

HOMOLOGOUS FUNCTIONAL STRUCTURE AND ORIGIN OF  
THE SPERMATOPHORES IN SIX PALAEMONID SHRIMPS  
(DECAPODA, CARIDEA)

BY

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RÉSUMÉ

Les structures du canal déférent et des spermatophores de six espèces de crevettes Palaemonidae (*Macrobrachium nipponense*, *M. formosense*, *M. japonicum*, *M. latidactylus*, *M. rosenbergii* et *Palaemon paucidens*) ont été comparées et se sont révélées homologues. Le spermatophore se compose d'une matrice adhésive, d'une matrice protectrice, et d'une masse spermatique. L'épithélium colonnaire périphérique et inférieur du canal déférent sécrète la matrice adhésive, alors que l'épithélium central et supérieur (le typhlosole) sécrète la matrice protectrice. La matrice qui correspond à la masse de spermatozoïdes a des qualités similaires à celles de la matrice protectrice mais provient des testicules, avec les spermatozoïdes. Les analogies entre les structures et les qualités du spermatophore chez les Palaemonidae et chez d'autres groupes sont discutées.

INTRODUCTION

A spermatophore is defined as a complex comprised of spermatozoa and male secretions which wrap or embed the sperm. Spermatophores play an important role in sperm transfer, sperm storage, and fertilization, for a wide range of animals (Mann, 1984). The origin, morphology, function and/or histology of the spermatophore have been reported for over 50 species of decapod crustaceans (see the review by Dudenhausen & Talbot, 1983). To the excellent general description about the origin and function of the decapod spermatophore by Dudenhausen & Talbot (1983), only a few details need to be added. A comparison of the functional structure of the spermatophores among taxa can, however, provide information for phylogenetic studies and evolutionary divergence.

We described the structure, origin, function, and alteration of the spermatophore in the palaemonid shrimp *Macrobrachium rosenbergii* (De Man, 1879) (cf. Chow et al., 1982). The present report summarizes observations on structures of vasa deferentia and spermatophores in six species belonging to the subfamily Palaemoninae, the origin and function of spermatophoric components

are discussed, and the palaemonid spermatophore structure is compared with those of other taxa.

#### MATERIALS AND METHODS

Six palaemonid shrimp species (*Macrobrachium nipponense* (De Haan, 1849), *M. formosense* (Bate, 1868), *M. japonicum* (De Haan, 1849), *M. latidactylus* (Thallwitz, 1891), *M. rosenbergii* (De Man, 1879) and *Palaemon paucidens* (De Haan, 1841)) were used. All of the species except *M. rosenbergii* are native species of Japan. The vasa deferentia and female sterna to which spermatophores were attached in each species were dissected, fixed in Bouin's fluid, and embedded in paraffin (m.p. 56°C). The enlarged distal portion of the vas deferens (see Chow et al., 1982) and sternum with spermatophore were sectioned transversely at 4-6  $\mu\text{m}$  thickness and stained with Delafield's hematoxylin and eosin.

#### RESULTS

Transverse sections of the enlarged distal portion of the vas deferens and the spermatophore are shown in figs. 1 and 2.

The structure of the vas deferens was similar among the five *Macrobrachium* species examined (fig. 1 A-E), as diagrammatically illustrated in fig. 1 F. The vas deferens is a tube which consists of an epithelial wall (*le* and *he*) inside, and muscle layer (*ml*) outside. The components of the vas deferens are gelatinous and consist of three parts; sperm mass (*sm*), basophilic matrix (*bm*), and eosinophilic matrix (*em*). The matrix which fills spaces between spermatozoa in the sperm mass, is also basophilic. As seen by light microscopy, there is no border between basophilic matrix (*bm*) and sperm mass (*sm*), suggesting that both of the matrices are equal in property. On the other hand, a clear boundary can be observed between the eosinophilic matrix (*em*) and the other matrices. The epithelium surrounding these matrices is a simple column, but can be distinguished into two epithelia; the peripheral low columnar epithelium (*le*) and the central high columnar epithelium (*he*). In all species examined the eosinophilic matrix (*em*) always co-exists along with the peripheral low columnar epithelium (*le*), and the basophilic matrix (*bm*) with the central high columnar epithelium (*he*). The muscle layer (*ml*) contracts to extrude the components of vas deferens at ejaculation. The tube-like components ejaculated from a pair of gonophores laterally, fuse with each other and attach to the female sternum during mating. The eosinophilic matrix (*em*) which surrounded the basophilic matrix (*bm*) and sperm mass (*sm*) in the vas deferens, is always positioned to the female sternum (*st*), while the basophilic matrix (*bm*) is exposed to the opposite side in the spermatophore (fig. 2). When newly extruded, both of the matrices are gelatinous but the eosinophilic matrix

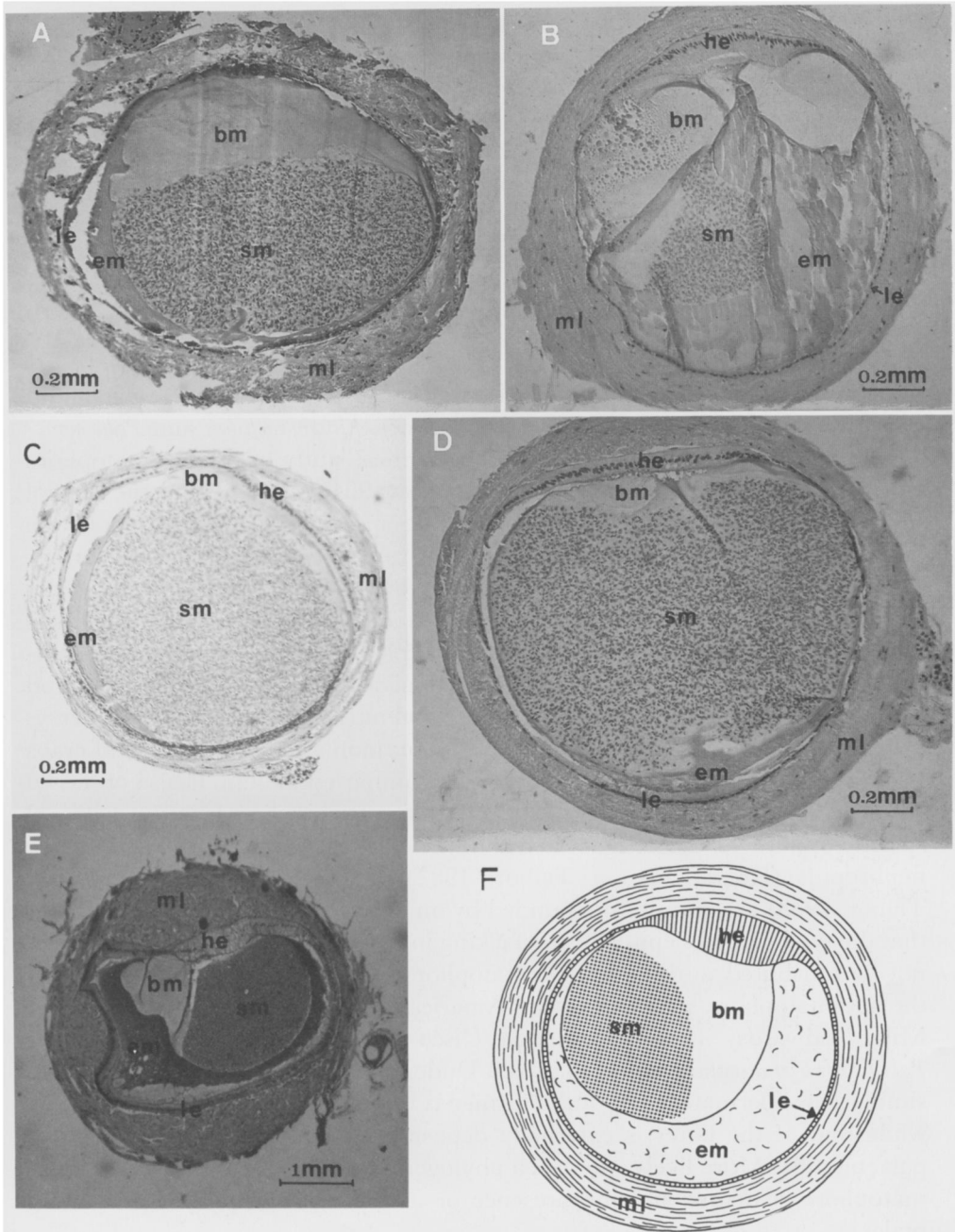


Fig. 1. Transverse sections of terminal portion of vasa deferentia in five *Macrobrachium* species; (A) *M. nipponense*, (B) *M. latidactylus*, (C) *M. formosense*, (D) *M. japonicum*, (E) *M. rosenbergii* and (F) diagrammatic illustration. Abbreviations are (bm) basophilic matrix, (em) eosinophilic matrix, (he) high columnar epithelium, (le) low columnar epithelium, and (sm) sperm mass.

(*em*) is more sticky than the basophilic matrix (*bm*). Functionally, therefore, the eosinophilic matrix and basophilic matrix in the spermatophore should be called adhesive matrix (*am*) and protective matrix (*pm*), respectively. Three *Macrobrachium* spp. and *Palaemon paucidens* are homologous in the spermatophore structure, although *Palaemon* lacked the sperm-free protective matrix observed in *Macrobrachium* spp. (fig. 2). In one instance, two neatly piled spermatophores were observed on the sternum of a twice-mated *M. latidactylus* (fig. 2 B).

#### DISCUSSION

These data, together with our previous observations (Chow et al., 1982) indicate homology in the functional structure and origin of the palaemonid spermatophore, with minor difference between *Macrobrachium* and *Palaemon*.

In a detailed ultrastructural and histochemical study of the spermatophore of *Macrobrachium rosenbergii*, Dougherty et al. (1984) reported that the medial mucus mass (equivalent here to "basophilic matrix") and sperm mass were similar in fine structure and histochemical reactivity except that the former lacked spermatozoa. Probably, the matrix of the sperm mass possesses the same properties as the basophilic matrix, but surely originated in the testis with the spermatozoa. The central high columnar epithelium which continuously secretes the basophilic matrix coincides with the typosole observed in other decapod vasa deferentia, notably palinurids (Matthew, 1951; Berry, 1970; Berry & Heydorn, 1970; Radha & Subramoniam, 1985) and sand crabs (Subramoniam, 1984). A peripheral low columnar epithelium is also observed in these species for secretion of an adhesive matrix to cement the external spermatophore to the female sternum. In contrast, the spermatophores of nephropids (Kooda-Cisco & Talbot, 1982) and astacids (Dudenhause & Talbot, 1983) are entirely surrounded by an outer bounding layer, suggesting that the typosole-like epithelium is lacking in these species. This difference can not be attributed to different spermatophore maintenance systems; although the spermatophore structure in the American Lobster *Homarus americanus* H. Milne Edwards, 1837 (cf. Kooda Cisco & Talbot, 1982) and crayfish *Pacifastacus leniusculus* (Dana, 1852) (cf. Dudenhause & Talbot, 1983) are quite similar, the spermatophore of the former is inserted into an annulus ventralis while that of the latter is externally deposited on the female sternum as in palaemonids. More likely, there is a phylogenetic relationship between the spermatophore structure and the presence or absence of a copulation organ in males.

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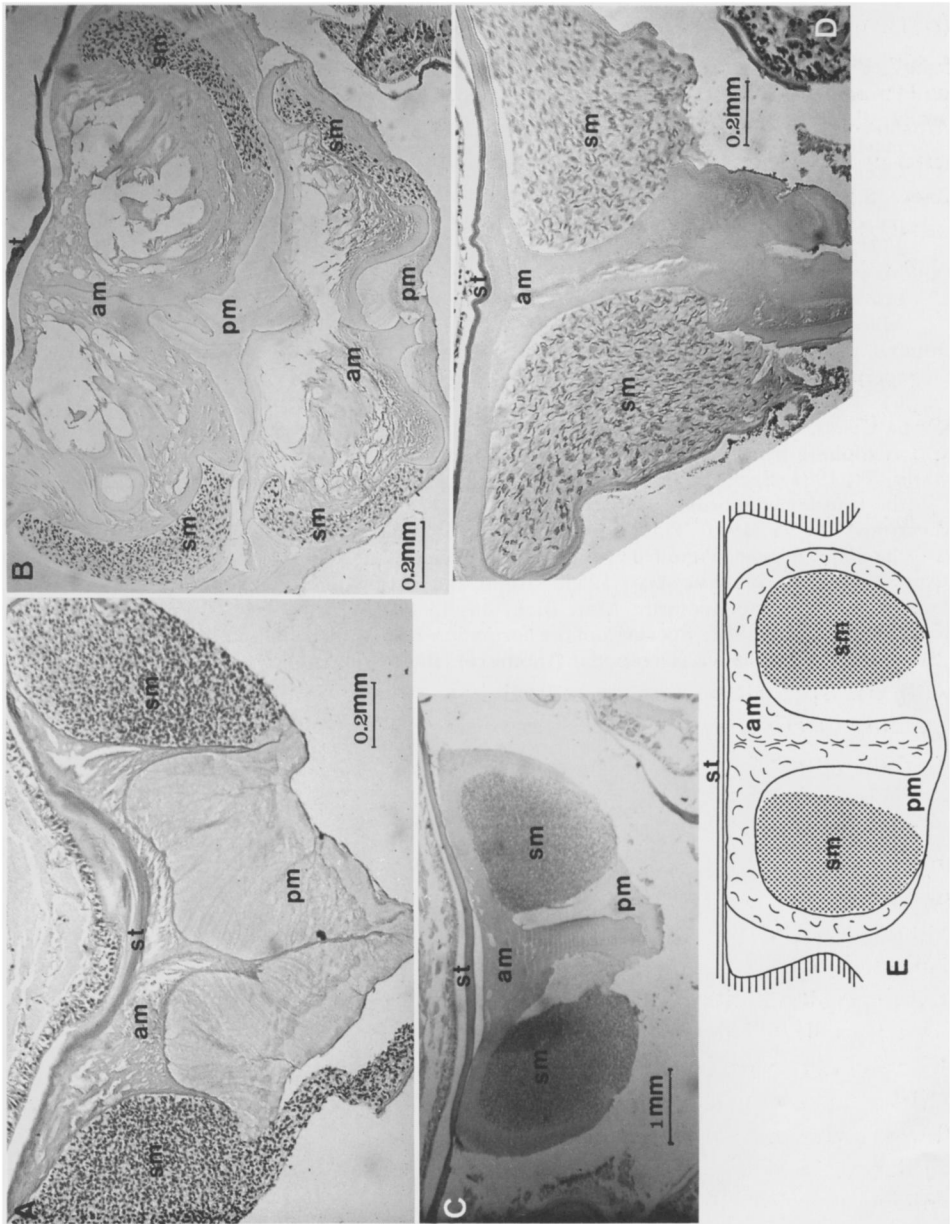


Fig. 2. Transverse sections of spermatophores deposited on the female sternum in three *Macrobrachium* species and in *Palaemon paucidens*; (A) *M. nipponense*, (B) *M. latidactylus*, (C) *M. rosenbergii*, (D) *P. paucidens* and (E) diagrammatic illustration. Abbreviations are (am) adhesive matrix, (pm) protective matrix, (sm) sperm mass, and (st) sternum.

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