Heterotremata (see Discussion). No microtubules are present in the arms or elsewhere in the sperm. The chromatin consists of fine, diffusely arranged putative DNA fibrils but is so electron pale as scarcely to be visible. The nuclear material is in direct contact with the plasma membrane (the combined membrane being termed the cell membrane) and a discrete nuclear membrane is not visible. Anteriorly, the concavity of the nucleus is separated from the acrosome and, medianly, from the cytoplasm by a thick dense irregular membrane.

Cytoplasm centrioles and other organelles

The cell membrane continues from the nucleus apically over the surface of the acrosome, as the plasma membrane, to which it is closely adherent. No cytoplasm intervenes between the plasma membrane and the acrosome but at the anterior pole the plasma membrane is more or less widely separated from the acrosome membrane. There is some evidence that this apical separation is artefactual (Figs 2A, *Homola* sp.; Figs 3A, B, *Paromola* sp.; Figs 4A, B, *Paromola petterdi*; Fig. 5A, *Homola* sp.).

The large mass of cytoplasm lies in the hiatus at the hind end of the perforatorium, extends thinly along the posterior face of the acrosome vesicle and anteriorly for a short distance axially as far as the base of the perforatorium (Fig. 2A, *Homola* sp.; Figs 3A, B, *Paromola* sp.; Figs 4A, B, *Paromola petterdi; Fig. 5A, Homola* sp.; see also transverse sections, Figs 2F, 3E). It contains posteriorly situated subspherical bodies with dense bounding membranes, some of which have what appear to be vestigial cristae (e.g. *Paromola petterdi*, Figs 4A, B) and are therefore deduced to be degenerate mitochondria. In *Paromola* sp. (Figs 3A, F), the contents of the putative mitochondria in some sperm is replaced with paracrystalline arrays, and the bounding membrane of the bodies are less well defined than in the other two species but the paracrystalline material is not always evident (Fig. 3B). The dense membranes bounding the degenerate mitochondria are continuous with highly convoluted membranes which fill the bulk of the cytoplasm. The cytoplasm is separated from the perforatorium and acrosome by a similar dense membrane which is itself frequently infolded as part of the tortuous membranes and of those limiting the putative mitochondria. The irregular membranes bounding the posterior and anterior faces of the cytoplasm pass laterally to join, and apparently combine with, the cell membrane at the anterior limit of the nuclear cup, shortly behind the equator of the acrosome. Centrioles are probably normally present in the cytoplasm as one has been seen in an area of the cytoplasm devoid of convoluted membranes (Fig. 4B, *Paromola petterdi*).

Dromiid, raninid, and heterotreme sperm

The sperm of *Petalomera lateralis* (Dromiidae, Fig. 5B), *Ranina ranina* (Raninidae, Fig. 6A) and *Portunus pelagicus* (Heterotremata, Portunidae, Fig. 6B) are illustrated for comparison with the homolid sperm. In Fig. 5B, for *P. lateralis* an apical interruption, of the operculum, previously unrecognized, is shown.

Discussion

Comparison of homolid sperm with those of dromiids, Ranina, and heterotreme Brachyura

The spermatozoa of *Homola* sp., *Paromola petterdi* and *Paramola* sp. are very similar and constitute a distinctive homolid sperm. This nevertheless appears to share more synapomorphies with dromiid sperm than with the sperm of *Ranina* (both in the Podotremata) or of the heterotreme–thoracotreme assemblage (see Jamieson 1991).

The homolid spermatozoon differs markedly from spermatozoa of the Heterotemata–Thoracotremata assemblage but agrees with the sperm of dromiids, in the strongly anteroposteriorly depressed acrosome and the capitate form of the perforatorium. The capitate perforatorium is a major synapomorphy seen nowhere else in the Crustacea. It is noteworthy, in view of the origin of dromiaceans near the palinurids suggested by Glaessner (1969) that the acrosome of *Scyllarus chacei* provides the only other known case in Crustacea of an acrosome with a radiating structure (the acrosome ray zone is a different phenomenon on a finer scale) in having electron-dense rays (40 in number compared with only about 12 in *Homola* sp.) radiating from a dense disc which lies at the apex of the bell-shaped vesicle, under the plasma membrane, like the struts of an umbrella (McKnight & Hinsch 1986). The palinurid structure occurs in the

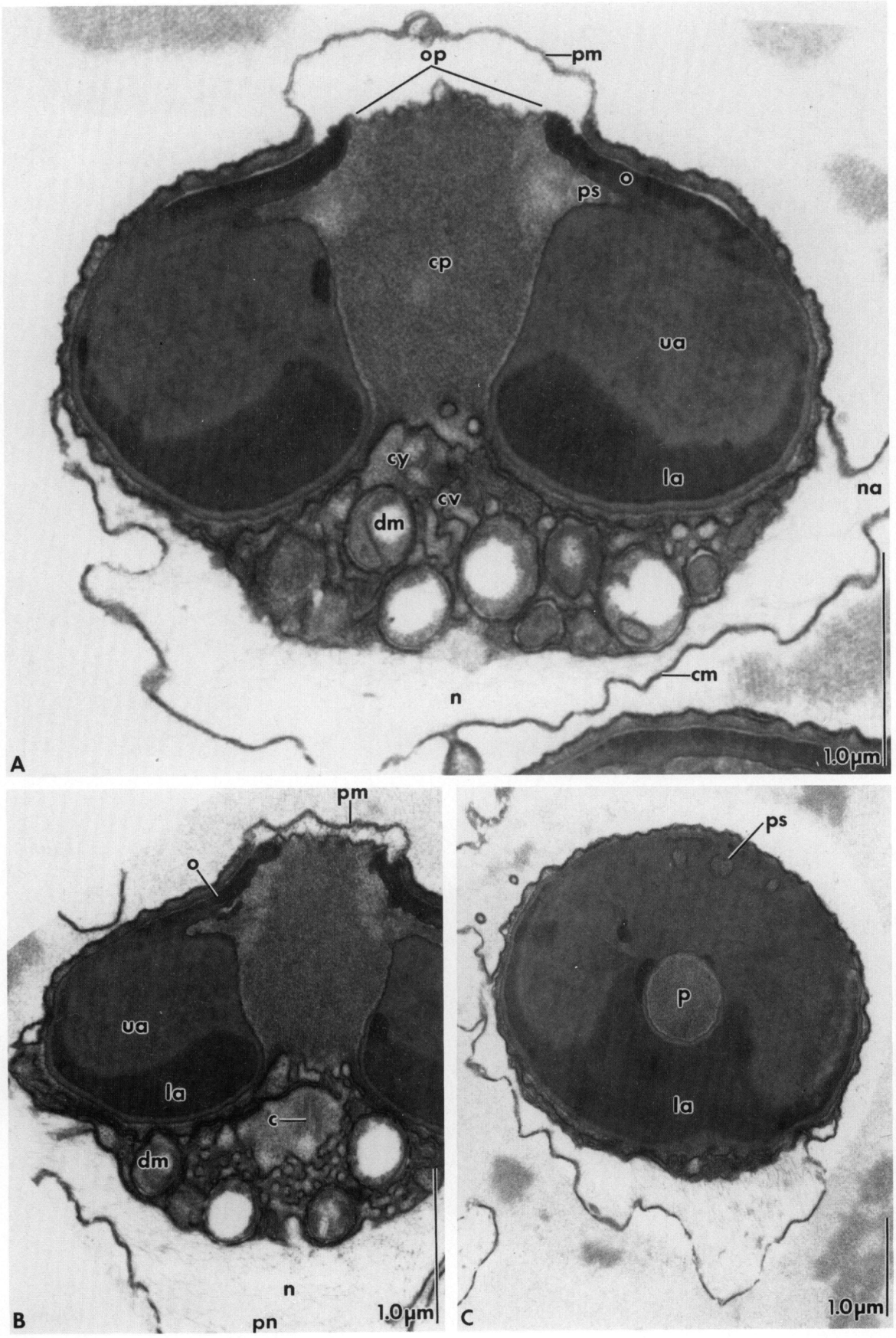

Fig. 4. Transmission electron micrographs of spermatozoa of *Paromola petterdi*.—*A*, *B*. Sagittal longitudinal sections.—*C*. Oblique TS through stalk of perforatorium and some of the radial spikes.