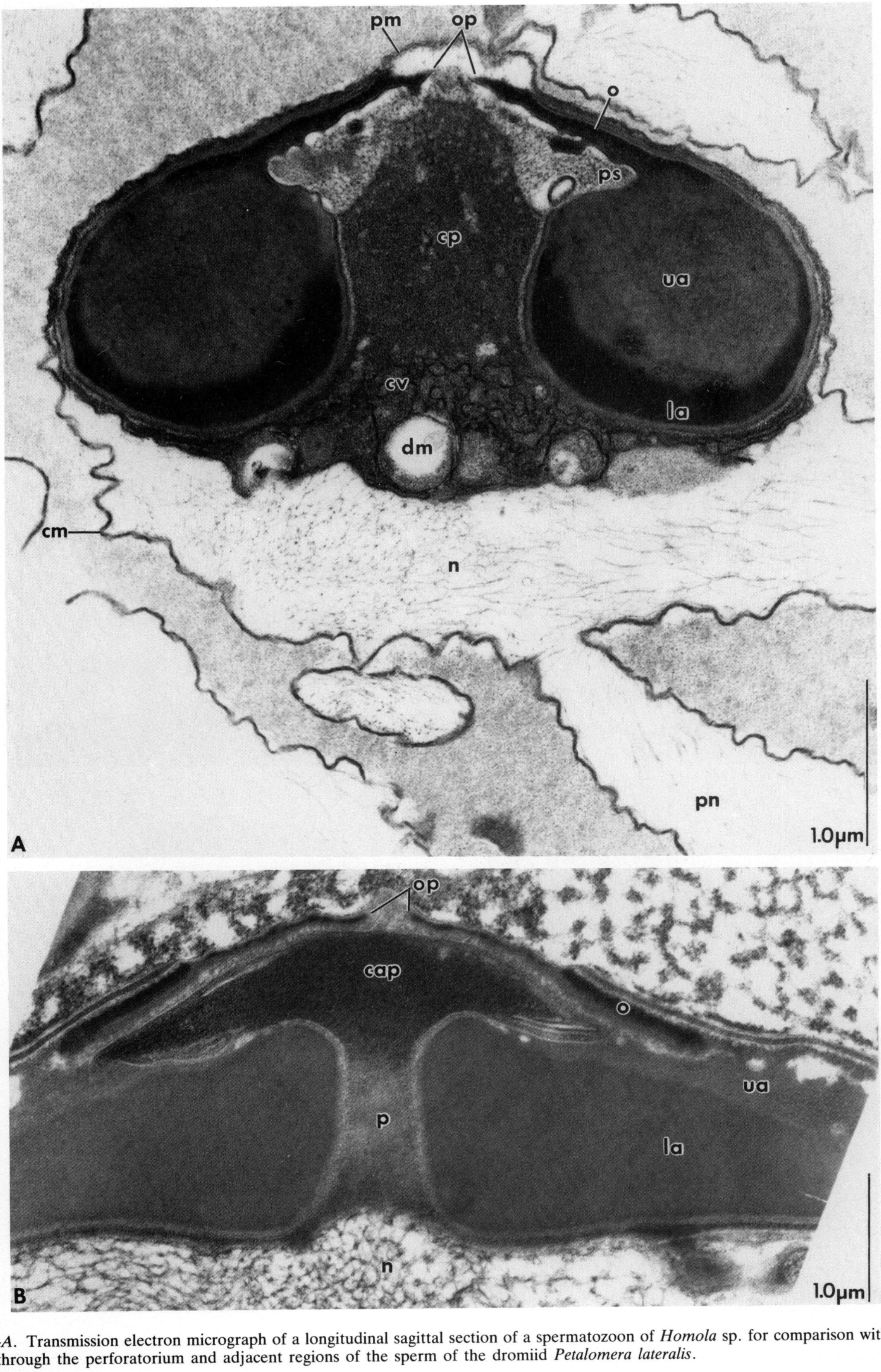

Fig. 5.—A. Transmission electron micrograph of a longitudinal sagittal section of a spermatozoon of *Homola* sp. for comparison with *B* a similar section through the perforatorium and adjacent regions of the sperm of the dromiid *Petalomera lateralis*.

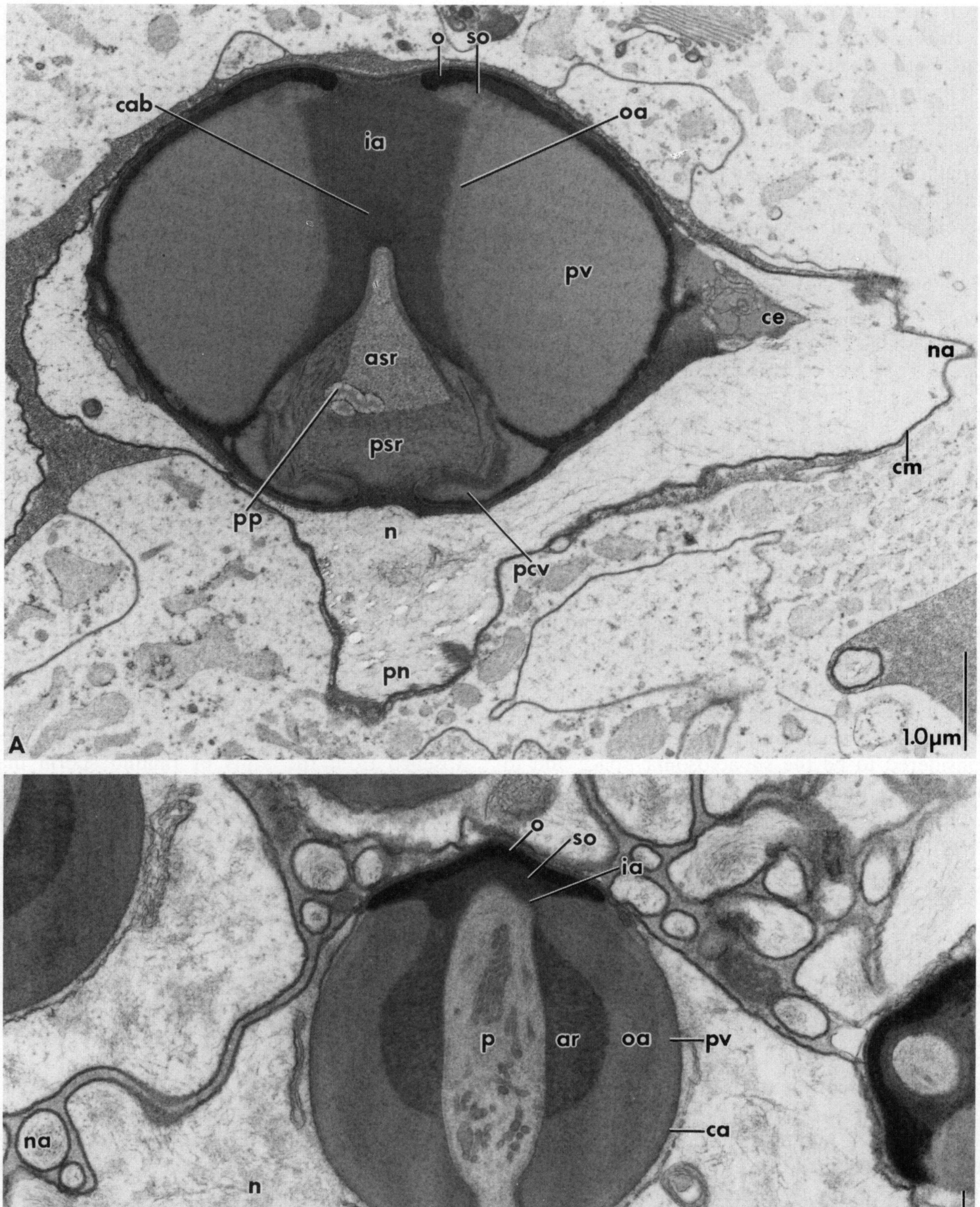

Fig. 6. Transmission electron micrograph of a sagittal longitudinal section of the spermatozoon of *A* the raninid *Ranina ranina* and *B* the portunid heterotreme *Portunus pelagicus*.

absence of a recognizable perforatorium and does not appear to be homologous with that in dromiids and homolids. Radiate structures more similar to, but again doubtfully homologous with, those of homolids are seen in the acrosome of the shrimp *Sicyonia ingentis* (see Kleve *et al.* 1980). In this shrimp there is a 'saucer-shaped plate' reminiscent of the head of the homolid capitate perforatorium. The unpaired anterior spike projecting at the tip of the shrimp acrosome vesicle is not seen in homolids.

Petalomera differs from homolids in that the acrosome is superficial on the nucleus, to which it presents an almost flat surface (see *Petalomera lateralis*, Jamieson 1990) whereas in homolids it is embedded approximately to its equator in the nucleus, though not as deeply embedded as in *Ranina* and heterotreme–thoracotreme crabs. However, in another dromiid, *Dromidiopsis edwardsi* Rathbun 1919, the acrosome is deeply embedded (Jamieson *et al.*, in prep.).

A broad area of the acrosome membrane at the anterior pole of the homolid acrosome is irregular (crenulated). In the dromiid *Petalomera* the central region of the operculum is also somewhat crenulate. In homolids, and as here shown to a lesser extent in *Petalomera* (and in *Dromidiopsis*) the operculum is interrupted centrally. In *Ranina* and Heterotremata the apical membrane is smooth; the operculum is apically interrupted in *Ranina* and in some Heterotremata.

Only in homolids does the perforatorium resemble the capitate perforatorium of dromiids in having a large anterolateral extension. In *Ranina* and Heterotremata–Thoracotremata the acrosome is penetrated by a broad central column. In *Ranina* the region of this considered to be the subacrosomal space and to be perforatorial is limited to a conical chamber which does not extend anterior of the equator of the acrosome. In Heterotremata the perforatorium forms a stout baton-like structure extending to the anterior end of the acrosome. The homolid perforatorium differs from that of dromiids in the spiked-wheel form of the anterior expansion, here interpreted as an autapomorphy for homolids.

Only in homolids does the acrosome, peripheral to the perforatorial chamber, resemble that of dromiids in being horizontally zonated (there is, however, both horizontal and concentric zonation in *Dromidiopsis*). In *Ranina* and Heterotremata–Thoracotremata the zonation is vertical and concentric. However, zonation in dromiids includes an acrosome ray zone not seen in homolids. The acrosomal rays also occur in the acrosomes of heterotremes, e.g. xanthids and portunids (Jamieson 1989*b*; Jamieson & Tudge 1990). Similar rays are, however, visible in published micrographs of the sperm of the astacids, *Pacifastacus leniusculus* (Dudenhausen & Talbot 1979) and *Cambarus* sp. (Anderson & Ellis 1967); and are well known in the sperm of hermit crabs (e.g. Hinsch 1980; Tudge 1992; Tudge & Jamieson 1991). They are therefore possibly plesiomorphic for reptantians.

There is no indication in homolids, dromiids or Heterotremata–Thoracotremata of the posterior subacrosomal region or of the posterior acrosomal chamber seen in *Ranina*.

Homolid sperm have irregular lateral arms but also (e.g. *Homolo* sp.), three radial nuclear vertices, little more than triangular projections, constituting short arms. Homolid arms contain only nuclear material as in *Ranina*, higher heterotremes and the Thoracotremata. Three 'stubby radial arms', lacking microtubular bundles, occur in *Dromidia antillensis* and apparently *Dromia vulgaris* (see Brown 1966; Grobben, 1878, respectively; both species junior synonyms of *Dromia personata* (Linné, 1758)) and are represented by three nuclear vertices in *Dromidiopsis edwardsi* (Jamieson *et al.*, in prep.). In *Petalomera lateralis*, although the ellipsoidal to subspherical nucleus frequently shows irregularities or distortions, no discrete arms were recognized ultrastructurally. Examination of further material of *Petalomera* is required, nevertheless, as it is possible that the three diminutive triangular prominences seen in *Dromidiopsis* are present. However, the plesiomorphic condition for heterotremes, seen in majiids, is the presence of arms which are nuclear but also contain bundles of microtubules. This is presumably the plesiomorphic condition for Heterotremata as it is also seen in other reptants, for instance, nephropids (see Talbot & Chanmanon 1980). Absence in brachyurans of purely microtubular arms is a notable distinction from anomurans such as the Paguroidea. Paguroid sperm otherwise have strong points of resemblance to heterotreme sperm which Jamieson (1993*b*) has considered indicative of relationship.

It is probable that absence of microtubules in the nuclear arms of dromiacean sperm is an independent loss representing a dromiid–homolid (and questionably raninid) synapomorphy. Absence of microtubules in the arms of higher heterotremes is clearly an independent and apomorphic loss from the majid-like condition. Absence from the arms of raninid sperm may be an independent development but could conceivably be synapomorphic with dromiids and homolids. We do not find evidence for a close raninid–dromiacean link.

Outside the Reptantia, arms questionably homologous with those of reptants have been reported for the sperm of the caridean shrimp *Rhynchocinetes typus* (Barros *et al.* 1986) and in branchiopods and Phyllocarida where they do not involve prolongation of the nuclear membrane, and are therefore probably not homologous with the thus characterized arms of decapods (see Jamieson 1991).

Similar in constitution to the nuclear arms is a posterior median process seen (transiently?) in homolid sperm, in *Ranina* and in majiids but absent from dromiid sperm. If homologous, this is, however, a symplesiomorphy as is seen in at least some paguroids (in some porcellanids it contains microtubules).

Presence of most of the cytoplasm (including tortuous membranes and degenerating mitochondria) below the acrosome is a homolid feature not seen in *Petalomera* (though seen in *Dromidia antillensis* with an intermediate condition in *Dromidiopsis*), nor in *Ranina* and the heterotreme–thoracotreme assemblage. In the absence of data on dynomenid and cyclodorippoid sperm it is difficult to establish that subacrosomal cytoplasm is a symplesiomorphy of dromiids and therefore of dromiids and homolids. In *Ranina* and the heterotreme–thoracotreme assemblage the small amount of cytoplasm is predominantly lateral to the acrosome with, in some heterotremes, a trace posteriorly. In *Petalomera* there is the merest vestige of cytoplasm beneath the acrosome.

Centrioles have been observed in the cytoplasm posterior to the acrosome in homolid sperm. They are unknown in dromiids and raninids and are variable in occurrence in heterotremes. Their greatest development is seen in *Potamonautes* (Jamieson 1993*a*) and *Potamon* (Jamieson & Guinot, unpubl.), in the Heterotremata, in which they show a unique elongation. The presence of short centrioles is symplesiomorphic for brachyurans and is seen in many other decapods.

Phylogenetic and taxonomic implications

Similarities of homolid and *Petalomera* sperm noted above, especially the capitate perforatorium, the partly, at least, horizontal zonation of the acrosome vesicle, and the depressed form of the acrosome, support inclusion of the Dromiidae and Homolidae in a single grouping, the Podotremata. Until the sperm of dynomenids and cyclodorippoids are known, it will not, however, be possible to test the validity of the proposition of Guinot (1977, 1978, 1991), illustrated in Fig. 7, that homolids should be removed from the Dromiacea and placed, with cyclodorippids and raninoids, in the Archaeobrachyura.

In Fig. 7 the phylogeny of brachyurans suggested from non-spermatozoal characters by Guinot (1978, 1979) and by Guinot & Tavares (in prep.) is used as a framework for summarizing sperm structure in the investigated groups of crabs. Sperm ultrastructure has supported placing dromiids and homolids in the same clade but, in the absence of data on dynomenids and cyclodorippoids, does not contraindicate relegation of a homolid–cyclodorippoid subclade to the Archaeobrachyura, with or without the raninoids. The apparently apomorphic nature of the homolid perforatorium relative to dromiids suggests that homolids were a relatively late offshoot of the dromiacean stock.

It must be stressed, however, that there is very little in the ultrastructure of homolid or dromiid sperm to associate them with either the Raninidae or the heterotreme–thoracotreme assemblage. The major finding of the present study is the apparent close relationship of homolids and dromiids as evidenced particularly by the shared capitate perforatorium, by the horizontal zonation of the acrosome vesicle and, less cogently, the absence of microtubules in the arms, and the distinc-

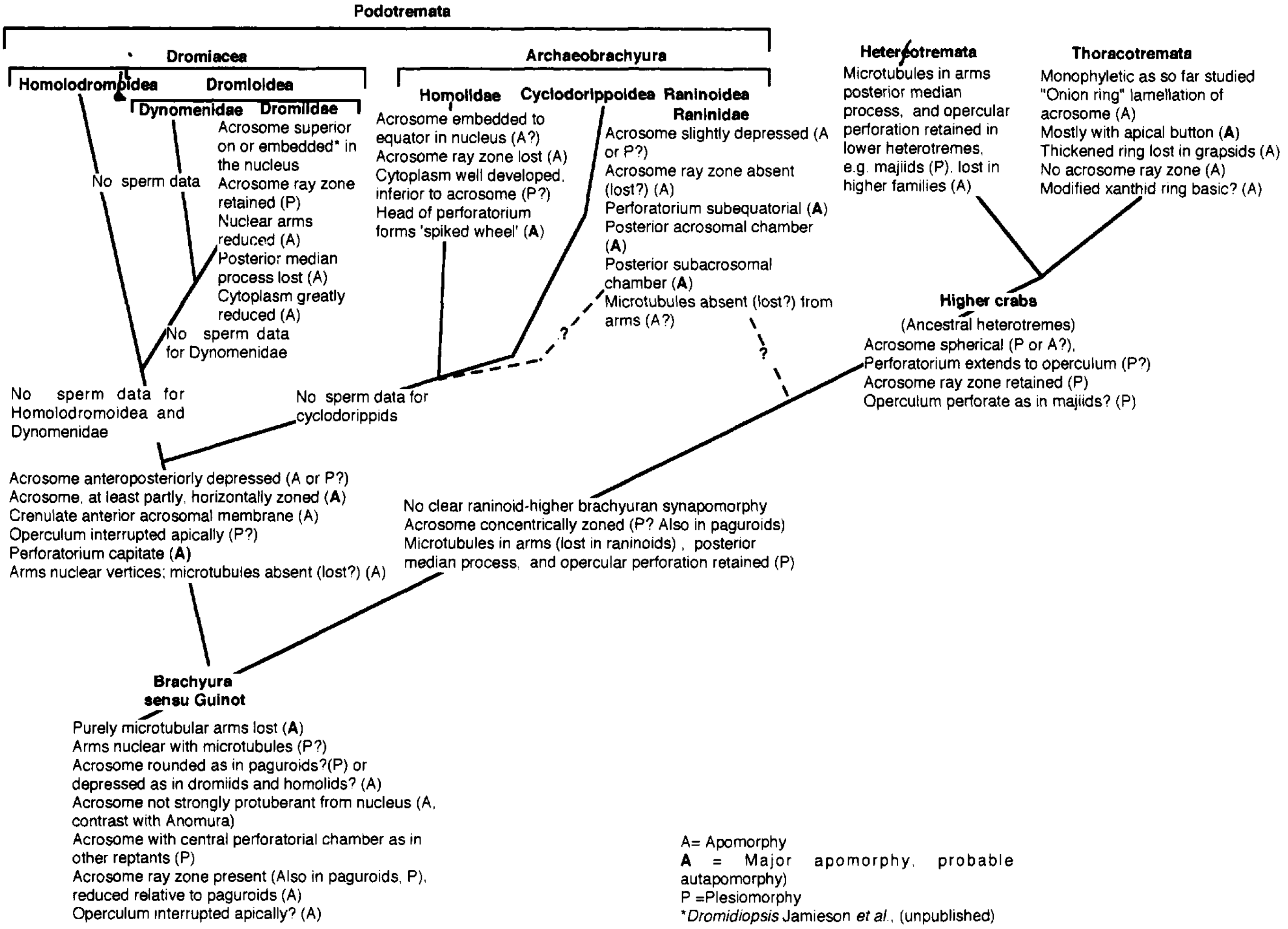

Fig. 7. Phylogeny of the Brachyura (*sensu lato*) after the classification of Guinot (1978, 1979, and in prep.), with spermatozoal characteristics superimposed. An attempt is made to distinguish apomorphies from plesiomorphies but more definitive polarization of characters must await a comprehensive review of anomuran and brachyuran spermatozoa. Note that if the Raninoidea are excluded from the Podotremata these and the Archaeobrachyura become paraphyletic groups.

tiveness of their sperm from those of raninids and heterotreme–thoracotremes.

The homogeneity of spermatozoal ultrastructure in the three species *Homola* sp., aff. *Paromola petterdi* and *Paromola* sp. provides few if any grounds for separating the three entities. Separation of these taxa as three distinct genera on the basis of somatic morphology has been argued by Guinot & Richer de Forges (in press). Spermatozoal homogeneity at the familial level, here the distinctive homolid type, is seen also in other crabs: dromiids (Brown 1966; Jamieson 1990), majiids (Hinsch 1973), xanthids (Jamieson 1989*b*), portunids (Jamieson 1991; Jamieson & Tudge 1990), and grapsids (Jamieson 1991), but species specific, if sometimes only metric, differences are observable and may yet prove to have taxonomic value. It remains to be seen whether small differences noted between homolid species, such as the more homogeneous composition of the perforatorium and the paracrystalline mitochondrial arrays in *Paromola* sp., or the lesser, though still strong depression of the acrosome in *Paromola petterdi* will prove to be reliable taxonomic characters for placement of these in distinct genera.

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Abbreviations Used in the Figures

ar	acrosome ray zone
asr	anterior subacrosomal region
c	centriole
ca	capsule
cab	central acrosomal body
cap	capitate region of perforatorium
ce	cytoplasmic extension into arm
cm	cell membrane
cp	core of perforatorium
cv	convoluted membranes
cy	cytoplasm
dm	degenerating mitochondrion
eo	extensions of the operculum into head of perforatorium
ia	inner acrosomal zone
ine	disrupted inner nuclear envelope
la	lower acrosomal zone
n	nucleus
na	nuclear arm
o	operculum
oa	outer acrosomal zone
op	apical perforation of operculum
p	perforatorium
pac	paracrystalline material
pcv	posterior chamber of acrosomal vesicle
pm	plasma membrane
pn	posterior median process of nucleus
pp	putative perforatorium
ps	perforatorial spike
psr	posterior subacrosomal region
pv	peripheral contents of acrosome vesicle
so	subopercular zone
tr	thickened ring
ua	upper acrosomal zone

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