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Author(s): Peter G. Beninger, Robert W. Elner and Yves Poussart

Source: *Journal of Crustacean Biology*, Vol. 11, No. 2 (May, 1991), pp. 217-228

Published by: Oxford University Press on behalf of The Crustacean Society

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GONOPODS OF THE MAJID CRAB *CHIONOECETES OPILIO* (O. FABRICIUS)

Peter G. Beninger, Robert W. Elner, and Yves Poussart

ABSTRACT

To further elucidate the reproductive processes of the snow crab *Chionoecetes opilio* (O. Fabricius) the first and second gonopods of adult specimens were examined using scanning electron microscopy and histology. Surface features and setal types are described for both gonopods. The gonopods are highly modified compared to other brachyuran crabs and lower crustaceans. Suggestions for setal function are presented, based on size, orientation, location, fine structure, and cuticular insertion. Tubulation of the endopod is observed in both the first and second gonopods. Rosette glands are abundant in the basal half of the first gonopod, but are absent in the second gonopod. A duct network from the rosette glands terminates in cuticular pores that are restricted to the ejaculatory canal, indicating that the rosette glands function in copulation, probably contributing to the seminal fluids. A mechanism for transfer of seminal fluids is proposed, based on the relative sizes of the gonopods and the morphology of the second gonopod.

RÉSUMÉ

Afin d'élucider davantage les processus reproducteurs du Crabe des neiges, *Chionoecetes opilio* (O. Fabricius), les premiers et deuxième gonopodes ont été examinés à l'aide de la microscopie électronique à balayage et de l'histologie. Les gonopodes sont très modifiés par rapport à ceux des autres Brachyours et des Crustacés plus primitifs. La topologie superficielle et les types de soies sont décrites pour les deux gonopodes. Des suggestions pour la fonction des soies sont présentées, selon leur dimension, leur orientation, leur structure, et leur insertion cuticulaire. Une tubulation est évidente dans les premiers et deuxième gonopodes. Des glandes rosettes sont abondantes dans la moitié basale du premier gonopode, mais absentes dans le deuxième gonopode. Un réseau de canalicules provenant des glandes se termine dans des pores distribués uniquement dans la cuticule du canal éjaculateur du premier gonopode, laissant présager une fonction copulatoire, notamment en tant que contribution aux fluides séminaux. Un mécanisme pour le transfert des fluides séminaux est proposé, basé sur les dimensions relatives et la morphologie des gonopodes.

The first and second pair of pleopods in male brachyuran crustaceans are variously modified as gonopods. Their role in the transfer of seminal fluids has been known for some time (Stephensen, 1946; Cronin, 1947; Ryan, 1967; Hartnoll, 1969, 1975; Bauer, 1976, 1986; Elner *et al.*, 1985). The specificity of gonopod function in copulation probably contributes to their observed intraspecific morphological stability. Due to its conservative nature, gonopod morphology has been proposed as an important taxonomic character (Chambers *et al.*, 1980; Martin and Abele, 1986). Furthermore, distinct trends are evident in the evolution of these appendages (Hartnoll, 1975; Bauer, 1986), and the importance of detailed studies of insemination morphology and function in the formulation of hypotheses concerning decapod phylogeny has been underscored (Bauer, 1986).

Despite the intrinsic importance of such work, data concerning the detailed structure of decapod gonopods are largely lacking. The bulk of the literature is confined to line drawings of gross morphology, usually of the first gonopod (Stephensen, 1946; Cronin, 1947; Garth, 1958; George, 1963; Nishimura, 1967; Tirmizi and Qureshi, 1970; Hartnoll, 1975; Martin and Abele, 1986). Although the utility of scanning electron microscopy (SEM) in the study of the surface features of gonopods has been demonstrated (Abele, 1971), SEM data remain scanty, being limited to special features of the gonopods of a few distantly related species (Bauer, 1976; Tombes and Foster, 1979; Nicol and Nicol, 1983; Diesel, 1989).

The internal anatomy of brachyuran gonopods has been studied somewhat more extensively, but again attention has focused primarily on the first gonopod, and partic-

ularly on the rosette-shaped glands beneath the hypodermis. Although the position and structure of these glands have been progressively elucidated, their function remains unresolved (Spalding, 1942; Cronin, 1947; Johnson and Talbot, 1987; Diesel, 1989).

Here we address these questions through a detailed study of the external morphology and internal anatomy of the gonopods of the snow crab *Chionoecetes opilio* (Decapoda: Majidae). A preliminary study of the gonopod morphology of several brachyuran crab species was performed in 1983–1984 (R. W. Elnor and J. Stanley, unpublished), serving to orient the present detailed examination of the gonopods of *C. opilio*. The work is part of ongoing studies designed to elucidate the reproductive biology of this commercially important species (Elnor and Gass, 1984; Davidson *et al.*, 1985; Elnor *et al.*, 1986; Beninger *et al.*, 1988).

MATERIALS AND METHODS

As considerable change has been shown to occur in the gross morphology of the first gonopod with developmental stages (Nishimura, 1967), the present study was restricted to morphometrically mature individuals (according to the criteria of Conan and Comeau, 1986), thus allowing eventual comparisons with adults of other crab species.

Live snow crabs collected in July and August 1989 off Cape Breton Island and kept in an open-circuit seawater system were examined under a dissecting microscope. Illustrations of the anatomical relationships of the first and second gonopods were made from these specimens.

Five morphometrically mature male snow crabs were collected from Cape Breton Island, Nova Scotia, and Bonne Bay, Newfoundland, during the summers of 1987 and 1989. They were transported live to Moncton, where the first and second gonopods were removed at the abdominal insertion. The gonopods of 1 male were fixed in aqueous Bouin's solution, dehydrated in an ascending alcohol-HemoDe (Fisher Scientific Co., 711 Forbes Avenue, Pittsburgh, Pennsylvania 15219) series, embedded in paraffin, and sectioned at 5–7 μm . The sections were rehydrated in a descending HemoDe-ethanol-water series and stained using the Goldner variation of the Masson Trichrome topological technique (Gabe, 1968). These slides were observed and photographed using clear-field microscopy. The gonopods of an additional 3 individuals collected from Cape Breton Island in the summer of 1990 were processed for histology and light microscopy as described above.

The gonopods of the remaining 4 specimens were fixed in 2.5% glutaraldehyde in 0.2 M sodium cacodylate buffer (pH 7.4), postfixated in 1% osmium tetroxide, and dehydrated in an ascending ethanol series. They were dried with liquid CO_2 in a critical point

apparatus, sputter-coated with gold or gold-palladium, mounted on SEM stubs, and observed using a JEOL 35 scanning electron microscope.

RESULTS

As in other higher brachyurans, the right and left gonopods and their respective penes each form a complete insemination unit. The general functional morphology of the first and second gonopods conforms to that reported by Spalding (1942) for *Carcinus maenas* and Cronin (1947) for *Callinectes sapidus*. However, as described below, the detailed anatomy of the gonopods of *Chionoecetes opilio* is quite distinctive.

First Gonopod.—The first gonopod consists of a basal protopodite and an elongated endopodite, in which the cuticle is infolded the length of the endopodite, forming a tube which functions as an ejaculatory canal (Hartnoll, 1975; Figs. 2C, 5A, B). The second pleopod fits into this fold, which is medial in *Chionoecetes opilio*, while the penis fits into a slit on the lateral face at the base of the endopodite (Fig. 1A, C). Ejaculate from the penis is presumably pushed down the ejaculatory canal by the pumping motions of the second gonopod. In the apical region, the cuticular folds are easily distinguished as outer and inner folds (Fig. 2C). The first gonopod is approximately five times longer than the second gonopod (Fig. 1).

The first gonopod terminates in a recurved process, at the apex of which the ejaculatory canal opening forms a distinct spout (Fig. 2A, B). Three related types of setae are quite conspicuous on the terminal third of the pleopod; these have been termed types I, II, and III (Nishimura, 1967). The first two types differ morphologically only in length, the longer setal type I being found along the ejaculatory canal, while the shorter setal type II is limited to two short double parallel rows on the face opposite the canal (Fig. 2A). Both setal types I and II possess serial depressions along the proximal two-thirds of their length, while the distal one-third is characterized by the presence of a variable number of knobby processes (Fig. 3B, C). These setae are inserted into the gonopod in characteristic cup insertions (Fig. 3D). Setal type III is considerably shorter than the preceding types, and arranged in two double parallel rows extending basally from the setal type II rows (Fig. 3A). They possess

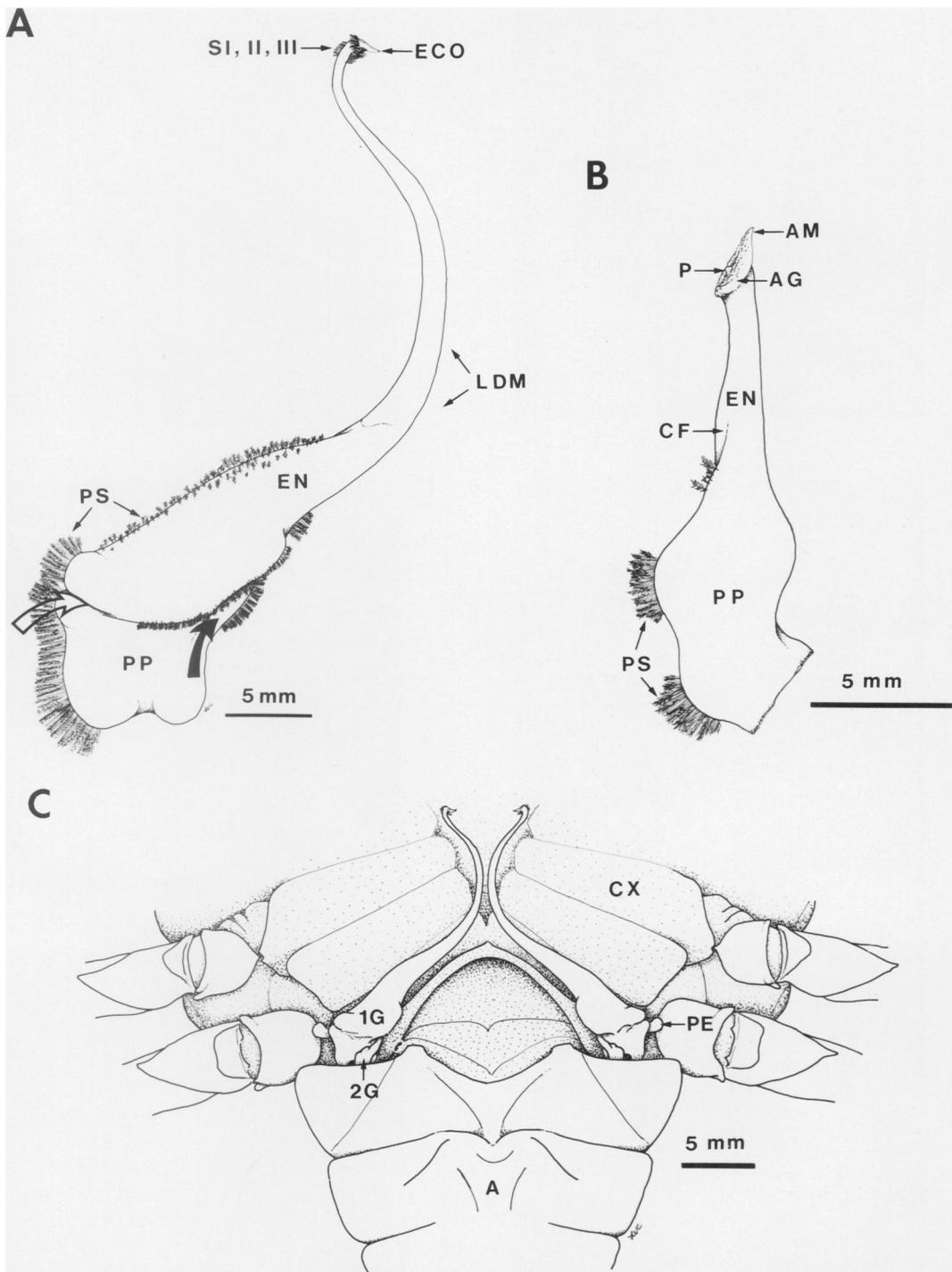
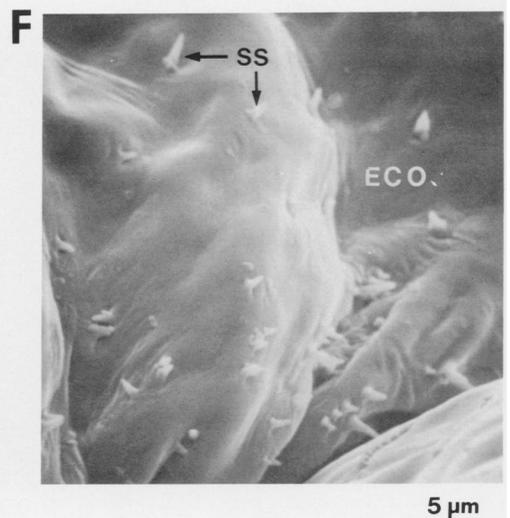
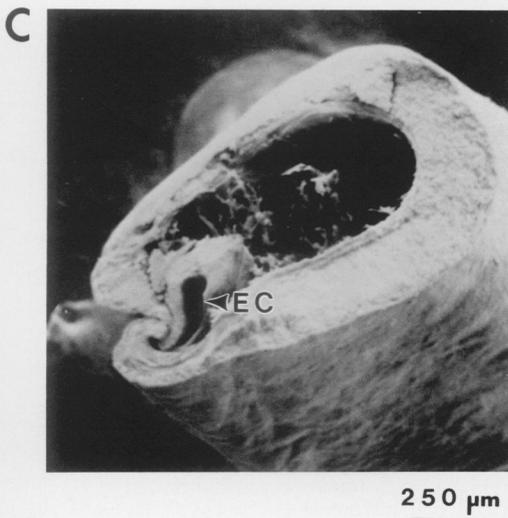
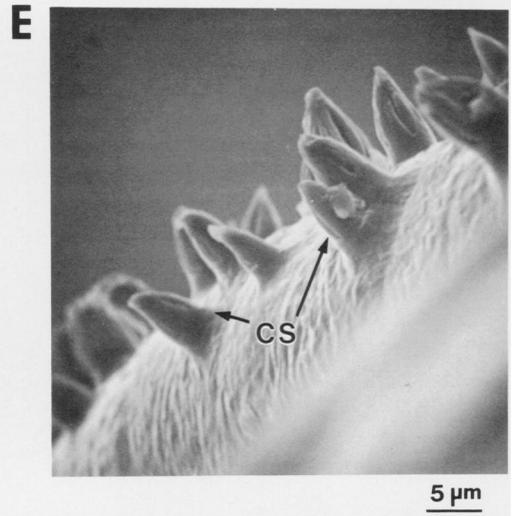
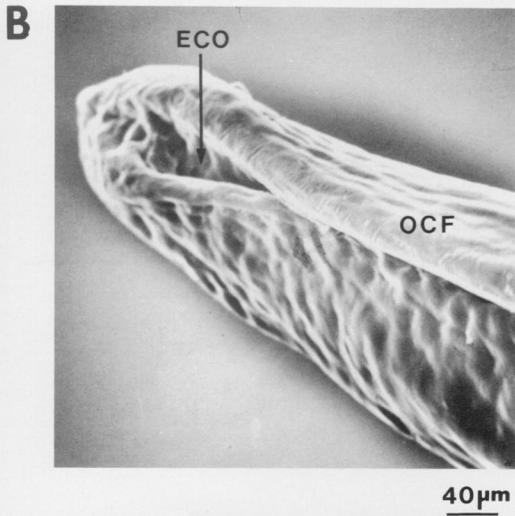
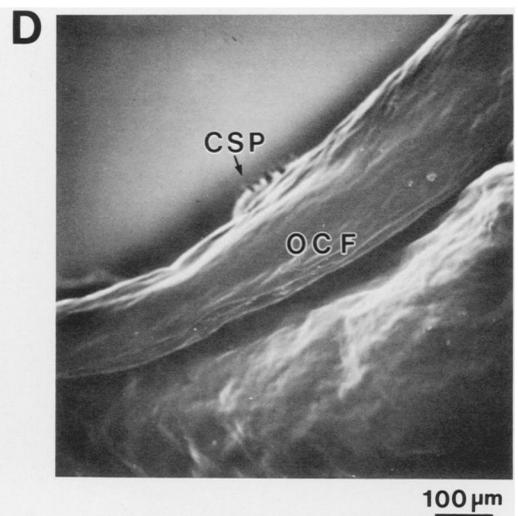
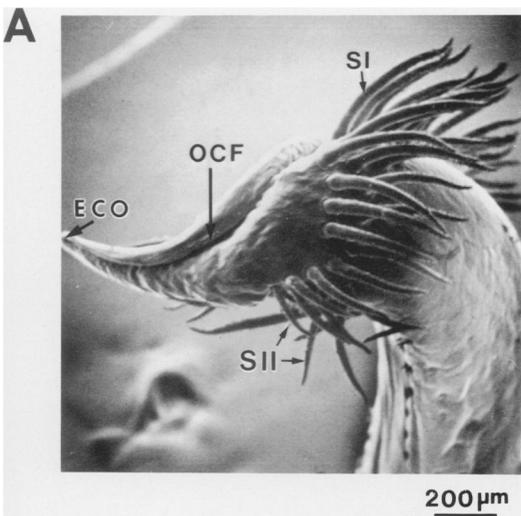


Fig. 1. *Chionoecetes opilio*. Illustration of gross morphology of first (A) and second (B) right gonopods, labeled 1G and 2G in (C), which shows anatomical relationships of gonopods in specimen viewed ventrally. Large solid arrow shows insertion of second gonopod; both ejaculatory canal and insertion of penis (large open arrow) are on face not in view. A, abdomen. AG, apical girdle. AM, appendix masculina. CF, cuticular fold of second gonopod. CX, cephalothorax. ECO, ejaculatory canal opening. EN, endopodite. 1G, first gonopod. 2G, second gonopod. LDM, laterodorsal margin. P, protuberance. PE, penis. PP, protopodite. PS, pinnate setae. SI, II, III, setal types I, II, III.



apically directed secondary setules along their distal half, while the seta itself is inserted in the gonopod via a cup insertion similar to that of types I and II (Fig. 3A, E).

Three additional setal types were identified on the first gonopod. The first of these was a very short, conical seta on the inner surface of the ejaculatory canal opening (Fig. 2F). It was not possible to ascertain whether this setal type was distributed throughout the ejaculatory canal. Another setal type, present on only one of the specimens examined, was a squat composite seta mounted on a mound-shaped protuberance (Fig. 2D, E). Pinnate setae are present on the medial and lateral margins of the basal part of the endopodite and the protopodite (Fig. 1). The pinnate setae are inserted via a characteristic annular insertion (Fig. 3F).

The internal anatomy of the first gonopod is relatively complex. The cuticle is thin in the region of the ejaculatory canal, progressively thickening around the rest of the gonopod (Figs. 2C, 5A, B). Beneath the hypodermis is a loose connective tissue, within which are two distinct sets of striated muscles which are oriented parallel to the long axis of the endopod (Fig. 5A, B). Radiating out from the ejaculatory canal are the rosette-shaped glands termed pleopod tegumental glands (Johnson and Talbot, 1987). Each gland consists of secretory cells and a canal cell. The canal cell contains a ductule leading to a network of similar ductules and terminating in pores which traverse the thin cuticle of the ejaculatory canal (Fig. 5A–F). Possible remnants of secretions can be observed in the ejaculatory canal (Fig. 5A, B, C). The number of rosette glands decreases steadily from the base to the distal extremity of the endopod.

Second Gonopod.—The second gonopod is much smaller than the first (Fig. 1), and presents a tendency to tubulation in the endopodite stalk region. The apical region is greatly modified, consisting of an apical girdle, a short appendix masculina, and a cen-

tral protuberance (Fig. 4A, B, C). The protuberance is variably developed in different individuals, and may represent a vestigial appendix interna.

The setae present in the apical region are of two types: shorter, pyramidal setae on the irregular surface of the apical girdle, and longer, needlelike setae directed toward the apex of the appendix masculina on its greatly folded surface (Fig. 4E, F). Three unequal tufts of pinnate setae are present on the medial margin of the protopodite, resting against the base of the first gonopod (Fig. 1). They are structurally similar to those of the first gonopod.

The tendency to tubulation in the second gonopod is quite pronounced in the basal region of the endopodite (Fig. 5G), attenuating distally (Fig. 5H). Striated muscle bundles run longitudinally up the length of the endopodite, but are absent in the apical region (Figs. 4D, 5F, G, H). The cuticle is quite thick on the lateral face of the endopodite, but comparatively thin on the median face surrounding the cuticular fold (Fig. 5G, H). In the apical region, the cuticle is uniformly thick and superficially folded (Fig. 4A–F).

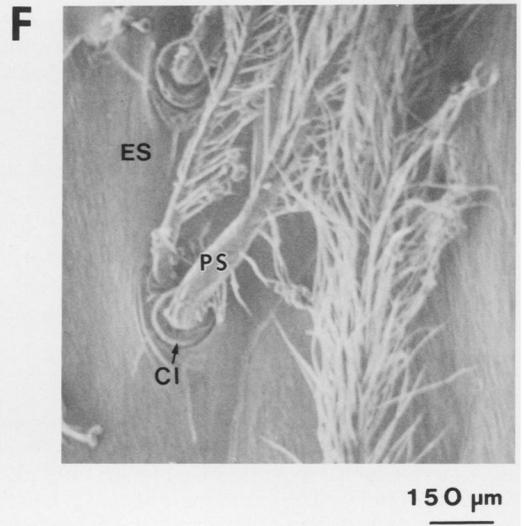
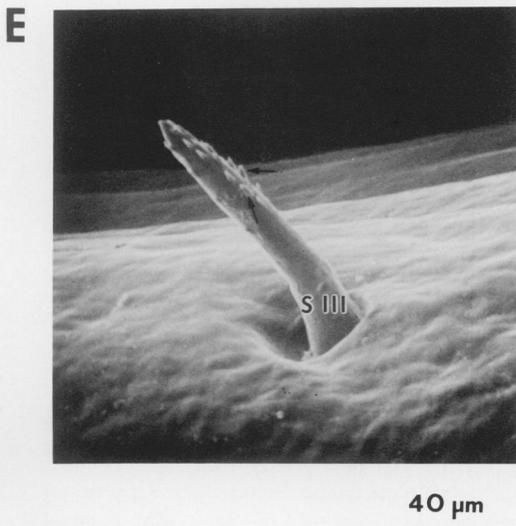
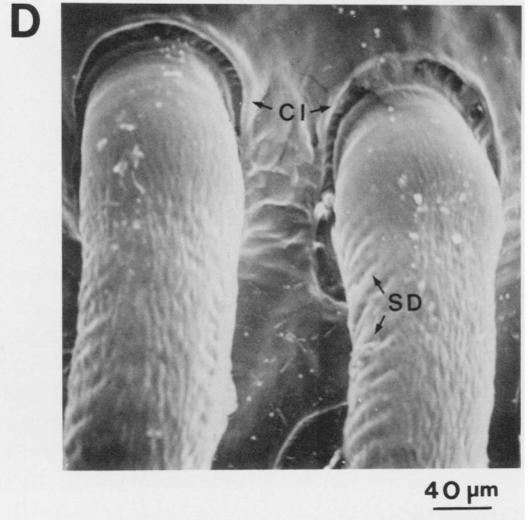
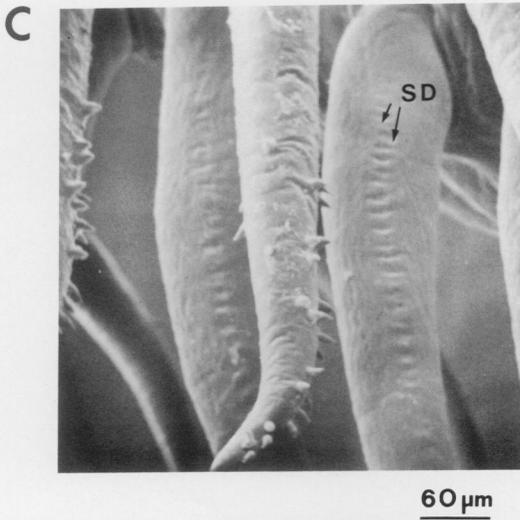
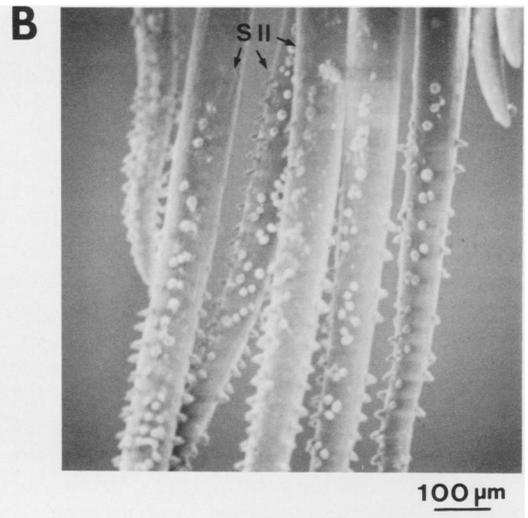
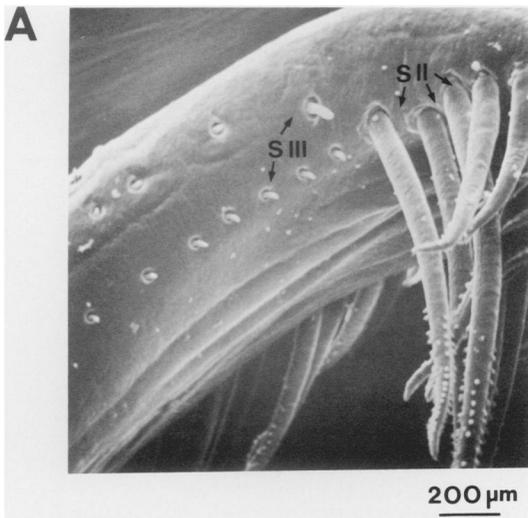
Rosette glands are not present in the second gonopods at any level. The subhypodermal tissues consist of the previously mentioned striated muscle bundles and loose connective tissue in the stalk region, and loose connective tissue only in the apical region (Figs. 4D, 5G, H).

DISCUSSION

Higher brachyurans present a number of evolutionary trends in their gonopods when compared to more primitive members of this order, notably a tendency toward tubulation of the endopodite of the first gonopod and the reduction and fusion of the appendix masculina with the endopodite of the second gonopod (Hartnoll, 1975). Whereas tubulation in the first gonopod acts

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Fig. 2. *Chionoecetes opilio*. Scanning electron micrographs of first gonopod. A, general view of distal region showing arrangement of type I and II setae (SI + SII) and outer cuticular fold (OCF) covering ejaculatory canal. B, detail of terminal spout showing opening of ejaculatory canal (ECO). C, transverse section at approximately one-third of endopodite length, showing configuration of cuticular folding around ejaculatory canal (EC). D and E, location and detail of protuberance (CSP) bearing composite setae (CS) found on 1 of 4 specimens. F, detail of ejaculatory canal opening, showing distribution of short setae (SS).



as a duct for the transmission of seminal fluids from the penis to the seminal receptacle at copulation, tubulation has not previously been reported for the second gonopod. Its existence indicates a certain structural homology with the first gonopod, but its function is not immediately obvious. A suggestion for its possible role in copulation will be given below.

The apical region of the second gonopod is characterized by a circular swelling and a thickening of the cuticle to produce the apical girdle. The medial face of the girdle is extended distally. This process probably represents a highly reduced and modified appendix masculina. The extremely short length of the second gonopod precludes a role in the direct physical transport of seminal fluids down the ejaculatory canal. However, the swelling and cuticular thickening in the apical girdle suggest that this region might act as a seal in the ejaculatory canal, allowing seminal fluids to be hydraulically pushed down the canal. In such a case, the seal would have to be broken at each return stroke of the endopodite, strokes which are presumably provided by abdominal flexion movements, as in *Cancer borealis* (see Elner *et al.*, 1985). The cuticular fold of the second gonopod might allow the seal to be broken, through an asymmetrical longitudinal force applied in its vicinity by the single set of endopodite muscles. The thinness of the cuticle in this region is consistent with this hypothesis.

Five types of setae are present in the apical region of the first gonopod based on their relative lengths, positions, and shapes. Nishimura's (1967) setal types I and II are, in fact, structurally identical and should be considered a single type with a specific distribution. The position and insertion of setal type III also indicate a close homology. The setules observed on this setal type resemble the knobby processes on setal types I and II. All three of these setal types, there-

fore, present a close relationship, and are probably homologous.

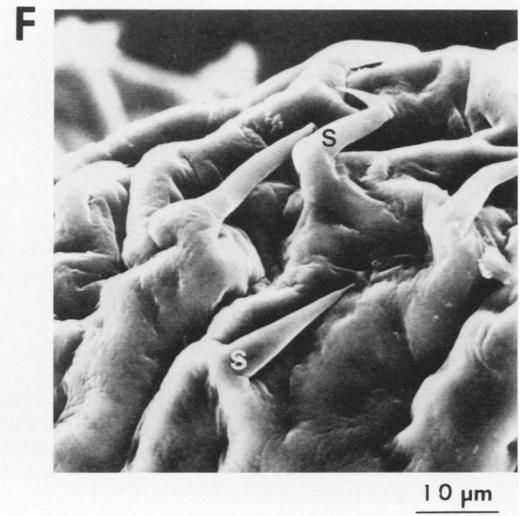
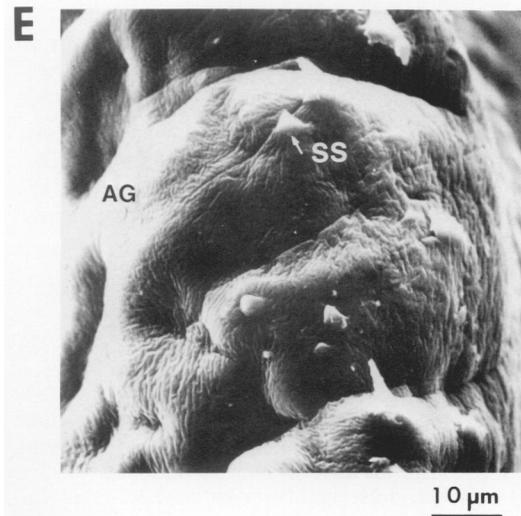
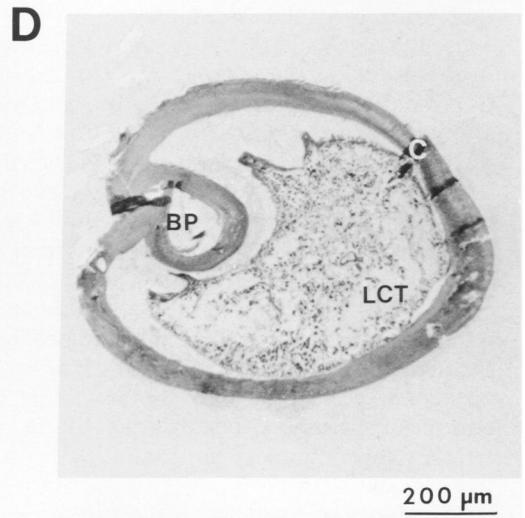
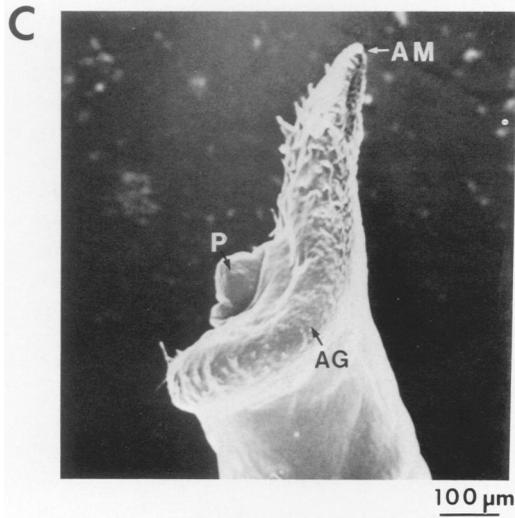
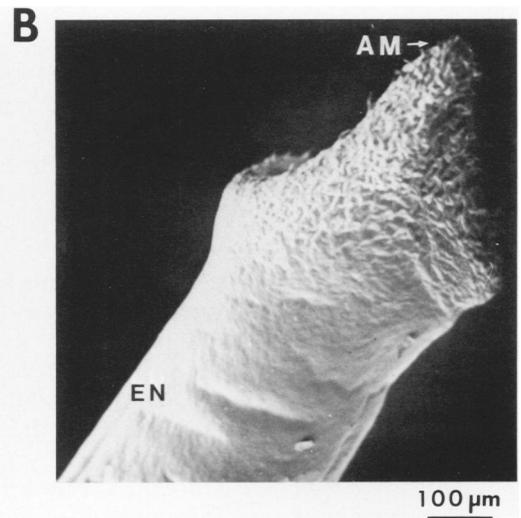
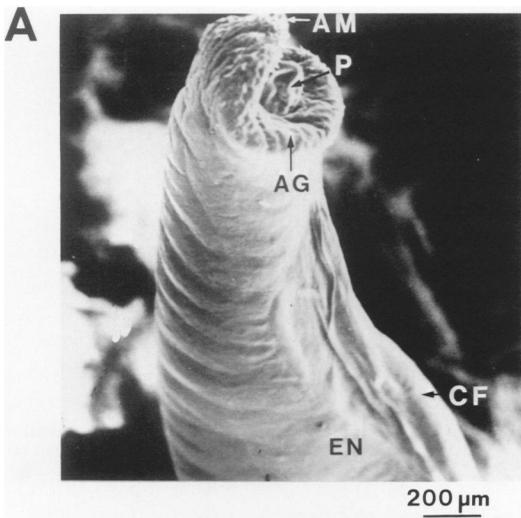
No explicit structure-function correlation has been established for any gonopod setae in crabs. However, several inferences may be made based on their position, orientation, structure and attachment to the cuticle. The distribution of the long, backwardly directed setal types I and II would certainly assist in stabilizing the insertion of the first gonopod in the vagina during copulation. The knoblike projections on the distal regions of these setae would also contribute to this function. The serial depressions of the cuticle on the proximal region of setal types I and II may represent local cuticular thinnings. Similar depressions have been suggested as having a chemosensory role in the antennules of *Carcinus maenas* (Fontaine *et al.*, 1982). The cup-shaped insertions of these setae allow basal movement in all directions, suggesting a mechanoreceptive function, possibly in the positioning of the first gonopod at the onset of copulation. The similar insertion of setal type III also suggests a mechanoreceptive function.

It should be noted that setal types I and II are oriented toward the base of the first gonopod. Together with the recurved distal extremity of this gonopod, a function in the removal of spermathecal contents prior to a consecutive mating seems quite plausible, as has been suggested for crayfish and damselflies (Waage, 1979; Berrill and Arsenault, 1984; Snedden, 1990). This would reduce sperm competition within the spermatheca.

The two compact setal types observed on the first gonopod are fused to the cuticle and probably do not have any mechanoreceptive function. With this in mind, it is difficult to conceive of a function for the short, pyramidal spines of the terminal spout. However, these spines are similar in size and shape to those of the apical girdle of the second gonopod, and may represent a vestigial homology. The significance of the

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Fig. 3. *Chionoecetes opilio*. Scanning electron micrographs of mid- and basal regions of first gonopod. A, midregion showing arrangement of setal types II (SII) and III (SIII). B and C, details of setal type II (SII), showing numerous cuticular knobs in distal region and serial depressions (SD) in proximal region. D, detail of insertion (CI) of setal type II into cuticle of first gonopod. E, detail of setal type III showing distal setules (arrows). F, pinnate setae (PS) on endopodite surface (ES) at base of first gonopod. Note typical annular cuticular insertion (CI) of plumose setae.



presence of composite setae found in only one of the four specimens examined is not apparent. Further studies are required to determine the occurrence and distribution of this feature.

The pinnate setae attached to the basal regions of the first and second gonopods are morphologically similar to those described for the antennae of *Panulirus cygnus*. These have been ascribed a function in the monitoring of vibrations along the antennal shaft (Phillips and Macmillan, 1987). A similar role could be envisaged for the pinnate setae of the gonopods. The pinnate setae of the first gonopod would rub against the abdomen during copulation, while those of the second gonopod would rub against the propodite of the first gonopod.

The presence of rosette-shaped glands inside crustacean gonopods has frequently been reported (see Johnson and Talbot, 1987, and Diesel, 1989, for references). Their structural homology to glands found not only in the first and second pleopods of females, but also in other pleopods and in hypodermal regions remote from the reproductive system, have led to the conclusion that these glands may have a specific function in females, such as egg attachment (Silberbauer, 1971; Johnson and Talbot, 1987) as well as a general function for both males and females in the hardening of the cuticle (Johnson and Talbot, 1987; Talbot and Zao, 1991). While Spalding (1942) suggested that in males these glands may contribute to the seminal fluid, Ryan (1967) refuted this argument, although the reason is unclear. In the present study, rosette glands were found only in the first gonopod, and not the second gonopod. This limited distribution within the first gonopod argues for a specific function in reproduction, probably as a contribution to the seminal fluid. Indeed, the complex duct network arising from these glands leads to pores in the ejaculatory ca-

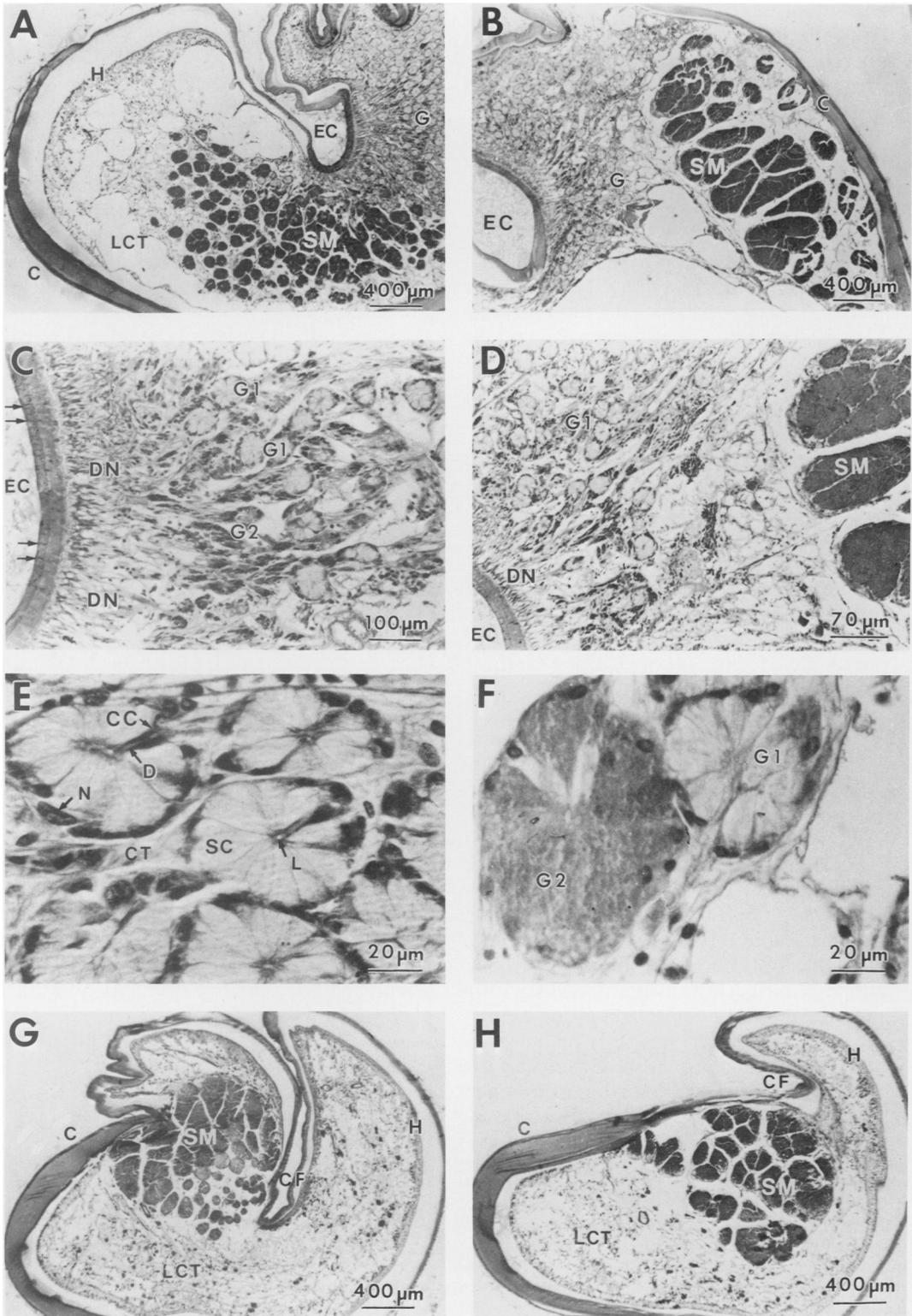
nal, and not to the general cuticular surface of the gonopod, as has been described for another member of the Majidae, *Inachus phalangium* (see Diesel, 1989), and the American lobster *Homarus americanus* (see Johnson and Talbot, 1987).

To the best of our knowledge, the variably developed protuberance situated in the center of the apical girdle of the second gonopod has not previously been reported. Since *C. opilio* and other higher brachyurans lack the primitive appendix interna of lower crustaceans (Hartnoll, 1975; Bauer, 1976; Tombes and Foster, 1979; Nicol and Nicol, 1983), this protuberance may represent a modified vestigial appendix interna. A more primitive arrangement has been reported for *Neptunus* (= *Portunus*) *sanguinolentus*, in which the apex of the second gonopod bears two blunt tips (George, 1963). The great degree of interindividual variation in development of this structure observed in the specimens examined in the present study suggests that it plays no crucial role in copulation. The distally directed, nonarticulating setae of the appendix masculina probably assist in the pumping of seminal fluids down the ejaculatory canal. The similar but smaller setae of the apical girdle may be homologous derivatives with reduced function in the pumping of seminal fluids.

The present study has established several fundamental points concerning the male genitalia of *Chionoecetes opilio*, notably the exact external morphology and surface anatomy, the distribution and probable copulatory role of the rosette glands, and suggestions for at least some functions of the gonopod setae. Directions for future research include electrophysiological studies of the setae, detailed anatomical comparisons with other crab species, functional studies using selective ablations, and histochemical/biochemical analysis of the rosette gland secretions.

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Fig. 4. *Chionoecetes opilio*. A–C, scanning electron micrographs of second gonopod. A, gross morphology showing endopodite (EN), appendix masculina (AM), and variably developed protuberance (P) which may represent vestigial appendix interna. Note pronounced cuticular fold (CF), extending from apical girdle (AG) and running length of endopodite (EN). B, dorsal view and C, lateral view of distal region. D, transverse histological section through apical girdle. Note thickness of cuticle (C) in entire region, including base of protuberance (BP). Gonopod is filled with loose connective tissue (LCT) at this level. Modified Masson trichrome stain. E, SEM detail of apical girdle surface (AG), showing presence of short setae (SS) and irregular topography. F, SEM detail of appendix masculina surface, showing longer setae (S) directed toward apex, and greatly folded cuticle.



ACKNOWLEDGEMENTS

The authors thank Drs. K. Benhalima and G. Jones for their technical expertise on those aspects of this work funded by the Department of Fisheries and Oceans. Dr. P. Odense made SEM facilities available and provided useful guidance, for which we are most grateful. Assistance with word processing was furnished by Mad. L. Briard. The drawings of Fig. 1 were prepared by Ms. L. V. Colpitts. Snow crabs from Bonne Bay were provided by Dr. G. Y. Conan, and Mad. C. Lanteigne arranged their transport to Moncton. Additional funding was provided by Natural Sciences and Engineering Research Council operating grant A3658 and by grant 20-53221-54-12 of the Faculté des Études Supérieures et de la Recherche de l'Université de Moncton to P.G.B.

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Fig. 5. *Chionoecetes opilio*. Transverse histological sections of first and second gonopods. A–F, basal region of endopodite of first gonopod. A and B, sections showing organization of cuticle (C), subjacent hypodermis (H), duct network (DN), ejaculatory canal (EC), rosette glands (G), and striated muscle (SM), surrounded by loose connective tissue (LCT). Note presence of secretions in ejaculatory canal. C and D, details of duct network (DN) and associated rosette glands on either side of ejaculatory canal. Note numerous secretory pores (arrows) in cuticle of ejaculatory canal. E, detail of rosette glands showing basal nuclei (N), secretory cells (SC), central lumen (L), and ductule (D) within canal cell (CC). Intergland spaces are filled with connective tissue (CT). F, detail of 2 rosette glands, one showing denser concentration of secretions (G1) than other (G2). G, second gonopod endopodite, basal region. Note pronounced cuticular fold (CF), loose connective tissue (LCT), and absence of rosette glands. H, endopodite of second gonopod, midlength region. Note reduced cuticular fold compared to basal region, and unequal cuticle thickness, as in G. All sections stained with modified Masson trichrome.

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RECEIVED: 12 September 1990.

ACCEPTED: 26 November 1990.

Addresses: (PGB) Département de Biologie et Centre de Recherches et d'Études sur l'Environnement, Université de Moncton, Moncton, New Brunswick, Canada E1A 3E9; (RWE) Pacific Biological Station, Nanaimo, British Columbia, Canada V9R 5K6; (YP) Département de Biologie, Université de Moncton, Moncton, New Brunswick, Canada E1A 3E9.