

# Ultrastructure and Phylogeny of the Spermatozoa of the Infraorders Thalassinidea and Anomura (Decapoda, Crustacea)

*Christopher C. TUDGE*

Zoology Department, University of Queensland  
Brisbane, Q 4072, Australia

## ABSTRACT

The spermatozoal morphology of 62 species of anomuran and thalassinidean decapod crab (including many species for which the spermatozoal ultrastructure is previously undescribed) is compared at the light and electron microscope level. Relationships between taxa are postulated on the basis of shared spermatozoal characters and comparisons made with existing ideas about the relationships and evolution of these taxa. Pronounced spermatozoal differences between representatives of some families in the Infraorder Thalassinidea support the separation and reclassification of this group into three superfamilies. In contrast, within the anomuran superfamily Paguroidea, the families Paguridae, Parapaguridae, Diogenidae and Coenobitidae are shown to be united by a suite of ultrastructural spermatozoal characters. Each of these families, however, can be distinguished by characteristic spermatozoal features. The anatomically diverse family Diogenidae exhibits a range of sperm morphologies intermediate between the Paguridae and Coenobitidae which may indicate a diphyletic origin for this family. The families Galatheidae and Porcellanidae, within the superfamily Galatheoidea, each show a set of distinctive spermatozoal characters, but share very few characters.

## RÉSUMÉ

**Ultrastructure et phylogénie des spermatozoïdes des sous-ordres Thalassinidea et Anomura (Decapoda, Crustacea).**

La morphologie du spermatozoïde de 62 espèces de Crustacés Décapodes Anomoures et Thalassinides, (y compris de nombreuses espèces dont le spermatozoïde n'avait jamais été décrit), est comparée en microscopie photonique et électronique. Les relations entre les taxons sont postulées sur la base de caractères spermatologiques partagés et des comparaisons sont faites avec les idées pré-existantes concernant leurs relations phylétiques et leur évolution. Les différences importantes entre les spermatozoïdes des représentants de quelques familles du sous-ordre Thalassinidea soutiennent la séparation et la re-classification de ce groupe en trois super-familles. Au contraire, à l'intérieur de la super-famille des Paguroidea, on montre que les familles Paguridae, Parapaguridae, Diogenidae et Coenobitidae sont unies par un ensemble de caractères ultrastructuraux du spermatozoïde. Toutefois, chacune de ces familles peut être distinguée par des caractéristiques spermatologiques. La famille Diogenidae, qui est anatomiquement diversifiée, montre des morphologies spermatiques intermédiaires entre les Paguridae et les Coenobitidae, qui pourrait indiquer le diphylétisme de son origine. Les familles Galatheidae et Porcellanidae, membres de la super-famille Galatheoidea, montrent chacune un ensemble de caractères spermatologiques distinctifs, mais ont peu de caractères en commun.

---

TUDGE, C. C., 1995. — Ultrastructure and phylogeny of the spermatozoa of the infraorders Thalassinidea and Anomura (Decapoda, Crustacea). In: JAMIESON, B. G. M., AUSIO, J., & JUSTINE, J.-L. (eds), *Advances in Spermatozoal Phylogeny and Taxonomy. Mém. Mus. natn. Hist. nat.*, **166** : 251-263. Paris ISBN : 2-85653-225-X.



Within the order Decapoda, the infraorder Anomura has undergone considerable revision since its introduction [27]. Classifications of the Anomura such as those of GLAESSNER [17] and BORRADAILE [3], recognize the four superfamilies, Thalassinoidea, Paguroidea, Galattheoidea and Hippoidea. More recently the thalassinoids have been excluded from the Anomura and the constituent anomuran superfamilies redefined as the Paguroidea, Lomoidea, Galattheoidea and Hippoidea [30, 31].

Some significant taxonomic changes have been proposed for the infraorder Thalassinidea and the group now comprises three superfamilies and is considered a monophyletic taxon, distinct from the Anomura [40]. In the past the thalassinids have been linked with the anomurans on the basis of larval morphology [18, 26], and adult somatic characters [28]. The thalassinids are considered to be an important pivotal group in the evolution and phylogeny of the other decapod infraorders [2, 6].

The superfamily Paguroidea consists of the families, Coenobitidae, Diogenidae, Paguridae, Parapaguridae, Pylochelidae and Lithodidae [30]. All except the Lithodidae are considered true hermit crabs [5] but recently it has been shown that the lithodids may have close links with the genus *Pagurus* in the Paguridae [13].

The superfamily Lomoidea contains the monospecific genus *Lomis* in the family Lomidae. Once considered a symmetrical hermit crab [4], this enigmatic crab has since been elevated to its own family and superfamily [29, 34] but continues to be problematic in regard to its relationship to the remainder of the Anomura [28].

The superfamily Galattheoidea contains the families Aeglidae, Chirostylidae, Galatheididae and Porcellanidae, of which the Aeglidae, containing the single genus *Aegla*, are ecologically (restricted to freshwater) and morphologically distinct [28].

The superfamily Hippoidea (the mole crabs) contains only two families, Albuneidae and Hippidae, which have been variously allied with the other families of the Anomura but appear to be very distinct. They have been postulated to be more closely related to the thalassinoids than to the Anomura [28].

The species of thalassinidean and anomuran crabs studied for spermatozoal morphology (light or transmission electron microscopy) and published up to 1994 are listed in Table 1. This list comprises 32 species from 17 genera in 9 families. A further 30 species have been investigated for spermatozoal morphology by the author (Table 2) and this brings the total number of thalassinidean and anomuran taxa for which the spermatozoal structure is known to 62 species from 33 genera in 15 families. In addition to the listed publications, the ultrastructure of anomuran spermatozoa is briefly covered in several general crustacean sperm reviews [16, 23, 25].

#### MATERIALS AND METHODS

The crab specimens were collected from a wide range of localities including Australia, the South-West Pacific, the Mediterranean and European waters. The testes and ducts of the vasa deferentia were removed from the crabs and fixed in cold (4°C) glutaraldehyde for a minimum of 2 hours, after which the remainder of the standard techniques for transmission electron microscopy [44] were carried out. This procedure was undertaken for all species except for *Thalassina squamifera*, which was deep frozen, thawed and fixed in neutral buffered formalin before removal of the testes and then subjected to the standard TEM fixation procedure. Micrographs were taken on Hitachi H-300, JEOL 100-s and Hitachi H-600 transmission electron microscopes at 80, 60 and 75 kV respectively.

#### RESULTS

##### *Infraorder Thalassinidea*

The spermatozoa of the three investigated taxa in this group are each different in morphology, although the sperm cells of *Callianassa australiensis* and *Axius glyptocercus* are more similar to each other than to those of *Thalassina squamifera*. The sperm cells of

TABLE 1. — Thalassinidean and anomuran taxa previously investigated for spermatozoal morphology.

Infraorder Thalassinidea	
Superfamily Callianassoidea	
Family Upogebiidae	
<i>Upogebia pusilla</i>	[24] (as <i>Gebia littoralis</i> )
Superfamily Axioidea	
Family Calocarididae	
<i>Calocaris macandreae</i>	[41]
Infraorder Anomura	
Superfamily Paguroidea	
Family Coenobitidae	
<i>Birgus latro</i>	[23; 44; 45]
<i>Coenobita clypeatus</i>	[20; 21; 44]
<i>Coenobita rugosus</i>	[32]
<i>Coenobita variabilis</i>	[44] (as <i>C. spinosus</i> )
Family Diogenidae	
<i>Clibanarius corallinus</i>	[23; 44]
<i>Clibanarius erythropus</i>	[24] (as <i>C. misanthropus</i> ); [46]
<i>Clibanarius longitarsus</i>	[14; 15; 32]
<i>Clibanarius nathi</i>	[32]
<i>Clibanarius taeniatus</i>	[44]
<i>Clibanarius virescens</i>	[44]
<i>Dardanus arrosor</i>	[24] (as <i>Pagurus striatus</i> )
<i>Dardanus crassimanus</i>	[44]
<i>Dardanus megistos</i>	[32] (as <i>Pagurus punctulatus</i> )
<i>Diogenes custos</i>	[44]
<i>Diogenes miles</i>	[15]
<i>Paguristes oculatus</i>	[24] (as <i>P. maculatus</i> )
Family Lithodidae	
<i>Lithodes maja</i>	[41]
Family Paguridae	
<i>Pagurus bernhardus</i>	[7-12; 35-39; 41] (as <i>Eupagurus bernhardus</i> )
<i>Pagurus excavatus</i>	[24] (as <i>Eupagurus angulatus</i> )
<i>Pagurus prideaux</i>	[24] (as <i>Eupagurus prideauxii</i> )
Superfamily Galattheoidea	
Family Galatheididae	
<i>Allogalatea elegans</i>	[23] (as <i>Allogalatea</i> sp.)
<i>Galathea squamifera</i>	[24; 41]
<i>Galathea strigosa</i>	[24]
<i>Munida rugosa</i>	[24]
<i>Pleuroncodes planipes</i>	[22]
Family Porcellanidae	
<i>Petrolisthes lamarckii</i>	[23]
<i>Pisidia longicornis</i>	[41] (as <i>Porcellana longicornis</i> )
Superfamily Hippoidea	
Family Hippidae	
<i>Emerita analoga</i>	[48-52]
<i>Emerita asiatica</i>	[43]
<i>Emerita talpoida</i>	[1; 33]

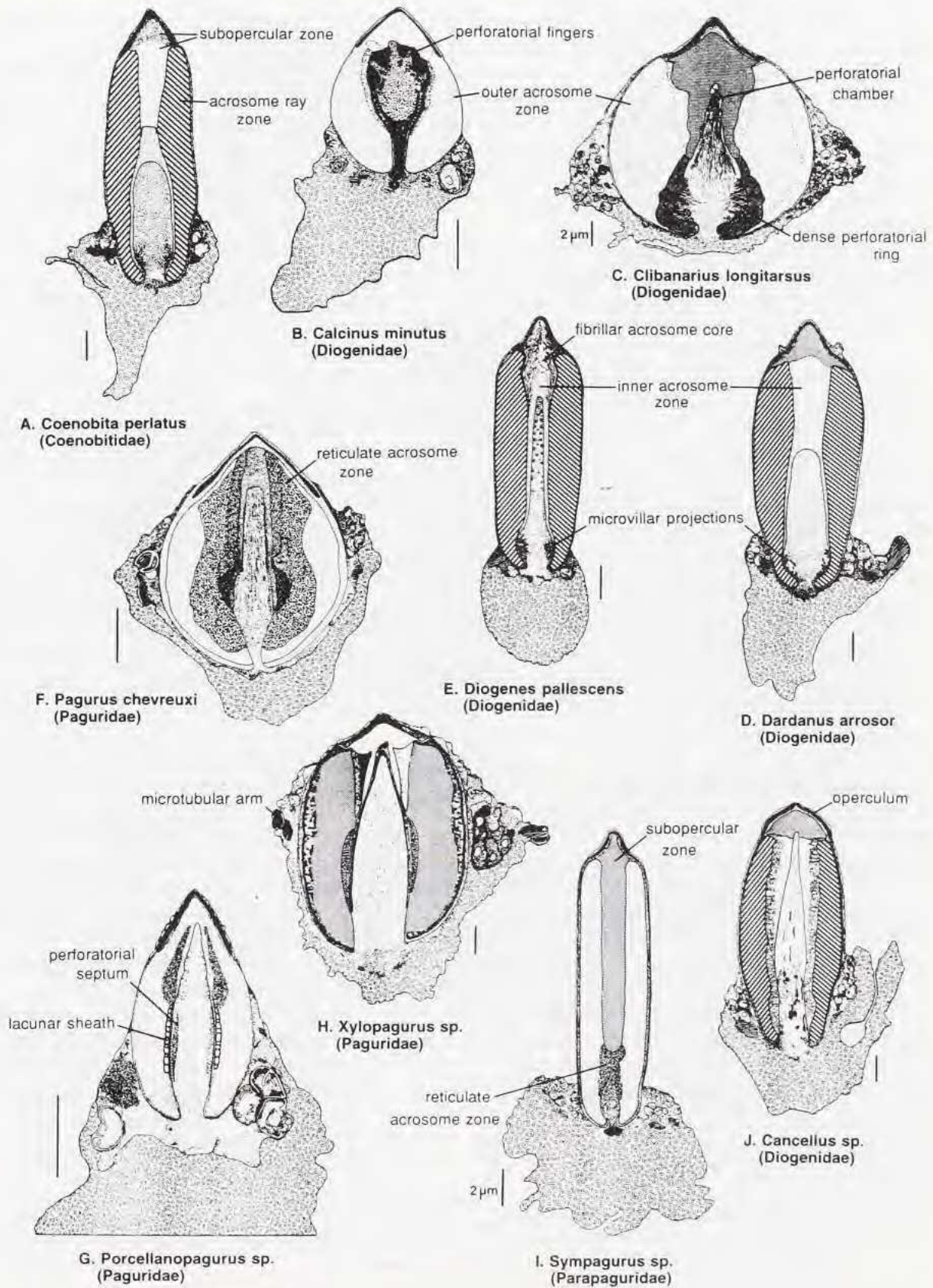


TABLE 2. — New thalassinidean and anomuran species investigated by the author for spermatozoal morphology.

Infraorder Thalassinidea	<i>Dardanus</i> sp.
Superfamily Thalassinoidea	<i>Diogenes pallescens</i>
Family Thalassinidae	G. n. sp. n.(cf. <i>Trizopagurus strigimanus</i> )
<i>Thalassina squamifera</i>	Family Paguridae
Superfamily Callianassoidea	<i>Pagurus chevreuxi</i>
Family Callianassidae	<i>P. hirtimanus</i>
<i>Callianassa australiensis</i>	<i>Porcellanopagurus</i> sp.
<i>C. arenosa</i>	<i>Xylopagurus</i> sp.
Superfamily Axioidea	Family Parapaguridae
Family Axiidae	<i>Sympagurus</i> sp.
<i>Axius glyptocercus</i>	Superfamily Lomoidea
Infraorder Anomura	Family Lomidae
Superfamily Paguroidea	<i>Lomis hirta</i>
Family Coenobitidae	Superfamily Galatheoidea
<i>Coenobita brevimanus</i>	Family Chirostylidae
<i>C. perlatus</i>	<i>Eumunida sternomaculata</i>
<i>C. purpureus</i>	<i>Uroptychus</i> sp.
Family Diogenidae	Family Galatheidae
<i>Calcinus gaimardii</i>	<i>Munida</i> sp.
<i>C. laevimanus</i>	<i>Munidopsis</i> sp.
<i>C. minutus</i>	Family Porcellanidae
<i>Cancellus</i> sp.	<i>Aliaporcellana suluensis</i>
<i>Dardanus lagopodes</i>	<i>Petrolisthes armatus</i>
<i>D. scutellatus</i>	<i>Polyonyx transversus</i>
	Superfamily Hippoidea
	Family Hippidae
	<i>Hippa pacifica</i>

*C. australiensis* and *A. glyptocercus* are spherical with prominent microtubular spines (probably four) radiating from the equatorial region. The sperm cell can be divided into two hemispheres, with the upper containing the cytoplasmic organelles and an electron-dense acrosome vesicle with operculum, while the lower hemisphere is composed of the nucleus (Fig. 2a). The microtubular spines originate in the nucleus and appear to pass completely through it. *A. glyptocercus* differs from *C. australiensis* in having a large columnar invagination (perforatorial chamber) penetrating the sperm cell from the posterior or lower pole to a subterminal position below the operculum (Fig. 2a). The spermatozoa of *T. squamifera* differs markedly in being composed of a large, ovoid, concentrically zoned acrosome vesicle, capped by a tri-layered operculum and posteriorly embedded in a ring of cytoplasm and nucleus (Fig. 2b). A number of microtubular arms originate in the posterior nucleus. The acrosome vesicle is penetrated posteriorly by a columnar perforatorial chamber which terminates below the operculum and appears to have an electron-dense thickened ring around its base.

FIG. 1. — A-J: Semidiagrammatic representations of longitudinal sections of hermit crab spermatozoa. Homologous regions between sperm cells are similarly shaded. Drawings based on tracings of micrographs. Scale bars = 1  $\mu$ m (except where indicated).





*Infraorder Anomura*

*Family Coenobitidae.* The spermatozoa of *Birgus latro* and the six investigated species in the genus *Coenobita* are all very similar in morphology [23, 44, 45]. The concentrically zoned acrosome vesicle is a large and oblong-ovoid (*Birgus*) to cylindrical (*Coenobita*) structure, penetrated posteriorly by a columnar perforatorial chamber in which the walls are drawn out into microvillar projections (Fig. 3a). The anterior pole of the acrosome vesicle is capped by a domed operculum, below which a divided subopercular zone occurs (Fig. 1a). The acrosome is largely composed of an acrosome ray zone which has the appearance of radiating dark and light bands (Fig. 3b). The acrosome vesicle is cupped posteriorly by the cytoplasm (with three microtubular arms) and nucleus.

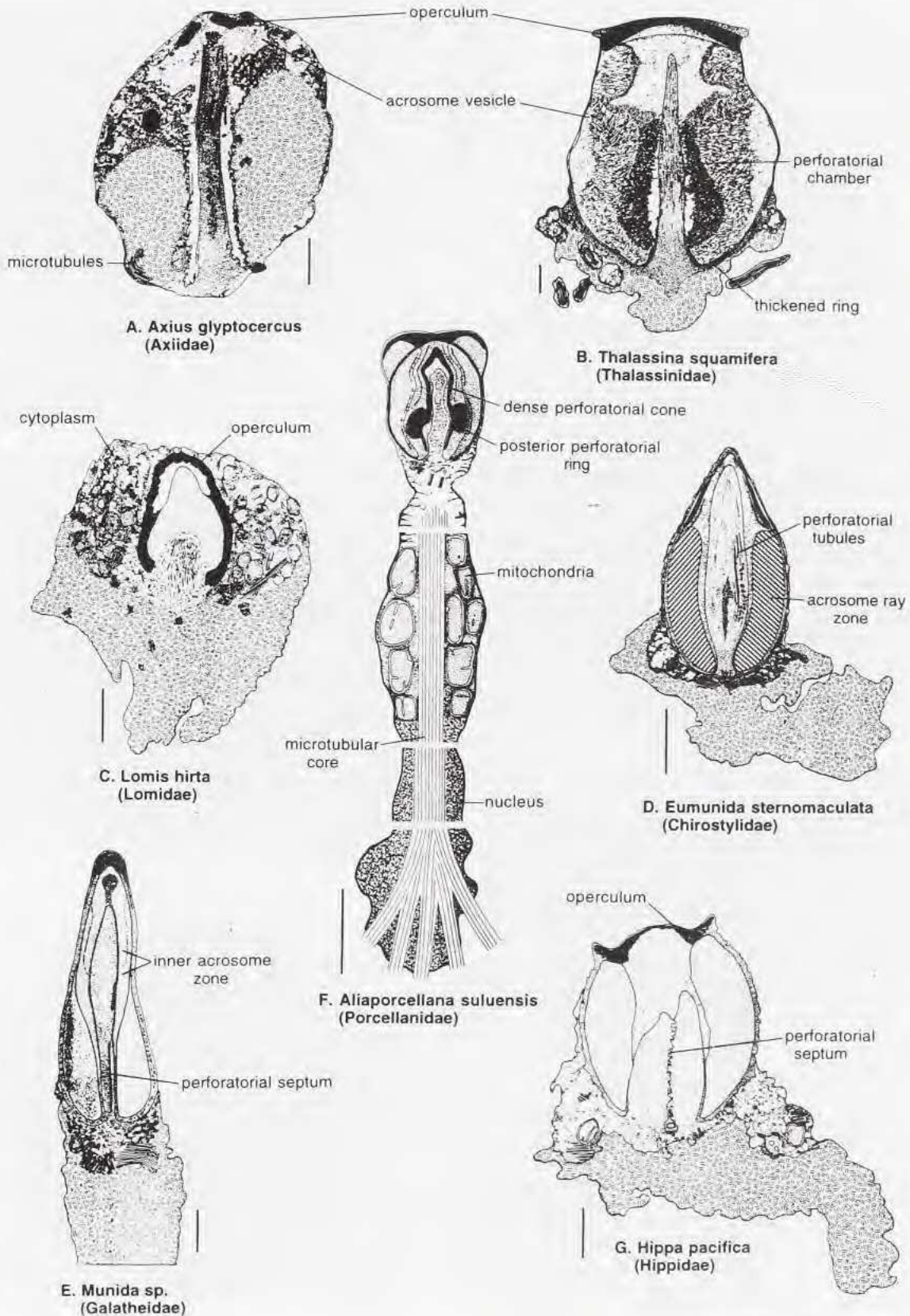
*Family Diogenidae.* The spermatozoa in the genus *Calcinus* are composed of a spherical acrosome vesicle, capped by a domed operculum, and posteriorly penetrated by a perforatorial chamber (Fig. 1b). The acrosome is embedded in the cytoplasm and nucleus and the perforatorial chamber walls project laterally to form short microvillar projections. An autapomorphy for this genus is the splitting of the anterior end of the perforatorial chamber into two or more fingers (Fig. 3c). The genus *Cancellus* has a spermatozoon with a cylindrical acrosome vesicle with a conspicuous acrosome ray zone, which is penetrated by a large tapering perforatorial chamber (Fig. 1j). Although perforatorial tubules are present in the chamber, there do not appear to be any microvillar projections and the operculum is unique among the paguroids in having a central perforation (Fig. 3d). The spermatozoa of the genus *Clibanarius* have an ovoid acrosome vesicle penetrated by a perforatorial chamber with microvillar projections but the chamber is distinctive in having a bulbous posterior region and a thin anterior projection. A dense ring (autapomorphy) occurs around the bulbous region of the perforatorial chamber (Fig. 1c). The sperm cells of the genus *Dardanus* are similar to the spermatozoa of the coenobitids but the acrosome vesicle (with conspicuous acrosome ray zone) (Fig. 3b) is generally shorter and more ovoid in shape and the subopercular zone is not divided into two distinct regions (Fig. 1d). The spermatozoa of the genus *Diogenes* are characterised by modification of the inner acrosome zone into a fibrillar core structure. The perforatorial chamber possesses microvillar projections and has the posterior bulb and anterior projection, like in clibanarids, but there is a prominent acrosome ray zone as in the coenobitids and dardanids (Fig. 1e).

*Family Paguridae.* The spermatozoa of the genus *Pagurus* lack microvillar projections in the perforatorial chamber, generally have ovoid acrosome vesicles with one or more reticulated acrosome zones (Fig. 3e) and the perforatorial chamber has a bulbous posterior region and a tapered anterior projection (Fig. 1f). *Porcellanopagurus* spermatozoa have a similarly shaped acrosome vesicle and perforatorial chamber (without microvillar projections) to *Pagurus* but the bulbous region of the perforatorial chamber has the walls sculpted into longitudinal septa and is surrounded by a vesiculated (lacunar) sheath (Fig. 1g). The spermatozoa of *Xylopagurus* differ from the other pagurids in having the microtubular arms emerging from the cytoplasm in the anterior part of the sperm cell and not posteriorly (this also differs from all other paguroids) and in possessing a larger, more cylindrical acrosome vesicle with unusual zonation (Fig. 1h).

*Family Parapaguridae.* The spermatozoa of *Sympagurus* share the bulbous shape of the posterior region of the perforatorial chamber, the lack of microvillar projections and the presence of a reticulated acrosome zone with members of the family Paguridae but differ in having the acrosome vesicle extended anteriorly to more than three times the length of any pagurid (Fig. 1i).

FIG. 2. — A-H: Semidiagrammatic representations of longitudinal sections of thalassinidean and anomuran crab spermatozoa. Homologous regions between sperm cells are similarly shaded. Drawings based on tracings of micrographs. Scale bars = 1  $\mu$ m.







*Family Lomidae.* The only representative in this family, *Lomis hirta*, has a spermatozoal morphology which is different from that of all other anomurans. The sperm cell is irregular, but basically globular, with one to three vertices which may be extended into microtubular arms (two arms have been observed in a single sperm but often three vertices are apparent). The acrosome vesicle is an inverted cup shape, penetrated by a perforatorial chamber, and is completely embedded in the cytoplasm. A discontinuous, electron-dense zone (interpreted as the operculum) extends around the entire acrosome vesicle (Fig. 2c).

*Family Chirostylidae.* The investigated genera in this family, *Eumunida* and *Uroptychus*, have spermatozoa with a spherical to ovoid acrosome vesicle, capped by a domed operculum and penetrated by a perforatorial chamber. The walls of the perforatorial chamber lack microvillar projections, but some perforatorial tubules are present in *Eumunida* (Fig. 2d). An acrosome ray zone is present in the posterior region of the acrosome vesicle in both.

*Family Galatheidae.* The spermatozoal morphology of *Allogalatea*, *Munida* and *Munidopsis* differs slightly in each species, but there are some characteristic features of the family. The acrosome vesicles are elongate and generally cylindrical, are capped by a domed operculum and penetrated for most of their length by a perforatorial chamber. The inner acrosome zone is divided into two regions of differing electron-density, the outer acrosome zone is situated posteriorly in the acrosome vesicle, and longitudinally arranged perforatorial septa are present in the posterior region of the perforatorial chamber (Fig. 2e).

*Family Porcellanidae.* The spermatozoal morphology found in the investigated members of this family can be divided into two types. In *Petrolisthes* the nucleus is globular in shape and the cytoplasm forms a thin, neck-like region between it and the acrosome while in the remaining genera, *Aliaporcellana*, *Pisidia* and *Polyonyx*, the sperm cells are elongate, with the cytoplasm and nucleus forming a veneer over a central microtubular core (Fig. 2f). The microtubular core splits posteriorly to form several external microtubular arms (Fig. 3f). The sperm cells of each have a complexly arranged, concentrically zoned acrosome vesicle, capped by a perforate operculum, penetrated by a perforatorial chamber (in which the walls are folded into septa) and share acrosomal features such as a dense perforatorial cone and posterior ring (Fig. 2f).

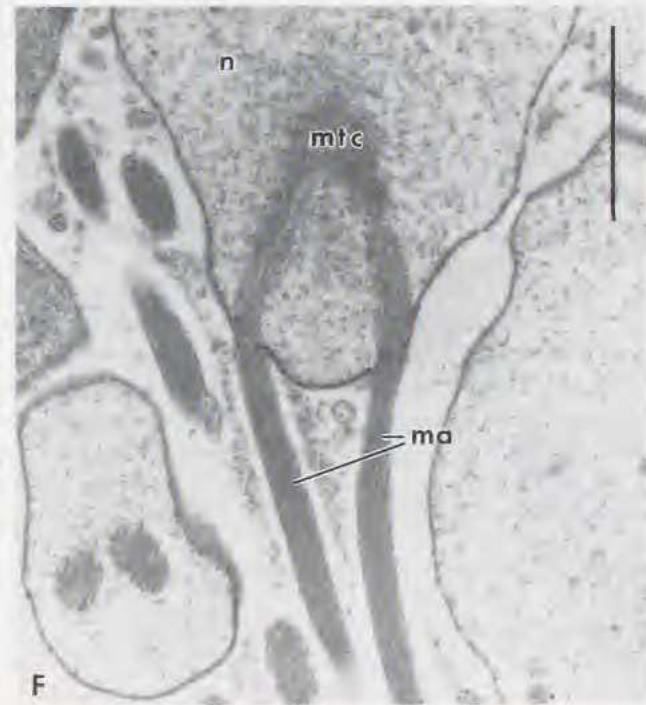
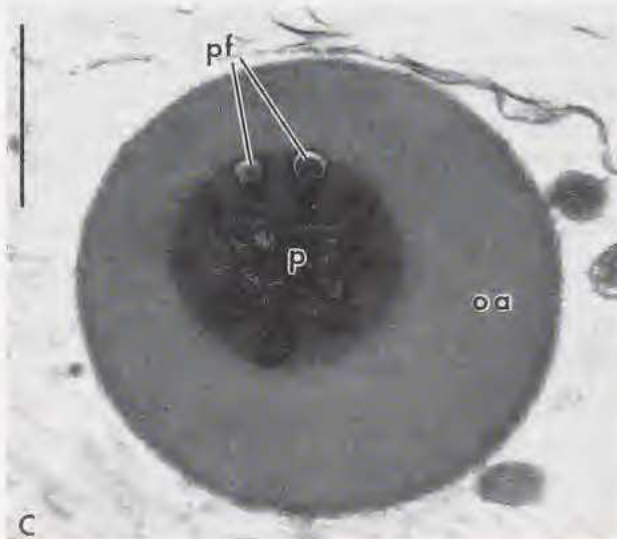
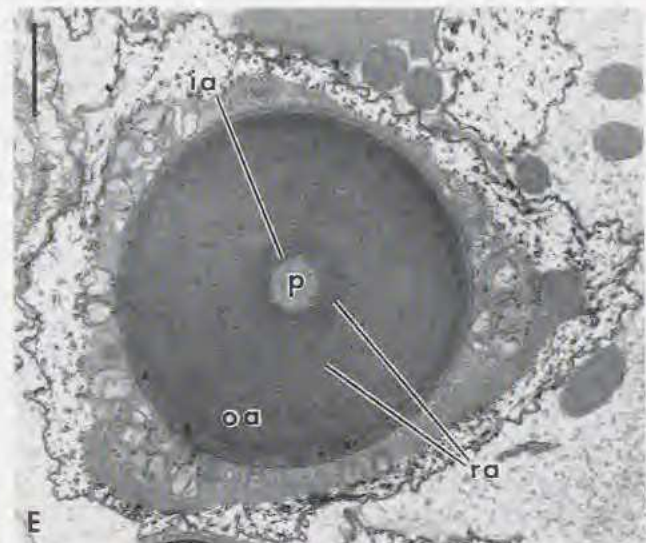
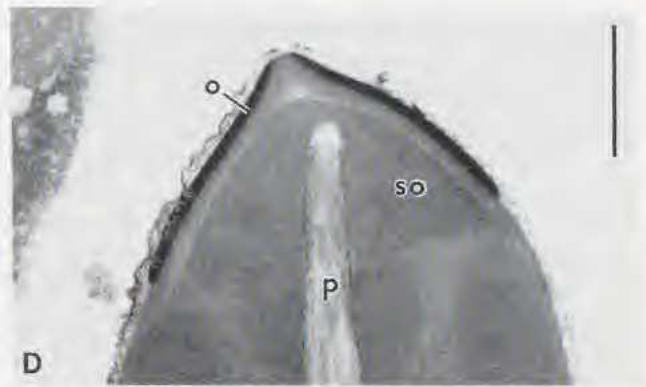
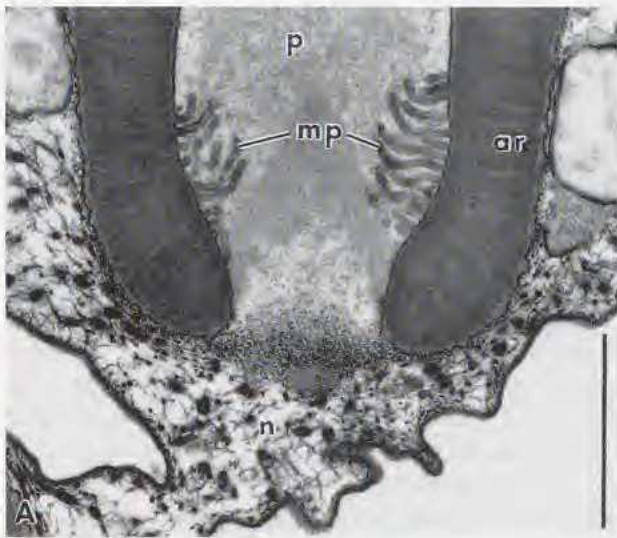
*Family Hippidae.* The sperm cell of *Hippa pacifica* is composed of a spherical to ovoid acrosome vesicle, capped by a broad operculum and penetrated by a wide perforatorial chamber. The unusual features of this spermatozoon are that the anterior end of the perforatorial chamber forms several tapered points, a membranous septum longitudinally divides the chamber and there are possibly up to five microtubular arms (Fig. 2g).

#### DISCUSSION

A recent reclassification of the infraorder Thalassinidea [40] has divided this group into three superfamilies. The available data from spermatozoal morphology would seem to vindicate this new arrangement, with *Thalassina*, *Callianassa* and *Axius* (from each of the superfamilies)

FIG. 3. — A-F: Transmission electron micrographs of longitudinal sections (LS) and transverse sections (TS) of spermatozoa of selected anomuran crabs. A: *Coenobita perlatus*. LS of perforatorial chamber showing microvillar projections. B: *Dardanus arrosor*. TS of acrosome vesicle showing conspicuous acrosome ray zone. C: *Calcinus minutus*. TS through upper acrosome vesicle showing splitting of the perforatorial chamber into separate fingers. D: *Cancellus* sp. LS of opercular region. E: *Pagurus chevreuxi*. TS through the acrosome vesicle showing reticulated acrosome zones. F: *Polyonyx transversus*. Oblique section through the posterior end of the nucleus showing the splitting of the microtubular core into discrete microtubular arms. Abbreviations: ar, acrosome ray zone; ia, inner acrosome zone; ma, microtubular arm; mp, microvillar projection; mtc, microtubular core; n, nucleus; o, operculum; oa, outer acrosome zone; p, perforatorial chamber; pf, perforatorial fingers; ra, reticulated acrosome zone; so, subopercular zone. Scale bars = 1  $\mu$ m.







showing a different spermatozoal ultrastructure. The overall sperm morphology for the Thalassinidea is sufficiently different from that of the Anomura to support the separation of the two based on evidence from somatic morphology [28]. Of interest is the fact that the spermatozoa of *Thalassina* possess an apparent thickened ring (Fig. 2b) which, so far, has been recorded only in heterotreme and thoracotreme brachyurans [23].

Within the superfamily Paguroidea, the investigated members of the Coenobitidae and Diogenidae share many spermatozoal characters, but many genera possess apomorphies which distinguish them. In the Diogenidae, the genus *Calcinus* has the splitting of the perforatorial chamber into separate fingers (Figs 1b, 3c), *Cancellus* sp. has a perforate operculum (Figs 1j, 3d), the clibanarids possess the dense perforatorial ring (Fig. 1c), and *Diogenes* species have modified the inner acrosome zone into a fibrillar core structure (Fig. 1e). Members of the genus *Pagurus* (Figs 1f, 3e), in the Paguridae, share the shape of the perforatorial chamber, the absence of microvillar projections and the reticulated acrosome zone with *Sympagurus* (Fig. 1i) in the Parapaguridae, but the other genera (*Porcellanopagurus* and *Xylopagurus*) appear more distinctive (Fig. 1g, h). The light microscope observation of *Lithodes* (Lithodidae) [41] is the only spermatozoal information available on this family. It shows a sperm cell with a spherical, concentrically zoned acrosome vesicle, penetrated by a perforatorial chamber, and three conspicuous microtubular arms. This description places it within the Paguroidea but an ultrastructural study is necessary to investigate the claim that the lithodids have close links with the genus *Pagurus* in the Paguridae [13].

The superfamily Lomoidea contains the monospecific genus *Lomis* in the family Lomidae. The spermatozoon of *Lomis* possesses spermatozoal characters, such as microtubular arms (possible three?) and an acrosome vesicle penetrated by a perforatorial chamber (Fig. 2c), which justify its position in the Anomura but its sperm morphology is distinct enough to confirm placement in its own family and superfamily [29].

Each of the three investigated families, Chirostylidae, Galatheidae and Porcellanidae, in the superfamily Galatheaidea shows a particular spermatozoal morphology which appears characteristic for that family. The chirostylid spermatozoal morphology is more similar to that of hermit crabs than to any other galatheid, particularly in the shape of the acrosome vesicle and the possession of an acrosome ray zone (Fig. 2d). The more elongate (fusiform) acrosome vesicle shape, division of the inner acrosome zone and the presence of septa in the perforatorial chamber characterise the members of the Galatheidae (Fig. 2e). The investigated members of the Porcellanidae all show a particular suite of acrosome vesicle characters which unite them but the overall sperm cell morphology divides the group. The globular nuclear form in *Petrolisthes* species clearly differentiates this genus from the other investigated genera which have an elongate sperm cell (Fig. 2f), reminiscent of flagellate spermatozoa. This basic division of the Porcellanidae is supported by larval [42, 47] and adult somatic morphology [19].

In the superfamily Hippoidea only representatives from the family Hippidae have been investigated for spermatozoal morphology. The spermatozoa observed in the genus *Emerita* (Table 1) have a more elongate acrosome vesicle than that described for *Hippa*. Though showing spermatozoal characteristics which place them in the Anomura (microtubular arms and acrosome vesicle structure), it is difficult to ally hippids with any other anomuran superfamily. The broad, horizontal operculum (Fig. 2g) has its nearest counterpart in members of the Porcellanidae (Fig. 2f) (though perforate in the latter case), or perhaps that seen in the thalassinidean, *Thalassina* (Fig. 2b). This last comparison may provide some evidence to support the statement that the hippids are the nearest relatives to the thalassinoids [28].



## ACKNOWLEDGEMENTS

The author acknowledges the assistance of Mrs Lina DADDOW (Zoology Department, University of Queensland) in all aspects of microscopy. Dr Shane LAVERY (Zoology Dept., University of Queensland), Dr Bertrand RICHER DE FORGES (ORSTOM, New Caledonia) and Dr Gary POORE (Museum of Victoria) are thanked for collecting many of the specimens and assistance in identifying the crabs was provided by Mr Peter DAVIE, Mr John SHORT (Queensland Museum), Dr Gary MORGAN (Western Australian Museum) and Prof. Jacques FOREST (Muséum National d'Histoire Naturelle, Paris). The constant support and guidance of Prof. Barrie JAMIESON is gratefully acknowledged.

## REFERENCES

1. BARKER, K. R. & AUSTIN, C. R., 1963. — Sperm morphology of *Emerita talpoida*. *Biological Bulletin*, **125**: 361-362.
2. BAUER, R. T., 1986. — Phylogenetic trends in sperm transfer and storage complexity in decapod crustaceans. *Journal of Crustacean Biology*, **6**: 313-325.
3. BORRADAILE, L. A., 1907. — On the classification of the decapod crustaceans. *Annals of the Magazine of Natural History*, **19**: 457-486.
4. BOUVIER, E. L., 1894. — Sur les caractères et l'évolution des Lomisinés, nouveau groupe de Crustacés anomoures. *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences, Paris*, **118**: 1353-1355.
5. BOWMAN, T. E. & ABELE, L. G., 1982. — Classification of the recent Crustacea. In: D. E. BLISS, *The Biology of Crustacea. Vol. 1. Systematics, the Fossil Record, and Biogeography*. New York, Academic Press: 1-27.
6. BURKENROAD, M. D., 1963. — The evolution of the Eucarida, (Crustacea, Eumalacostraca), in relation to the fossil record. *Tulane Studies in Geology*, **2**: 3-16.
7. CHEVAILLIER, P., 1966a. — Structure et constitution cytochimique de la capsule du spermatozoïde des Crustacés Décapodes. *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences, Paris*, **262**: 1546-1549.
8. CHEVAILLIER, P., 1966b. — Contribution à l'étude du complexe ADN-histone dans le spermatozoïde du pagure *Eupagurus bernhardus* L. (Crustacé Décapode). *Journal de Microscopie*, **5**: 739-758.
9. CHEVAILLIER, P., 1967a. — Nouvelles observations sur la structure des fibres intra-nucléaires du spermatozoïde du pagure *Eupagurus bernhardus* L. (Crustacé Décapode). *Journal de Microscopie*, **6**: 853-856.
10. CHEVAILLIER, P., 1967b. — Mise en évidence et étude cytochimique d'une protéine basique extranucleaire dans les spermatozoïdes des crustacés décapodes. *Journal of Cell Biology*, **32**: 547-556.
11. CHEVAILLIER, P., 1967c. — Relations DNA-Histones au cours de la spermatogenèse des Crustacés Décapodes. *Comptes Rendus Hebdomadaires de la Société de Biologie*, **161**: 435-436.
12. CHEVAILLIER, P., 1968. — Étude cytochimique ultrastructurale des nucléoprotéines dans le spermatozoïde du pagure *Eupagurus bernhardus* L. (Crustacé Décapode). *Journal de Microscopie*, **7**: 107-114.
13. CUNNINGHAM, C. W., BLACKSTONE, N. W. & BUSS, L. W., 1992. — Evolution of king crabs from hermit crab ancestors. *Nature*, **355**: 539-542.
14. DHILLON, B., 1964. — Sperm nucleus of *Clibanarius longitarsis*. *Experientia*, **20**: 505-506.
15. DHILLON, B., 1968. — Radial processes of decapod sperm. *Microscope*, **76**: 365-368.
16. FELGENHAUER, B. E. & ABELE, L. G., 1991. — Morphological Diversity of Decapod Spermatozoa. In: R. T. BAUER & J. W. MARTIN, *Crustacean Sexual Biology*. New York, Columbia University Press: 322-341.
17. GLAESSNER, M. F., 1969. — Decapoda. In: R. C. MOORE, *Treatise on Invertebrate Paleontology, Arthropoda 4. Part R, vol. 2*. Lawrence, Geological Society of America and University of Kansas Press: R399-R533.
18. GURNEY, R., 1942. — *Larvae of Decapod Crustacea*. London, Ray Society.
19. HAIG, J., 1965. — The Porcellanidae (Crustacea, Anomura) of Western Australia with descriptions of four new Australian species. *Journal of the Royal Society of Western Australia*, **48**: 97-118.
20. HINSCH, G. W., 1980a. — Spermiogenesis in *Coenobita clypeatus*, I. Sperm structure. *International Journal of Invertebrate Reproduction*, **2**: 189-198.
21. HINSCH, G. W., 1980b. — Spermiogenesis in a hermit crab, *Coenobita clypeatus*. II. Sertoli cells. *Tissue and Cell*, **12**: 255-262.
22. HINSCH, G. W., 1991. — Ultrastructure of the sperm and spermatophores of the anomuran crab *Pleuroncodes planipes*. *Journal of Crustacean Biology*, **11**: 17-22.
23. JAMIESON, B. G. M., 1991. — Ultrastructure and phylogeny of crustacean spermatozoa. *Memoirs of the Queensland Museum*, **31**: 109-142.
24. KOLTZOFF, N. K., 1906. — Studien über die Gestalt der Zelle. I. Untersuchungen über die Spermien der Decapoden, als Einleitung in das Problem der Zellengestalt. *Archiv für Mikroskopische Anatomie und Entwicklungs-Geschichte*, **67**: 364-572.



25. KROL, R. M., HAWKINS, W. E. & OVERSTREET, R. M., 1992. — Reproductive Components. In: F. W. HARRISON & A. G. HUMES, *Microscopic Anatomy of Invertebrates. Vol. 10. Decapod Crustacea*. New York, Wiley-Liss: 295-343.
26. MACDONALD, J. D., PIKE, R. B. & WILLAMSON, D. I., 1957. — Larvae of the British species of *Diogenes*, *Pagurus*, *Anapagurus* and *Lithodes* (Crustacea, Decapoda). *Proceedings of the Zoological Society of London*, **128**: 209-257.
27. MACLEAY, W. S., 1838. — Illustrations of the Annulosa of South Africa; being a portion of the objects of natural history chiefly collected during an expedition into the interior of South Africa, under the direction of Dr. Andrew Smith, in the years 1834, 1835, and 1836; fitted out by "The Cape of Good Hope Association for exploring Central Africa". In: A. SMITH, *Illustrations of the Zoology of South Africa (Invertebrate)*. London, Smith, Elder & Co: 1-75, pls. 1-4.
28. MARTIN, J. W. & ABELE, L. G., 1986. — Phylogenetic relationships of the genus *Aegla* (Decapoda: Anomura: Aegliidae), with comments on anomuran phylogeny. *Journal of Crustacean Biology*, **6**: 576-616.
29. MCLAUGHLIN, P. A., 1983a. — A review of the phylogenetic position of the Lomidae (Crustacea: Decapoda: Anomala). *Journal of Crustacean Biology*, **3**: 431-437.
30. MCLAUGHLIN, P. A., 1983b. — Hermit crabs - are they really polyphyletic? *Journal of Crustacean Biology*, **3**: 608-621.
31. MCLAUGHLIN, P. A. & HOLTHIUS, L. B., 1985. — Anomura versus Anomala. *Crustaceana*, **49**: 204-209.
32. NATH, V., 1942. — The decapod sperm. *Transactions of the National Institute of Sciences of India*, **2**: 87-119.
33. PEARSE, A. S., HUMM, H. J. & WHARTON, G. W., 1942. — Ecology of the sand beaches at Beaufort, N. C. *Ecological Monographs*, **12**: 135-190.
34. PILGRIM, R. L. C., 1965. — Some features in the morphology of *Lomis hirta* (Lamarck) (Crustacea: Decapoda) and a discussion of its systematic position and phylogeny. *Australian Journal of Zoology*, **13**: 545-557.
35. POCHON-MASSON, J., 1963. — Origine et formation de la vésicule du spermatozoïde d'*Eupagurus bernhardus* (Décapode Anomoure). *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences, Paris*, **256**: 2226-2228.
36. POCHON-MASSON, J., 1965a. — L'ultrastructure des épines du spermatozoïde chez les Décapodes (Macroures, Anomoures, Brachyoures). *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences, Paris*, **260**: 3762-3764.
37. POCHON-MASSON, J., 1965b. — Schéma général du spermatozoïde vésiculaire des Décapodes. *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences, Paris*, **260**: 5093-5095.
38. POCHON-MASSON, J., 1968a. — L'ultrastructure des spermatozoïdes vésiculaires chez les Crustacés Décapodes avant et au cours de leur dévagination expérimentale. I. Brachyoures et Anomoures. *Annales des Sciences Naturelles, Zoologie et Biologie Animale*, **10**: 1-100.
39. POCHON-MASSON, J., 1968b. — L'ultrastructure des spermatozoïdes vésiculaires chez les Crustacés Décapodes avant et au cours de leur dévagination expérimentale. II. Macroures. Discussion et conclusions. *Annales des Sciences Naturelles, Zoologie et Biologie Animale*, **10**: 367-454.
40. POORE, G. C. B., 1994. — A phylogeny of the families of Thalassinidea (Crustacea: Decapoda) with keys to families and genera. *Memoirs of the Museum of Victoria*, **54**: 79-120.
41. RETZIUS, G., 1909. — Die spermien der Crustaceen. *Biologische Untersuchungen*, **14**: 1-54.
42. SANKOLLI, K. N., 1965. — Studies on larval development in Anomura (Crustacea, Decapoda) - I. *Proceedings of the Symposium on Crustacea. Held at Ernakulam (January 12-15, 1965). Part II*. Marine Biological Association of India. Bangalore Press, Bangalore: 744-775.
43. SUBRAMONIAM, T., 1977. — Aspects of sexual biology of the anomuran crab *Emerita asiatica*. *Marine Biology*, **43**: 369-377.
44. TUDGE, C. C., 1992. — Comparative ultrastructure of hermit crab spermatozoa (Decapoda: Anomura: Paguroidea). *Journal of Crustacean Biology*, **12**: 397-409.
45. TUDGE, C. C. & JAMIESON, B. G. M., 1991. — Ultrastructure of the mature spermatozoon of the coconut crab *Birgus latro* (L.) (Coenobitidae, Paguroidea, Decapoda). *Marine Biology*, **108**: 395-402.
46. TUDGE, C. C. & JUSTINE, J.-L., 1994. — The cytoskeletal proteins actin and tubulin in the spermatozoa of four decapod crabs (Crustacea, Decapoda). *Acta Zoologica (Stockholm)*, **75**: 277-285.
47. VAN DOVER, C. L., FACTOR, J. R. & GORE, R. H., 1982. — Developmental patterns of larval scaphognathites: an aid to the classification of anomuran and brachyuran Crustacea. *Journal of Crustacean Biology*, **2**: 48-53.
48. VAUGHN, J. C., 1968a. — Histone metabolism in the crab *Emerita analoga*: Spermio-genesis and early embryogenesis. *Journal of Cell Biology*, **39**: 138a.



49. VAUGHN, J. C., 1968b. — Changing nuclear histone patterns during development. I. Fertilization and early cleavage in the crab, *Emerita analoga*. *Journal of Histochemistry and Cytochemistry*, **16**: 473-479.
50. VAUGHN, J. C., CHAITOFF, J., DELEON, R., GARLAND, C. & THOMSON, L., 1969. — Changing nuclear histone patterns during development. II. Isolation and partial characterization of "Decapodine" from sperm cells of the crab *Emerita analoga*. *Experimental Cell Research*, **54**: 362-366.
51. VAUGHN, J. C. & LOCY, R. D., 1969. — Changing nuclear histone patterns during development. III. The deoxyribonucleic acid content of spermatogenic cells in the crab *Emerita analoga*. *Journal of Histochemistry and Cytochemistry*, **17**: 591-600.
52. VAUGHN, J. C. & THOMSON, L. A., 1972. — A kinetic study of DNA and basic protein metabolism during spermatogenesis in the Sand crab, *Emerita analoga*. *Journal of Cell Biology*, **52**: 322-337.