

Phylogeny of the Brachyura (Crustacea, Decapoda): Evidence from Spermatozoal Ultrastructure

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ABSTRACT

Spermatozoa of *Dynomene* aff. *devaneyi* (Dynomeniidae) and *Homolodromia kai* (Homolodromiidae) are described. Parsimony analyses affirm the classification of the Brachyura by GUINOT (1978), notably the groupings Podotremata and Heterotremata *sensu lato*, as sister-groups, and Thoracotremata are confirmed. In the Podotremata, association of the Raninoidea and Cyclodorippoidea is upheld (as sister-groups), each with convincing and unique synapomorphies, but sperm data considered alone do not support alliance of the Homolidae, (a very clearly defined group) with this couplet and therefore do not endorse the grouping Archaeobrachyura which is, however, upheld by combined spermatozoal and non-spermatozoal data. The Dromiacea *sensu* Guinot (Dromiidae, Dynomeniidae and Homolodromiidae) is confirmed spermatologically as a monophyletic grouping but the discreteness of the three constituent families is not upheld. *Homolodromia* displays a mixture of dromiid and dynomenid spermatozoal features. The Dynomeniidae and Dromiidae are each found to be paraphyletic. *Latreillia* sp., considered an homoloid by GUINOT (1978) and GUINOT & RICHER DE FORGES (1995), forms a polytomy either with Homolidae+Raninoidea-Cyclodorippoidea with the combined, spermatozoal and non-spermatozoal, data set or with Homolidae+Dromiidae-Dynomeniidae-Homolodromiidae, for sperm data only. The association by GUINOT (1978) of the Dorippoidea, Portunoidea, Xanthoidea, and Majoidea in the non-thoracotreme Heterotremata is fully supported spermatologically. Spermatozoal data give majids the most basal position in the Heterotremata whereas for the combined data *Neodorippe* (with carrying behaviour, like most podotremes) appears the least modified member of the heterotreme-thoracotreme assemblage. The Thoracotremata is unequivocally supported.

RÉSUMÉ

Phylogénie des Brachyura (Crustacea, Decapoda): le témoignage de l'ultrastructure des spermatozoïdes

Les spermatozoïdes de *Dynomene* aff. *devaneyi* (Dynomeniidae) et *Homolodromia kai* (Homolodromiidae) sont décrits. Les analyses de parcimonie confirment la classification des Brachyura par GUINOT (1978), particulièrement les groupements Podotremata et Heterotremata *sensu lato* comme groupes-frères, et les Thoracotremata sont confirmés. Chez

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les Podotremata, l'association des Raninoidea et des Cyclodorippoidea est maintenue (comme groupes-frères), chacun avec des synapomorphies originales et convaincantes, mais les données spermatologiques utilisées seules ne permettent pas d'affirmer les relations des Homolidae (groupe très clairement défini) avec ces deux taxons, et donc ne supportent pas le groupement des Archaeobrachyura. Ce dernier est toutefois maintenu si l'on utilise à la fois les données spermatologiques et non spermatologiques. Les Dromiacea *sensu* Guinot (Dromiidae, Dynomenidae et Homolodromiidae) sont confirmés par les données spermatologiques comme un groupe monophylétique, mais le caractère séparé des trois familles n'est pas prouvé. *Homolodromia* montre un mélange de caractères spermatologiques de Dromiidae et de Dynomenidae. Les Dynomenidae et les Dromiidae ont tous deux été trouvés paraphylétiques. *Latreillia* sp., considéré comme un Homoloidea par GUINOT (1978) et GUINOT & RICHER DE FORGES (1995), forme une polytomie ou bien avec les Homolidae+Raninoidea-Cyclodorippoidea si on utilise les données spermatologiques et non-spermatologiques combinées, ou avec les Homolidae+Dromiidae-Dynomenidae-Homolodromiidae en utilisant les données spermatologiques seules. L'association par GUINOT (1978) des Dorippoidea, Portunoidea, Xanthoidea et Majoidea dans les Heterotremata non-thoracotrèmes est parfaitement confirmée par la spermatologie. Les données spermatologiques donnent aux Majidae la position la plus basale dans les Heterotremata alors que, avec les données combinées, *Neodorippe* (un 'porteur', comme la plupart des Podotremata) apparaît le membre le moins évolué de l'assemblage Hétérotrèmes-Thoracotrèmes. Les Thoracotremata sont confirmés de manière non équivoque.

The literature on sperm ultrastructure in Crustacea, and its relevance to phylogeny, a subject briefly addressed earlier for the Brachyura by BROWN [2], has been reviewed by JAMIESON [18]. Several papers on brachyuran ultrastructure have since appeared [19, 20, 23-27] and have culminated in a cladistic, parsimony analysis of brachyuran phylogeny [21] which is extended in the present chapter. The analyses apply the principles of phylogenetic systematics propounded by HENNIG [13] and computer procedures for phylogenetic analysis under the principle of parsimony which are enunciated by SWOFFORD [32].

The internal relationships and classification of brachyuran crabs, and particularly of the Podotremata, have been the subject of controversy. GUINOT [4-8] divides the Brachyura into three sections mainly on the basis of the location of the male and female pores: the Podotremata, the Heterotremata and the Thoracotremata. Nevertheless, GUINOT ([5]: p. 218) recognized that the coxal positions of male and female pores, with external fertilisation, characterizing the podotremes, were symplesiomorphies.

The Podotremata *sensu* GUINOT contain the Dromiacea and Archaeobrachyura. The Dromiacea consist of the Dromioidea and Homolodromioidea. The Archaeobrachyura contain the Homoloidea, Raninoidea, and Cyclodorippoidea (= Tymoloidea). In other classifications the superfamily Homoloidea, which includes three families (Homolidae, Latreilliidae and Poupiniidae) is often associated with or placed in the Dromiacea (see [5, 6, 12]).

The Heterotremata and Thoracotremata share a sternal location of the female pores and development of a sternal vulva on sternite 6, in direct communication with the seminal receptacle, allowing for internal fertilization. The Thoracotremata differ in the additional sternal location of the male pores. Whereas the Thoracotremata appeared to be a monophyletic group, the Heterotremata were suspected by JAMIESON to be paraphyletic [18].

In some contrast with the classification of GUINOT, nucleotide sequences of 18S ribosomal RNA support the exclusion of a mono- or poly-phyletic Dromiidae from the Brachyura, and their association with the Anomura, but support inclusion of the Raninidae in the Brachyura [1, 30, 31]; homolids were not considered in the molecular analyses.

This chapter adds to the former data matrix [21] new spermatozoal data on two families of questionable relationships, the Dynomenidae, represented by *Dynomene* aff. *devaneyi*, and the Homolodromiidae, represented by *Homolodromia kai*. The augmented matrix is subjected to parsimony analysis. In a second analysis, a minimum of non-spermatozoal characters, defining the Podotremata, Heterotremata and Thoracotremata and separating these from the Anomura, is added and effects on the original phylogram observed, pending a more comprehensive inclusion of non-spermatozoal characters.

MATERIAL AND METHODS

The species examined and sources of material are listed by JAMIESON [21]. In addition, the material of *Dynomene* aff. *devaneyi* and *Homolodromia kai* was obtained on the BATHUS 3 cruise in New Caledonian waters, at stations CP 805 and CC 848 respectively, on 22 November 1993.

Electron microscopy. Transmission electron microscopy procedures were as in [27].

Cladistics. Methods employed in the parsimony analysis are given in [21]. Characters employed are given in Table 1 and the data matrix is shown in Table 2. The parameters and specifications for the phylograms obtained are given in the legends of Fig. 1A and B.

TABLE 1. — Character coding employed

Spermatozoal characters

- (1) Acrosome length:width: 0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1.0 1.1 1.2 1.3 1.4 1.5 1.6 1.7 1.8 1.9 2.0,
- (2) Zonation of the contents of the acrosome vesicle predominantly: horizontal 0, concentric 1, intermediate 2,
- (3) Operculum: imperforate 0, perforate, open 1, perforate, closed with apical button 2,
- (4) Opercular projections into subopercular material absent 0, present 1,
- (5) Operculum: discontinuous with capsule 0, continuous with capsule 1,
- (6) Operculum: moderately thick 0, very thin double lamina 1,
- (7) Operculum width: not extremely wide 0, extremely wide 1,
- (8) Periopercular rim: absent 0, weak 1, well developed 2, —
- (9) Accessory opercular ring: absent 0, present 1,
- (10) Subopercular protuberance through operculum: absent 0, weak 1, well developed 2,
- (11) True acrosome ray zone: absent 0, present 1, lost 2,
- (12) Outer acrosome zone border with peripheral zone: not ragged 0, ragged 1,
- (13) Anterolateral pale zone of acrosome contents: absent 0, present 1,
- (14) Flangelike peripheral extension of lower acrosome zone: absent 0, present 1,
- (15) Xanthid ring: absent 0, present 1, modified and short 2, modified and elongate 3,
- (16) Subacrosomal chamber or perforatorium: postequatorial 0, extending preequatorially 1,
- (17) Head of perforatorium: non-capitate 0, amoeboid 1, spiked wheel 2, bilateral 3,
- (18) Corrugations of wall of perforatorial chamber: absent 0, simple invaginations 1, branched invaginations 2, invaginations with filaments 3, filaments only 4, evaginations only 5,
- (19) Lateral arms: absent 0, one 1 (not found), two 2, three 3, several 4
- (20) Lateral arms: absent 0, microtubular with chromatin 1, nuclear only 2, microtubular only 3,
- (21) Centrioles: absent 0, present 1, elongate 2. (Excluded).
- (22) Posterior median process of nucleus: absent 0, present 1,
- (23) Thickened ring: absent 0, present 1,
- (24) Concentric lamellae: absent 0, present 1,
- (25) Capsular chambers: absent 0, one chamber 1, several 2,
- (26) Capsular projections: absent 0, present 1,
- (27) Capsular flange: absent 0, present 1,

Non-spermatozoal characters

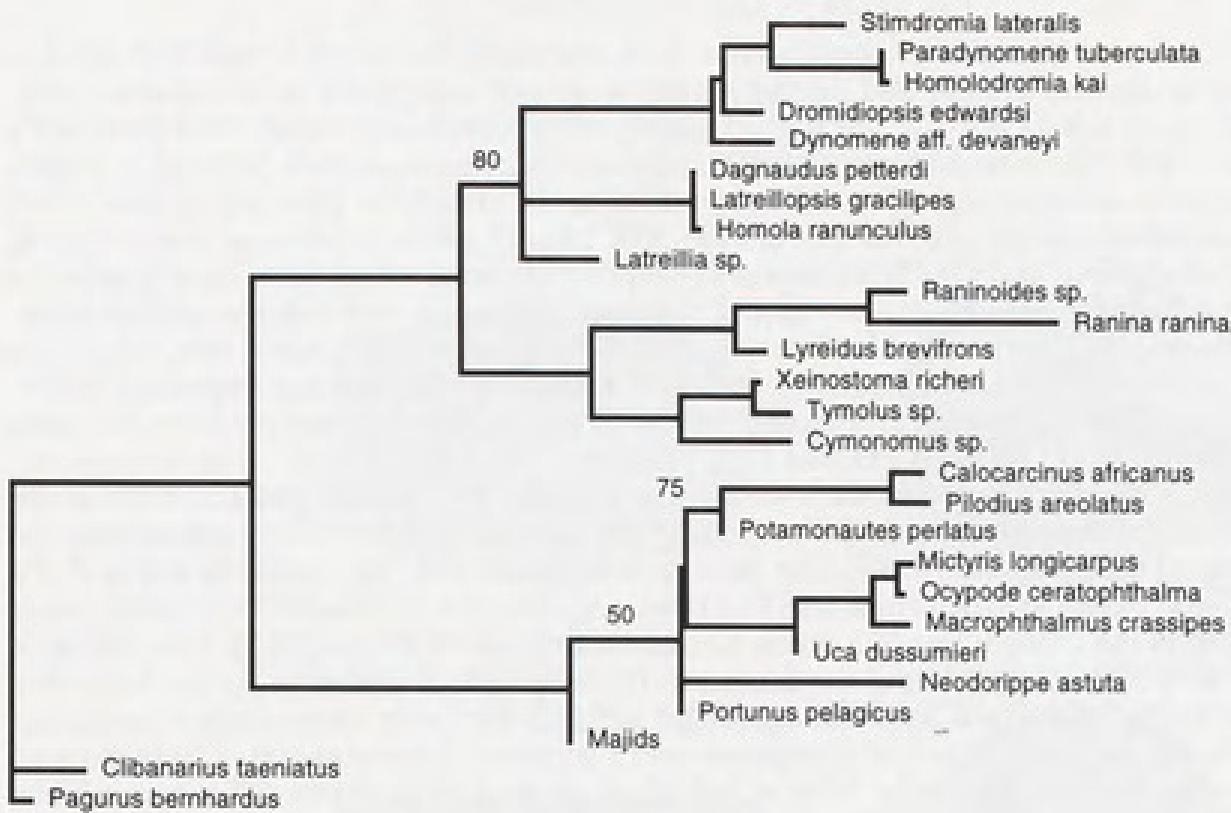
- (28) Genital pores: all coxal 0, female sternal 1, male and female sternal 2,
- (29) Separate spermatheca: absent 0, present 1,
- (30) P5, reduction of: absent 0, present 1,
- (31) P5, dorsal or subdorsal origin: absent 0, present 1,
- (32) P5, subcheliform or cheliform modification: absent 0, weak 1, strong 2,
- (33) Sella turcica: absent 0, present 1,
- (34) Uropods: present 0, vestigial 1, absent 2

In the present analyses, characters were unordered excepting 1, 8, 11, 25 and 32 (ordered) and 34 (irreversible, up).

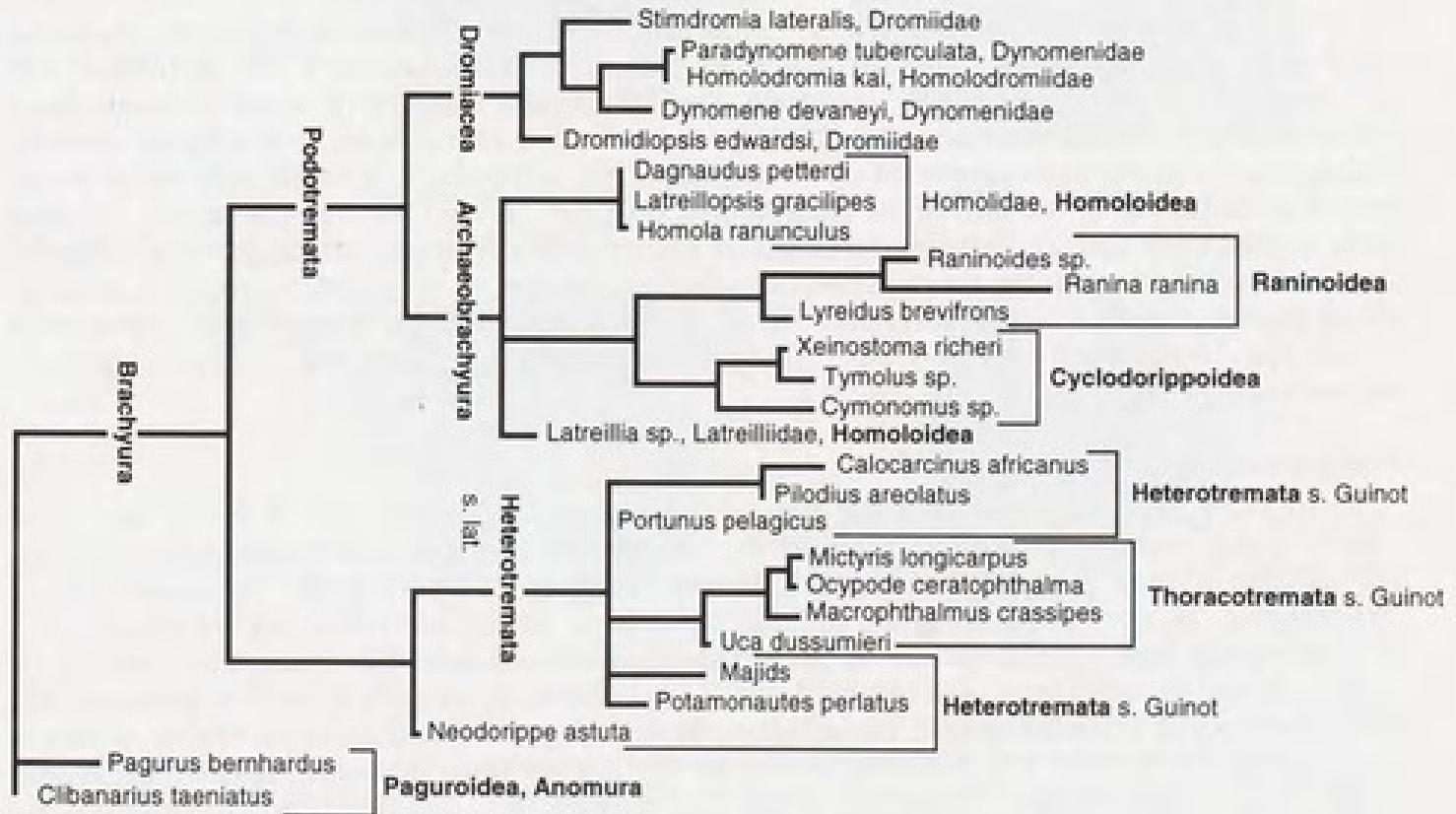
TABLE 2. — Data matrix

Taxon	11111111111222222222233333
	1234567890123456789012345678901234
<i>Stindromia lateralis</i>	3010000002001001300000000100111211
<i>Dagnaudus petterdi</i>	6011000001000001203211000000111212
<i>Calocarcinus africanus</i>	8100000210110021004210100001000012
<i>Dromidiopsis edwardsi</i>	3210000002001001303200000000111211
<i>Paradynomene tuberculata</i>	30100000020011013000?0000000111111
<i>Latreilopsis gracilipes</i>	6011000001000001203211000000111212
<i>Raninoides</i> sp.	7210100000000001023201002110111012
<i>Lyreidus brevifrons</i>	5210100000000001113201000100111012
<i>Xeinostoma richeri</i>	5010011000000001033211000100111112
<i>Cymonomus</i> sp.	60000010000001010332?1000100111112
<i>Tymolus</i> sp.	6010011000000001033211000100111212
	1
<i>Neodorippe 'astuta'</i>	B100000000100001004200100001011212
<i>Portunus pelagicus</i>	A100000000100001004210100001000012
<i>Mictyris longicarpus</i>	C120000000200031004200110002000012
<i>Ocyopode ceratophthalmus</i>	9120000000200031004200110002000012
<i>Uca dussumieri</i>	9120000000200001004200100002000012
<i>Macrophthalmus crassipes</i>	A100000000200001004200110002000012
<i>Pilodius areolatus</i>	9100000010110011004200100001000012
<i>Ranina ranina</i>	8110100000000000023211001110101012
<i>Homola ranunculus</i>	50110000010000012032?1000000111212
<i>Majids</i>	A11000000010000100?111100001000012
	2
<i>Potamonautes perlatus</i>	9100000200100001004220100001000012
<i>Latreillia</i> sp.	6210000000000000130?2?1000000111212
<i>Pagurus bernhardus</i>	F1000000000000001043111000000010200
<i>Clibanarius taeniatus</i>	C1000000000000001043100000000010200
<i>Homolodromia kai</i>	401000000200110130000?000000111111
<i>Dynomene</i> aff. <i>devaneyi</i>	5010000002001001302200000000111111

FIG 1. — Trees of the Brachyura. **A:** Heuristic 50% Majority rule consensus tree of 959 shortest and equally parsimonious trees for spermatozoal characters only. Heuristic search settings: Addition sequence: simple. One tree(s) held at each step during stepwise addition. Tree-bisection-reconnection (TBR) branch-swapping performed. MULPARS option in effect. Steepest descent option not in effect. Branches having maximum length zero collapsed to yield polytomies. Topological constraints not enforced. Trees rooted by outgroup. Multi-state taxa interpreted as polymorphism. Character 21 excluded. Character-state optimization: Accelerated transformation (ACCTRAN). Tree length = 49771. Consistency index (CI) = 0.665. Homoplasy index (HI) = 0.352. CI excluding uninformative characters = 0.647. HI excluding uninformative characters = 0.359. Retention index (RI) = 0.885. Rescaled consistency index (RC) = 0.588. Clades are supported by 100% of trees unless otherwise indicated. **B:** Heuristic strict consensus tree of 36 shortest and equally parsimonious trees, for spermatozoal and non-spermatozoal characters, using the outgroup method. Setting as for (A). Tree length = 47210. Consistency index (CI) = 0.701. Homoplasy index (HI) = 0.317. CI excluding uninformative characters = 0.682. HI excluding uninformative characters = 0.324. Retention index (RI) = 0.902. Rescaled consistency index (RC) = 0.632.



A Spermatozoal characters only



B Spermatozoal and non-spermatozoal characters

RESULTS AND DISCUSSION

In the parsimony analysis of spermatozoal data, the heuristic search option was used as computations under the branch and bound option were not completed in reasonable time. Nevertheless, the resultant phylograms agreed closely with branch and bound trees previously obtained [21]. The combined, spermatozoal and non-spermatozoal data yielded a highly structured strict consensus tree (Fig. 1B). Spermatozoal data alone gave an unstructured, completely pectinate strict consensus tree but the 50% Majority Rule consensus tree (Fig. 1A) was highly dichotomous and clearly meaningful, despite criticisms which have been levelled at the validity of majority consensus, in terms of resultant groupings, notably the dromiaceans, homolids, raninoids, cyclodorippoidea, heterotremes *sensu lato*, and thoracotremes, which are supportable on other grounds. Conclusions from the two consensus trees are discussed below. Non-spermatozoal characters will be discussed only where especially relevant but have had more extensive treatment in the previous analysis [21].

The chief difference between the two trees is that the Homolidae and Latreillidae are associated with the Raninoidea+Cyclodorippoidea in the analysis of combined, spermatozoal and non-spermatozoal data (hereafter termed the combined analysis) (Fig. 1B), but associate with the Dromiacea in the purely spermatozoal analysis (Fig. 1A). The former assemblage corresponds with and supports the recognition of a taxon Archaeobrachyura by GUINOT [5]. Discussion of the succession of spermatozoal apomorphies and of group synapomorphies in the following account will chiefly be derived from the combined analysis but, with the exception noted and some others to be discussed, there is strong agreement between the two analyses. It is stressed that a larger and more refined suite of morphological characters is required for a combined analysis (GUINOT *et al.*, in preparation).

Brachyura

The Brachyura is a monophyletic taxon relative to the anomuran outgroup, *Pagurus bernhardus* and *Clibanarius taeniatus*. Although the sperm of the Anomura [34] and Brachyura are distinctive relative to other decapods, the Brachyura have only weak spermatozoal synapomorphies relative to anomurans despite forming a monophyletic brachyuran clade. Brachyuran monophyly is supported by shortening of the acrosome to a nearly spheroidal form; loss of corrugations of the wall of the perforatorial chamber, though these reappear in a different form in raninoids and cyclodorippoidea; loss of microtubules from the lateral arms, a doubtful synapomorphy in view of their presence in at least some majids [14]; and, somatically, development of a sella turcica and reduction of the uropods. Although spermatozoal support for a monophyletic Brachyura is weak, many constituent groups are, in contrast, strongly supported.

Podotremata

In both the combined and the solely spermatozoal analysis, the Podotremata is a monophyletic taxon and the sister-group of the heterotreme-thoracotreme assemblage (Fig. 1A, B), as also shown previously [11, 21]. Synapomorphies of podotreme spermatozoa, as indicated in the combined analysis, include depression of the acrosome; development of a predominantly horizontal zonation of the acrosome compared with the concentric zonation of paguroids and heterotremes; and (ambiguously) a bilaterally symmetrical capitate perforatorial head (developing from the simple, non-capitate form in paguroids and ancestral crabs), which is lost in some members. The bilateral perforatorial head is seen in dromiids (*Dromidiopsis edwardsi* and *Stimdromia lateralis*); in the two investigated dynomenids (*Paradynomene tuberculata*, [21], and *Dynomene aff. devaneyi*) and in *Homolodromia kai* and contrasts with that of homolid sperm which has the form of a horizontally disposed spiked wheel [21, 27].

PODOTREMATA

- 1 Acrosome depressed
- 2 Zonation of acrosome horizontal
- 3 Operculum perforate

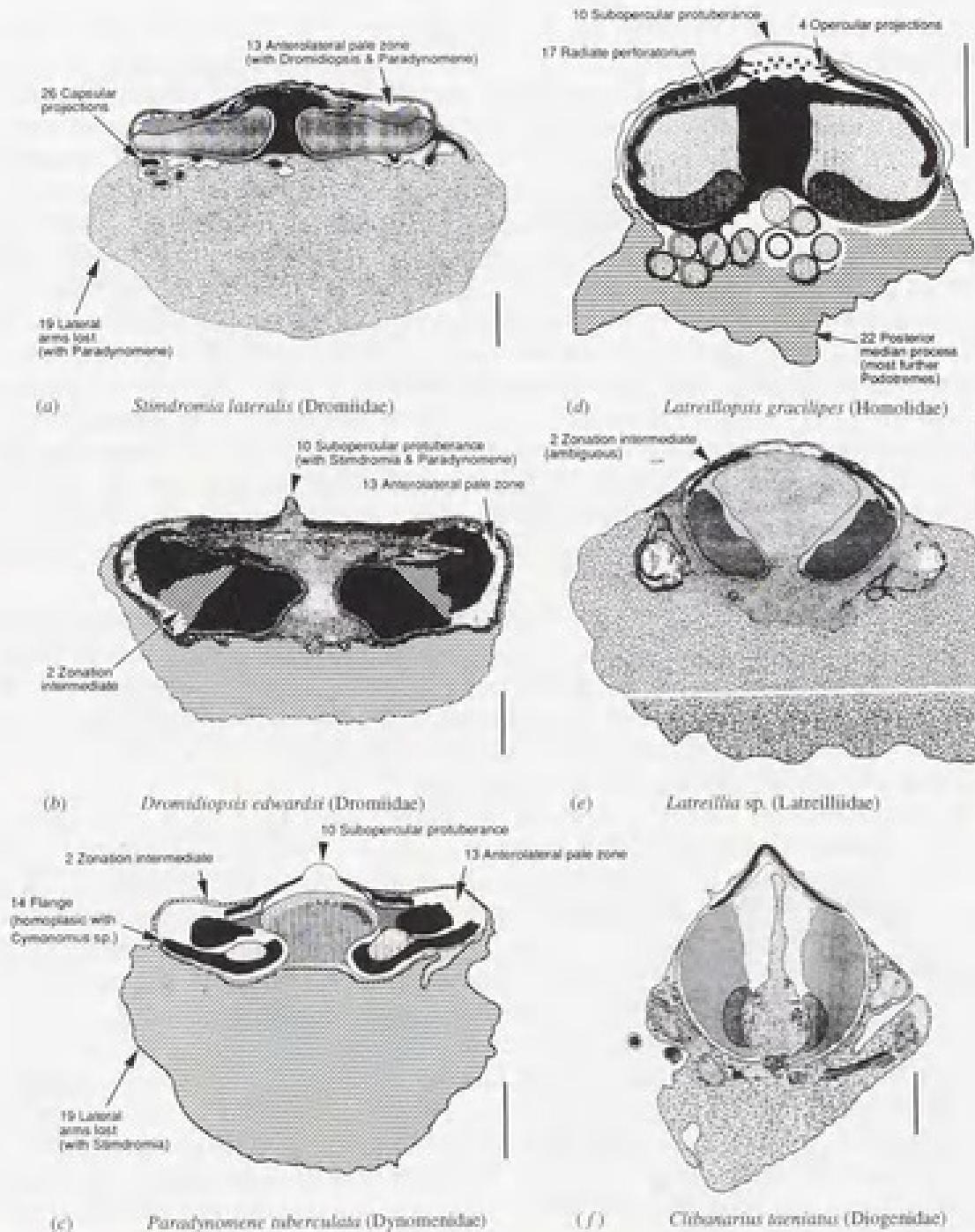


FIG. 2. — Drawings of spermatozoa of some podotremes and an anomuran used in this analysis. a: *Stimdromia lateralis* (Dromiidae). b: *Dromidiopsis edwardsi* (Dromiidae). c: *Paradynomene tuberculata* (Dynomenidae). d: *Latreillopsis gracilipes* (Homolidae). e: *Latreillia* sp. (Latreilliidae). f: *Clibanarius taeniatus* (Anomura, Diogenidae). The chief apomorphies are indicated but see text for a more detailed explanation. The section of *Stimdromia* (first described as *Petalomera* [17]) is not precisely sagittal; in micrographs which are sagittal, perforation of the operculum is seen. Scale bar 1 μ m. After [21].

Apical perforation of the spermatozoal operculum is a further synapomorphy of podotremes, the same condition in majids being, it appears, independently derived (homoplasic). Monophyly of the Podotremata as deduced from species examined for sperm ultrastructure to date, does not exclude, nor does it support, the possibility that some supposed dromiids, notably *Hypoconcha* [31], have been missclassified and may be closer phylogenetically to anomurans than they are to other brachyurans.

Dromiacea. The Dromiacea as constituted by GUINOT for the Dromiidae, Homolodromiidae, and Dynomenidae [5, 10], is confirmed as a monophyletic group in both analyses (Fig. 1A, B). Its spermatozoal synapomorphies, from the combined analysis, are further depression of the acrosome, well developed protrusion of subopercular material through the operculum (a lesser protrusion occurs in homolids), and development of an anterolateral pale zone of the acrosome. Although the Dromiacea forms a monophyletic clade, neither the constituent Dromiidae nor the Dynomenidae appears monophyletic spermatologically. Thus, in the combined analysis (Fig. 1B) *Paradynomene* pairs with *Homolodromia*, and these have *Dynomene* as their sister-group, the three being closer to *Stimdromia* than this is to the other dromiid, *Dromidiopsis*, which forms the sister-group of the other dromiaceans. In the purely spermatozoal analysis (Fig. 1A), *Paradynomene* again pairs with *Homolodromia* but sister-groups, in descending order, are *Stimdromia*, *Dromidiopsis* and *Dynomene*. It can thus be said that although there is distinctive dromiacean spermatozoal ground plan, sperm structure does not distinguish the constituent families Dromiidae, Homolodromiidae and Dynomenidae. This does not necessarily challenge definition of these families on the grounds of non-spermatozoal morphology (e.g. [10, 29]) and further analysis of non-spermatozoal characters is in progress to further ascertain the relationships of these families (GUINOT, JAMIESON & RICHER DE FORGES, and GUINOT & TAVARES, in preparation).

Dromiidae. The Dromiidae (see [29]) are elusive of definition spermatologically as shown in the previous section (see also [21]), being a paraphyletic group in both analyses. In the combined analysis (Fig. 1B), a monophyletic dromiid clade (including dynomenids and *Homolodromia*) is identical with the dromiacean clade. Spermatozoa of *Stimdromia* (= *Petalomera*) *lateralis*, *Dromidiopsis edwardsi* and *Paradynomene tuberculata* are illustrated in Fig. 2A-C and that of *Homolodromia kai* in Fig. 6B.

In the combined analysis (Fig. 1B), *Dromidiopsis edwardsi* is the sister-taxon of the other dromiaceans. The sole, and somewhat subjective, apomorphy of the sperm of *Dromidiopsis edwardsi* [28] is a zonation of the acrosome which is intermediate between the horizontal and concentric conditions. Synapomorphies of the dromiid-dynomenid-*Homolodromia* melange are weak, being loss of the three arms basic to the anomuran-brachyuran assemblage, and with them any microtubules in these arms. As arms are present in *Dynomene* aff. *devaneyi*, their basal loss is questionable, but they may well be labile in occurrence. *Stimdromia lateralis* (Fig. 2A) is diagnosed by the presence of capsular projections. *Dynomene* aff. *devaneyi*, which computes as basal relative to these taxa, appears to be unique in the Brachyura, in having only two nuclear arms. A further apomorphy is slight lengthening of the acrosome. *Paradynomene* (Fig. 2C) and *Homolodromia* (Fig. 6B) have a striking similarity, computing as a synapomorphy: a flange like lateral extension of the lower acrosome zone. *Paradynomene* is distinguished (ambiguously) by slight lengthening of the acrosome whereas *Homolodromia* shows no individual apomorphy; in the spermatozoal analysis, it is distinguished from *Paradynomene* only by its slightly more depressed acrosome.

Centrioles are unknown in dromiid sperm but are present in homolids. The difficulty in unequivocally demonstrating their presence or absence has led to their exclusion from the parsimony analyses.

Homolodromiidae This family is placed in a monotypic superfamily Homolodromioidea,

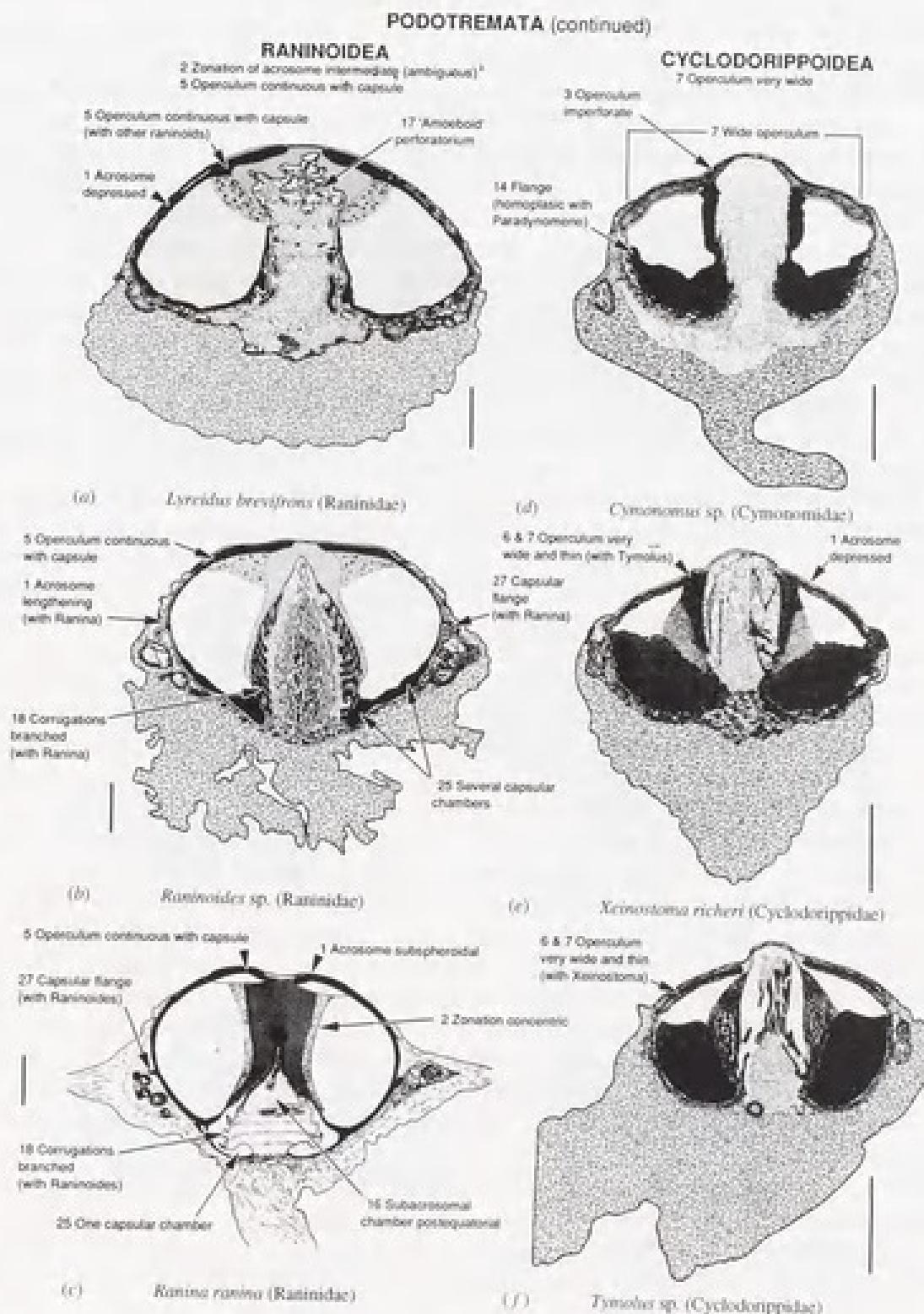


FIG. 3. — Drawings of spermatozoa of further podotremes used in this analysis. a: *Lyreidus brevifrons* (Raninidae, Lyreidinae). b: *Raninoides* sp. (Raninidae, Raninoidinae). c: *Ranina ranina* (Raninidae, Ranininae). d: *Cymonomus* sp. (Cymonomidae). e: *Xeinostoma richeri* (Cyclodorippidae, Xeinostominae). f: *Tymolus* sp. (Cyclodorippidae, Cyclodorippinae). The chief apomorphies are indicated but see text for a more detailed explanation. Scale bar 1 μ m. Sources as listed in Material and methods. After JAMIESON [21].

within the Dromiacea, by GUINOT [5, 10]. She considers that the Homolodromioidea represent, without doubt, the most primitive [members] of the Podotremata and lists a long series of characters in support of this contention. It is difficult, therefore, to evaluate the relatively advanced position which *Homolodromia* appears to occupy, in terms of spermatozoal ultrastructure, relative to other dromiaceans (Fig. 1A, B). It is noteworthy, in view of origin of *Homolodromia* in the phylograms between *Paradynomene* on the one hand and *Dynomene*, with or without intervention of dromiids, that GUINOT [5] stated that in some regards it is the dynomenids which seem closer to the Homolodromiidae than do the Dromiidae. The fact that *Homolodromia* lies within a dromiid clade is also of interest with regard to GUINOT'S [5, 10] statement (drawing on [35] and others) that the level of organization of the fossil Prosopidae, the most ancient crabs known, survives on the one hand in the form (without doubt little modified) of the Homolodromioidea, which inhabit deep waters, and on the other hand in the form of the Dromioidea (Dromiidae and Dynomenidae), much more numerous and diversified, which have developed special adaptations (in most Dromiidae the carapace is protected by a sponge, an ascidian or a bivalve shell) [29]. The Homolodromiidae have a unique combination of morphological characters, though mostly plesiomorphic. These are, *inter alia*, fusion of the ophthalmic segment to the anterior carapace (in *Homolodromia*); the soft branchiostegite; endophragmal skeleton with anastomoses; abdominal pleura developed; and retention of abdominal pleopods in the male on segments 3 to 5. Occurrence of uropods which are not dorsal and are represented by small lobes on the abdominal segment 6 appears to be a homolodromiid synapomorphy [10]. The phylograms (Fig. 1A, B) are heuristic for reconsideration of the validity and relationships of the families Dromiidae, Homolodromiidae and Dynomenidae.

In terms of the ultrastructural characters used in the parsimony analyses, the spermatozoon of *Homolodromia kai* has the following characteristics. The ratio of length to width of the acrosome is 0.4; zonation of the acrosome is predominantly horizontal; the operculum is perforate and lacks opercular projections such as are diagnostic of homolids; the operculum is not continuous with the acrosomal capsule, and, in contrast with raninoids, it is moderately thick and is of moderate width, not thin and occupying much of the width of the acrosome as in cyclodorippoids; there is no periopercular rim nor an accessory opercular ring; protrusion of subopercular material through the operculum is well developed; a true acrosome ray zone of the type seen in paguroids, other anomurans and in brachyurans of the Heterotremata *sensu stricto*, is absent although a "finger-print" like zone is possibly homologous with this; the ragged outer acrosomal zone and the xanthid ring, typical of xanthids and some of their relatives, are absent; an anterior pale zone of the acrosome, seen also in *Stindromia*, *Dromidiopsis*, *Dynomene* and *Paradynomene*, is present; the subacrosomal chamber extends pre-equatorially in the acrosome as in all investigated species excepting *Ranina ranina*; the head of the putative perforatorium is bilaterally symmetrical, as in *Stindromia*, *Dromidiopsis* and *Paradynomene*; corrugations of the wall of the perforatorial chamber, a thickened ring, concentric lamellae, capsular chambers, projections and flanges are absent. Nuclear arms and a definite posterior median process are not demonstrable.

Dynomenidae. GUINOT [5, 8, 10], and GUINOT, JAMIESON & RICHER DE FORGES [11], ranked dynomenids as a family in the superfamily Dromioidea, placed with the Homolodromioidea in the subsection Dromiacea, within the section Podotremata. This placement of dynomenids is wholly supported in both analyses but as indicated above, the Dynomenidae does not have spermatological support as a monophyletic group (Fig. 1A, B).

Separation of the Dynomenidae from the Dromiidae is justified, in non-spermatozoal characters, by a large number of differences [6] which include complete modification of the coxa of P5 as a penis. Furthermore, dynomenids show reduction of P5 instead of P4 and P5 as in the

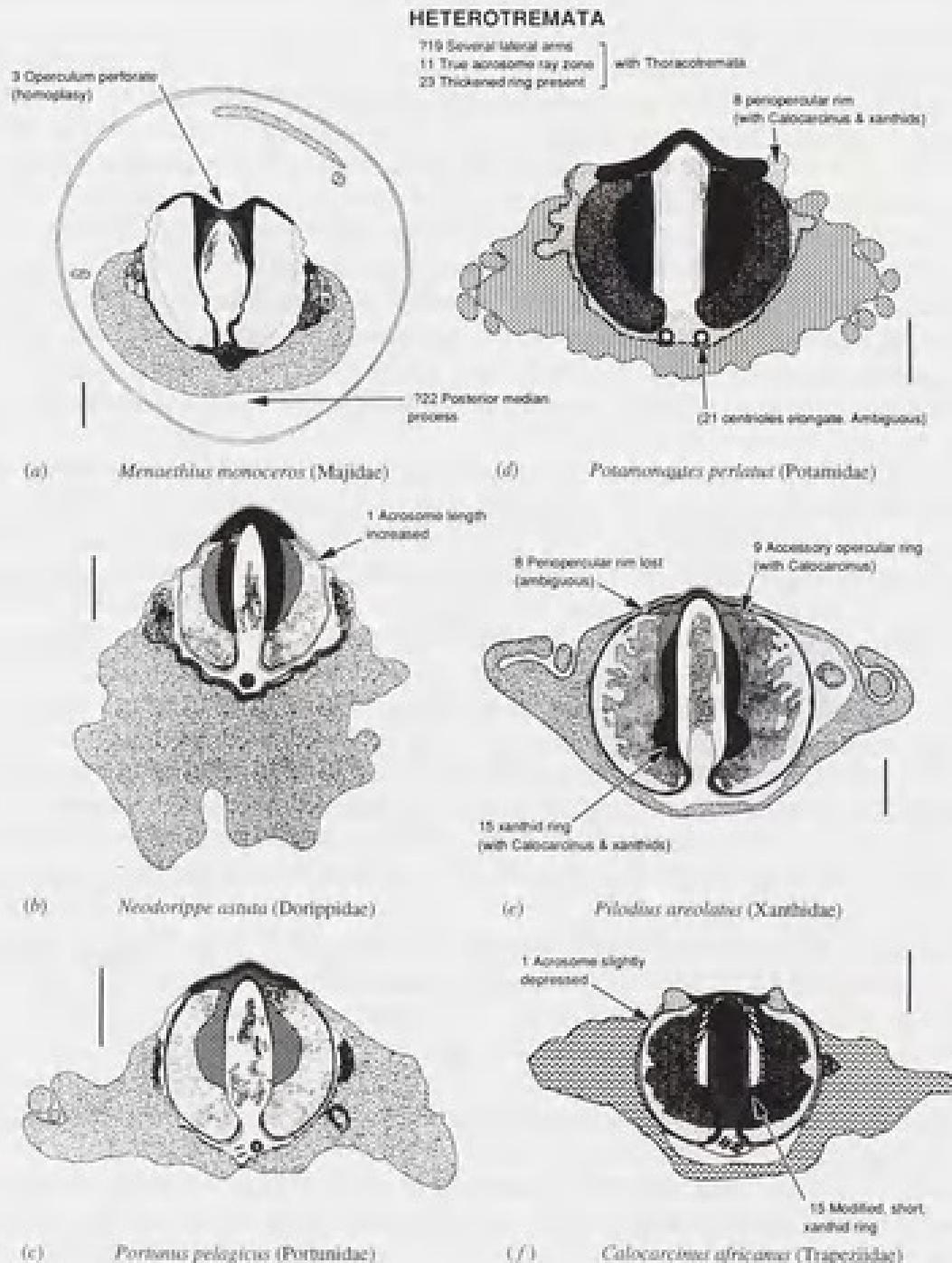


FIG. 4. — Drawings of spermatozoa of Heterotremata used in this analysis. a: *Menaethius monoceros* (Majidae). b: *Neodorippe 'astuta'*, now considered close to *N. callida* (Dorippidae). c: *Portunus pelagicus* (Portunidae). d: *Potamonectes perlatus* (Potamidae). e: *Pilodius areolatus* (Xanthidae). f: *Calocarcinus africanus* (Trapeziidae). The chief apomorphies are indicated but see text for a more detailed explanation. Scale bar 1 μ m. Sources as listed in Material and methods. After [21].

Dromiidae. Despite the more brachyuran facies of some species, several features of the Dynomenidae appear to be plesiomorphic and to accord with the earlier appearance of dynomenids in the fossil record relative to dromiids.

The sperm of *Dynomene* aff. *devaneyi* (Fig. 6A) resembles that of *Homolodromia kai*, described above, in all features mentioned, with the exception of the following. The ratio of length to width of the acrosome is 0.5; two nuclear arms are detectable; and a posteromedian process is absent.

Archaeobrachyura. The phylogram for combined data (Fig. 1B), as previously [21], supports recognition of the Archaeobrachyura of GUINOT [5], containing the superfamilies Homoloidea, Raninoidea and Cyclodorippoidea (=Tymoloidea). The single spermatozoal synapomorphy for the Archaeobrachyura is weak: the presence of a posterior median process. It is, however, reinforced by the somatic character loss of the uropods [21]. The grouping Archaeobrachyura is not, however, supported in the purely spermatozoal analysis (Fig. 1A) in which *Latreillia* and the homolids group with the Dromiacea (Dromiidae, Dynomenidae and Homolodromiidae) and not with the raninoid+cyclodorippoid assemblage.

Homolidae. Spermatozoal ultrastructure has been examined in seven species of the Homolidae: *Homola ranunculus*, *Paramola bathyalis* and *Dagnaudus* (= *Paramola*) *petterdi* [11, 12] and in *Homologenus* sp., *Latreillopsis gracilipes* (Fig. 2D), *Homolomannia sibogae*, and *Paromolopsis boasi* [27].

From spermatozoal ultrastructure, the Homolidae is a convincingly monophyletic entity in the combined and the spermatozoal analyses (Fig. 1A, B, and [21]). Synapomorphies of homolid spermatozoa are the following. The presence of numerous radial arranged extensions of the acrosomal operculum into the perforatorium has been established as an autapomorphy of the homolids [27] seen in no other brachyurans. Projection of subacrosomal material into the opercular perforation occurs but is weaker than the strong protrusion which is apparently independently developed in dromiaceans. Thirdly, the spiked-wheel form of the anterior expansion of the perforatorium is restricted to the Homolidae for which it is thus an autapomorphy. Whether a preexisting bilateral form of the head of perforatorium is a basic condition of all podotremes or the non-capitate condition is basic computes ambiguously. The radial spikes, approximately 12 in number, extend far laterally. They are supported by fibrous cores which radiate from the central core of the perforatorium. The spikes are much longer in *Latreillopsis gracilipes* (Fig. 2D) than in the other species, curving around the inner aspect of the vesicle almost to its base.

Raninoidea and Cyclodorippoidea. The Raninoidea (Fig. 3A-C) and Cyclodorippoidea (Fig. 3D-F) form a monophyletic (but unnamed) clade in both analyses (Fig. 1A, B, and [21]). Spermatozoal synapomorphies are not striking and two are ambiguous: reversal from a bilateral to a non-capitate condition of the perforatorium; and development of simple corrugations of the wall of the perforatorial chamber. Unambiguous are development of outward projections of the capsule (present study and [21]), seen homoplasically in *Stimdromia*; and, somatically, though confined to the Raninoidea, loss of the subcheliform development of pereopods 5.

Raninoidea. Spermatozoal ultrastructure has been investigated in *Ranina ranina* [16] (Fig. 3C), in the subfamily Ranininae, *Raninoides* sp. [26] (Fig. 3B), in the subfamily Raninoidinae (reinstated by GUINOT [9]), and *Lyreidus brevifrons* Sakai, 1937 [26] (Fig. 3A), in the subfamily Lyreidinae [9]. These raninoids, as a group, are well defined spermatologically (Fig. 1A, B) by virtual continuity of the operculum with the capsule and alteration of the zonation of the acrosome vesicle to an intermediate condition, with development of a concentric condition in *Ranina ranina*. The intermediate condition is homoplastic with *Dromidiopsis* and *Latreillia*. Somatically raninoids have lost subcheliform modification of pereopods 5 (this study and [21]), perhaps correlated with a burrowing or swimming habit.

Ranina [16] and *Raninoidea* [26] share strong synapomorphies: development of posterior capsular chambers, one in *Ranina* (Fig. 3C) increasing to several in *Raninoidea* (Fig. 3B); and the remarkable lateral flange on the capsule. An ambiguous change, not shown in some parsimony analyses [21], is development of branched septum-like corrugations of the wall of the perforatorial chamber from the unbranched form basal to the raninoid-cyclodorippoid clade and persistent in *Lyreidus*. There is also a strong trend towards a subspheroidal form of the acrosome, most developed in *Ranina* in which zonation becomes concentric; and in which the perforatorium, apparently secondarily, becomes only postequatorial. In *Lyreidus* (Fig. 3A), the acrosome becomes secondarily depressed; and the "amoeboid" form of the head of the perforatorium is seen as development of a capitate condition independently of that in dromiids and homolids (This study and [21]).

Cyclodorippoidea. The Cyclodorippoidea form the sister-group of the Raninoidea in both analyses (Fig. 1A, B). The sperm of the three cyclodorippoids (Fig. 3D-F) [25] are well defined by the extreme width of the operculum relative to the acrosome. As an ambiguous change, corrugations of the wall of the perforatorial chamber are invaginations with filaments. A synapomorphy of *Xeinostoma* (Fig. 3E) and *Tymolus* (Fig. 3F) is the extreme thinness of the operculum. *Xeinostoma* is apomorphic in further depression of the acrosome. *Cyonomus* (Fig. 3D) is apomorphic for all investigated podotremes in losing the opercular perforation. This supports erection of a separate family Cyonomidae [33]. It appears to have developed the flange-like extension of the lower acrosome zone independently of *Paradynomene* and *Homolodromia* but the similarity is striking and cyclodorippoid relationships require further investigation (This study and [21], GUINOT & TAVARES, in preparation).

Latreilliidae. The position of *Latreillia* sp. (Fig. 2E) is equivocal, as in the previous cladistic analyses [21]. It forms a polytomy either with Homolidae+Raninoidea-Cyclodorippoidea with the combined data set (Fig. 1B) or with Homolidae+Dromiidae-Dynomenidae-Homolodromiidae, for sperm only (Fig. 1A). This archaeobrachyuran status of *Latreillia* for the combined data is in accordance with placement of the Latreilliidae by GUINOT [5] near the Homolidae and contradicts the view of WRIGHT AND COLLINS (see [5]) that the accepted close relationship between the Homolidae and Latreilliidae is based on no more than a few primitive features. Confirmation of the ultrastructural characteristics of *Latreillia* sperm is desirable as many spermatozoa of this species used in the cladistic study appeared malformed. The sole detected apomorphy of *Latreillia* is development, homoplasically with *Dromidiopsis*, of an intermediate condition of the acrosome vesicle contents from the horizontally zoned condition. In the combined analysis this condition is an ambiguous apomorphy as it could alternatively be basal to the Podotremata but it is unequivocal in the purely spermatozoal analysis.

Heterotremata and Thoracotremata

In the cladistic analyses (present study and [21]) (Fig. 1A, B), it is seen that within the heterotreme-thoracotreme assemblage, the Thoracotremata (Fig. 5) is a monophyletic taxon whereas the Heterotremata *sensu stricto* (Fig. 4) is a paraphyletic grouping.

The combined Heterotremata-Thoracotremata, which may be termed the Heterotremata *sensu lato* [21], is defined by a convincing synapomorphy, presence of the thickened ring. Other spermatozoal synapomorphies, although unambiguous, are less convincing. Multiplication of lateral arms from three, common to paguroids and podotremes, to several is a trend rather than a diagnostic basal apomorphy as it results from polymorphism, there being three in at least some majids as in the leucosiid *Iliacantha subglobosa* [3]. Presence of a true acrosome ray zone appears to be a synapomorphy but is seen, apparently homoplasically, in paguroids.

Cladistically (present study and [21]), the Heterotremata *sensu lato* form a grouping whether or not non-spermatozoal characters are included but the sternal female pores constitute, as GUINOT [5, 6] suggested, their non-spermatozoal synapomorphy. In the combined analysis

(Fig. 1B) as previously [21], *Neodorippe* forms the plesiomorphic sister-group of all other included crabs. Its sole (ambiguous) spermatozoal apomorphy is very slight elongation of the acrosome beyond a spheroidal shape. It is noteworthy, in view of their relatively plesiomorphic spermatozoal ultrastructure, that dorippids exhibit carrying behaviour, like most dromiids, *Neodorippe callida* attaching to leaves. The dorippid included here, and referred to as *Neodorippe astuta* (see [22]), is close to *N. callida* but definitive identification has not been made. There are, however, no spermatozoal apomorphies distinguishing the remaining crabs of the Heterotremata *sensu lato* from *Neodorippe*, though somatic synapomorphies are loss of subcheliform development of pereopods 5 (and also P4). On the basis of purely spermatozoal data, as in the former analysis [21], the Majidae occupy this basal position (Fig. 1A).

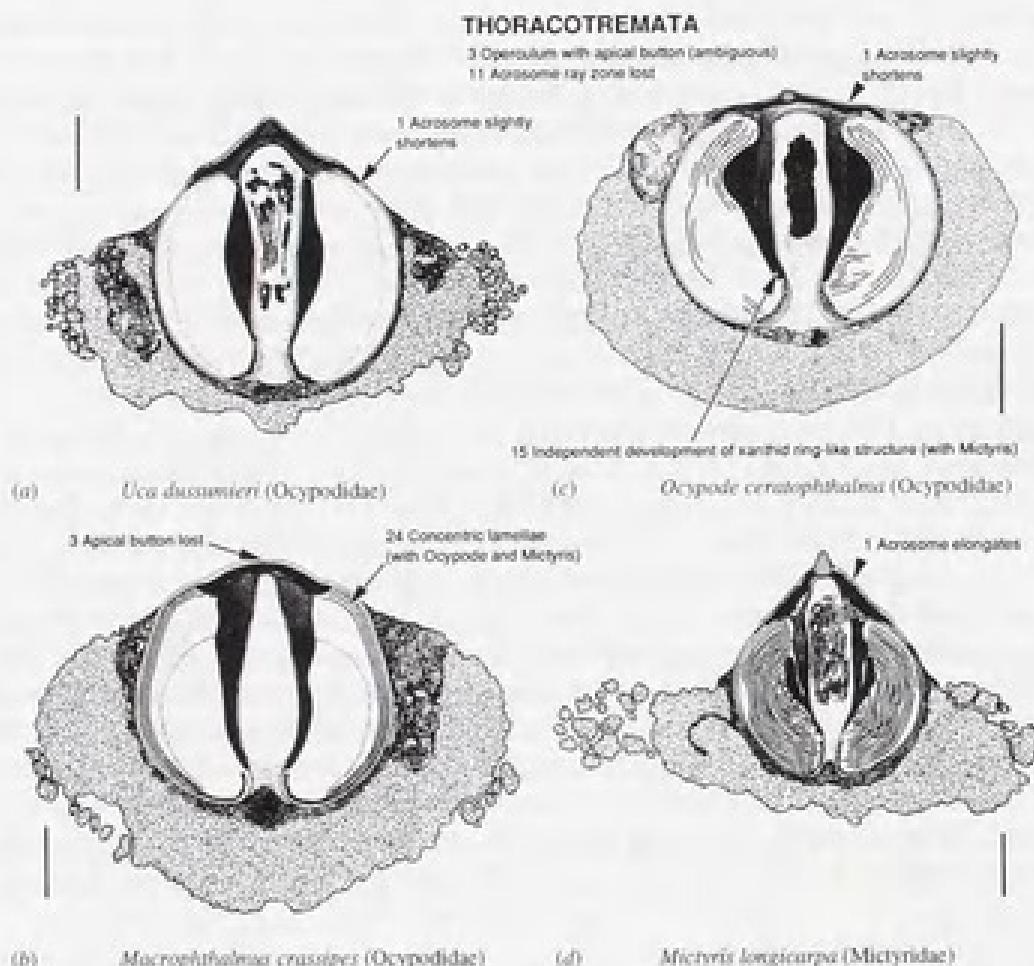
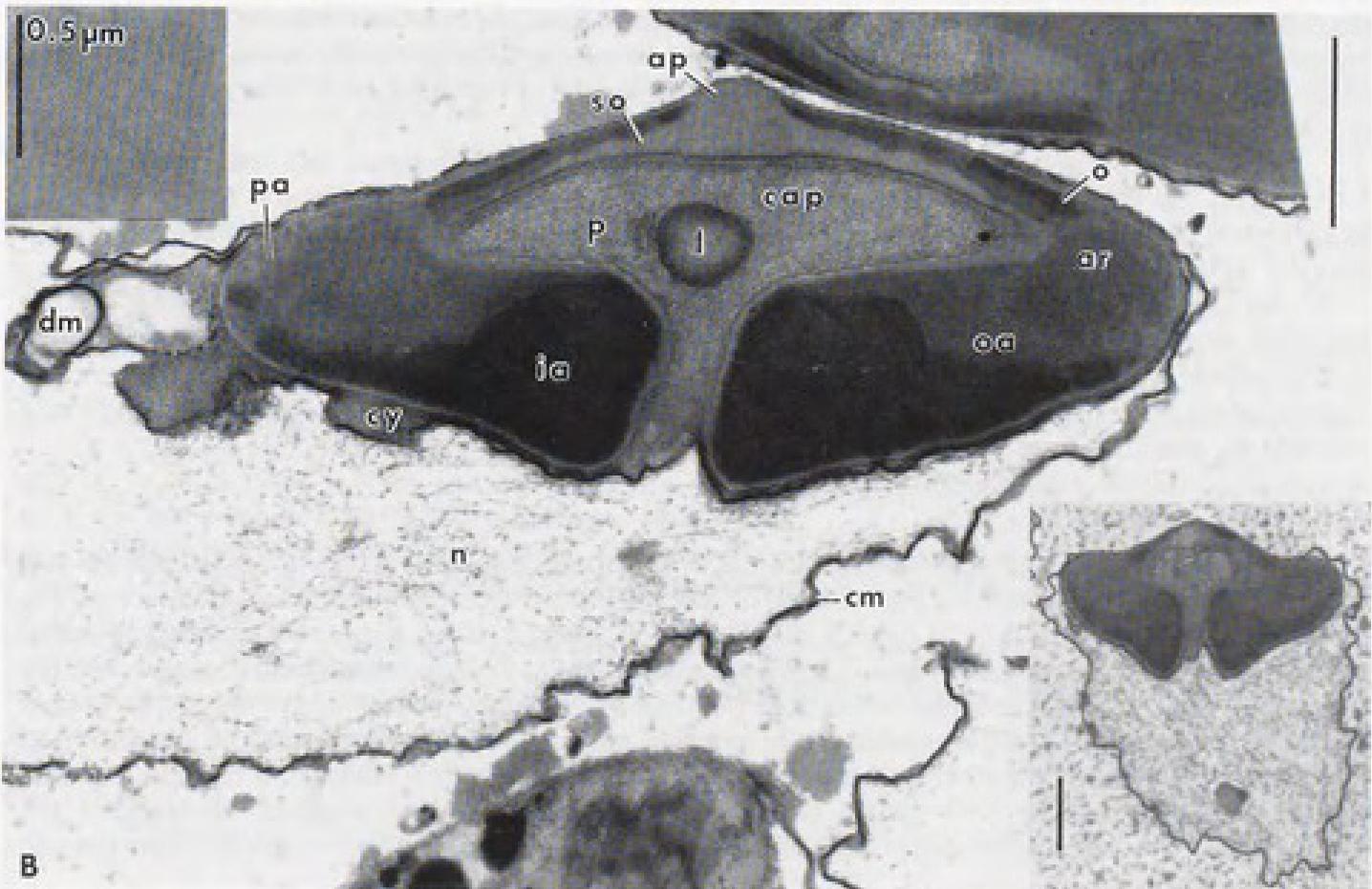


FIG. 5. — Drawings of spermatozoa of Thoracotremata used in this analysis. a: *Uca dussumieri*. b: *Macrophthalmus crassipes*. c: *Ocypode ceratophthalma* (all Ocypodidae). d: *Mictyris longicarpus* (Mictyridae). The chief apomorphies are indicated but see text for a more detailed explanation. Scale bar 1 μ m. Sources as listed in Material and methods. After [21].

FIG. 6. — Transmission electron micrographs of longitudinal sagittal sections of the sperm of two podotreme species described in this chapter. A: *Dynomene* aff. *devaneyi*. Short diameter of perforatorium in main micrograph, long diameter right inset. B: *Homolodromia kai*. Long diameter of perforatorium in main micrograph, short diameter in right inset, detail of acrosome ray zone ("fingerprint" zone) in left inset. ap, apical protuberance; ar, acrosome ray zone; cap, capitate region of perforatorium; cm, cell membrane; cy, cytoplasm; dm, degenerating mitochondrion; ia, inner acrosome zone; l, lamellae; n, nucleus; o, operculum; oa, outer acrosome zone; p, perforatorium; pa, anterolateral pale acrosome zone; so, subopercular zone.



Within the heterotremes above *Neodorippe* (combined data, Fig. 1B), or above the majids (sperm only, Fig. 1A), *Calocarcinus* and the xanthid *Pilodius* group together but there is ambiguity as to whether development of a simple xanthid ring is basic to the two and is retained in xanthids but transformed in *Calocarcinus* (as seems likely), whether the supposedly transformed condition is basal, or whether each developed a form of the xanthid ring *de novo*. Their ancestor may have slightly shortened the acrosome. Other significant synapomorphies, retained in *Calocarcinus* and *Pilodius*, are development of an accessory opercular ring and the ragged form of the outer acrosome zone. However, too literal an acceptance of the precise sequence of changes should be avoided as it was found in the previous analysis [21] that *Potamonautes* (Fig. 4D), *Calocarcinus* (Fig. 4F) and the two xanthids included were unified by a periopercular rim, remaining well developed in *Potamonautes* (Fig. 4D) and *Calocarcinus* (Fig. 4F), becoming weak in the xanthid *Etisus* (excluded from the present analyses), and lost in *Pilodius* (Fig. 4E) but that this character is ambiguous. When the character was treated as ordered, it was unambiguous, being represented weakly in the ancestor of this clade and in *Etisus* (excluded from the present study), developing from this state to well developed in *Calocarcinus* and *Potamonautes*, and being lost in *Pilodius* [21]. From intuitive studies, xanthids are united by the presence of a ring around the base of the inner acrosome zone, the xanthid ring [15]. In the present study strong development of a periopercular rim occurred independently in *Potamonautes* relative to *Calocarcinus*. Majids are characterized by development of perforation of the operculum and of a posterior median process independently of that in podotremes. *Portunus pelagicus* shows no apomorphies beyond those of basal heterotremes.

The Thoracotremata (Fig. 5A-D) selected for the cladistic studies (This study and [21]) were found to be monophyletic (Fig. 1A, B) on the basis of two unambiguous characters: loss of the acrosome ray zone and movement of the male pores (following that of the female pores basic to heterotremes) onto the sternum. Development of the characteristic apical button in the perforatorium appears ambiguous owing to its alternative absence or loss in *Macrophthalmus* (Fig. 5B). A more detailed investigation of thoracotremes might resolve the issue of whether the button is basic to thoracotremes. In view of the close relationship generally recognized between *Macrophthalmus* and *Ocypode* (Fig. 5C), it seems likely that the absence in *Macrophthalmus* is due to loss of a basic thoracotreme condition.

Concentric lamellae in the acrosome appear to be a development, not seen in *Uca* (Fig. 5A), basal to the higher thoracotremes, *Mictyris* (Fig. 5D), *Ocypode* (Fig. 5C) and *Macrophthalmus* (Fig. 5B). *Uca* differs from the basic thoracotreme condition only in slight shortening of the acrosome.

An interesting outcome of the cladistic analyses is that the "modified xanthid ring" which has been recognized as a characteristic of some thoracotreme sperm and considered to suggest derivation of thoracotremes from a xanthid stock [18] computes as an entirely independent development not related to the xanthid structure (this study and 21). This does not completely rule out the possibility of derivation from the xanthid ring, however.

Concluding remarks

The parsimony analyses, whether using only spermatozoal characters or spermatozoal and non-spermatozoal characters, provide a remarkable affirmation of the classification of the Brachyura by GUINOT [4, 5] which differed so markedly from pre-existing and, in some schools, still current classifications. Thus the validity of, and phylogenetic justification for, the groupings Podotremata and Heterotremata (though only in *sensu lato*) and Thoracotremata is affirmed. Podotremes and Heterotremata *sensu lato* are confirmed as sister-taxa. Association of the Raninoidea and Cyclodorippoidea is upheld (as sister-groups), each with convincing and unique synapomorphies, but sperm data considered alone do not support alliance of the Homolidae, though equally clearly defined, with this Raninoidea+Cyclodorippoidea couplet and

therefore do not endorse the grouping Archaeobrachyura. Combined spermatozoal and non-spermatozoal data do, however, support the Archaeobrachyura. There is, nevertheless, molecular evidence [31] that raninoids are more closely related to the heterotreme-thoracotreme assemblage than they are to other podotrematous crabs. Within the Podotremata, the Dromiacea *sensu* GUINOT (Dromiidae, Dynomenidae and Homolodromiidae) is confirmed spermatologically as a monophyletic grouping but the discreteness of the three constituent families is not upheld. *Homolodromia* displays a remarkable mixture of dromiid and dynomenid spermatozoal features while lacking any distinctive apomorphy, and does not appear spermatologically to occupy the basal position in the Dromiacea indicated by GUINOT [5, 10] (the apparent agreement of the combined analysis, in this respect, is due solely to the spermatozoal characters.) The Dynomenidae and Dromiidae are each found to be paraphyletic. An 18S rRNA study [31] also found little support for the Dromiidae as a monophyletic group but, unlike the present study, excluded one dromiid from the Brachyura; the two dromiids included in the molecular analysis never formed a clade. In a bootstrap analysis the dromiid *Hypoconcha arcuata* grouped with a hermit crab while *Dromidia antillensis* formed their sister taxon [31]. Examination of the spermatozoa of *Hypoconcha* would be very desirable. Relationships of *Latreillia* sp., the sole representative in the present study of the Latreilliidae and considered an homoloid by GUINOT [5] and GUINOT & RICHER DE FORGES [12], are equivocal. It forms a polytomy either with Homolidae+Raninoidea-Cyclodorippoidea with the combined data set or with Homolidae+Dromiidae-Dynomenidae-Homolodromiidae, for sperm only. The association by GUINOT [5] of the Dorippoidea, Portunoidea, Xanthoidea, and Majoidea in the non-thoracotreme Heterotremata is fully supported spermatologically (calappoids, corystoids, parthenopoids, bellioids and leucosioids, also included by GUINOT, were not included in computations). The Thoracotremata is unequivocally supported as a monophyletic group.

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NOTE ADDED IN PROOF

In a valuable paper received as this chapter was going to press, SCHOLTZ & RICHTER (1995) conclude, from a preliminary, mainly morphological analysis, that the Homolodromiidae are the sister-group of all other brachyurans. If this is so, the similarity of the sperm of *Homolodromia* to that of *Paradynomene* is problematical.

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