カラノイドかいあし類のコペポダイト期における皮殻器官の出現状態

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The Occurrence of Integumental Organs in Copepodid Stages of Calanoid Copepods[1)]

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Abstract

The occurrence of integumental organs, which are sensilla and the openings of glands, was examined in the adults and copepods of *Pareuchaeta norvegica* (BOECK, 1872), *Calanus plumchrus* MARUKAWA, 1921 and *C. cristatus* KRØYER, 1848. These organs are developed throughout the sequential copepodid stages, stages I and II having none or very few present. The organs are, like any other complex character of the adults, developed ontogenetically. Previous observations suggested that only those on the abdomen were developed ontogenetically and that consequently they are of primary importance in mating and speciation of copepods. This investigation suggests that organs of the head, thorax and abdomen are of equal importance.

Introduction

Integumental organs, consisting of sensilla and gland openings, are distributed over the entire integument of the body of all crustaceans (MAUCHLINE, 1977). These were first described in detail in species of the calanoid copepod genus *Eucalanus* Dana, 1853 by FLEMINGER, 1973. BRADFORD (1974) has since described their occurrence in two species of the genus *Arietellus* GIESBRECHT, 1892 and FLEMINGER and HULSEMANN (1977) map their occurrence on the abdominal segments of three species in the genus *Calanus* LEACH, 1816.

Investigations of their occurrence and function and the possible taxonomic and phylogenetic significance of the patterns of distribution of these organs in the integuments is at a preliminary stage (FLEMINGER,1973; FLEMINGER and HULSEMANN, 1977; MAUCHLINE, 1977). Their potential as tools for investigating taxonomic relationships between species and genetic variation within species has already been outlined by FLEMINGER.

It is important, however, before any discussion of function of these organs in the context of mating and speciation to discover whether they are indeed characteristic of adult stages only, or also of the larvae. FLEMINGER (1973) states that copepodid stages III-V of *Eucalanus* species, in general, have the complete pattern of integumental organs on the head and thorax but that the pattern on the abdomen is only developed in the adult. The abdominal organs are therefore considered by FLEMINGER to be secondary sexual characteristics of the adult.

A preliminary examination of some northeast Atlantic copepods suggested that those on

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the head and thorax were not all present in the copepodid stage III but were progressively developed, like those on the abdomen, throughout the successive copepodid stages. The results of a more detailed study confined to three species is described here.

Materials and Methods

Samples of adults and copepodids of *Pareuchaeta norvegica* (BOECK, 1872) were taken in Loch Etive, Scotland and off the western coast of Ireland at approximately 55°N 12°30′ W. The other two species, *Calanus plumchrus* MARUKAWA, 1921 and *Calanus cristatus* KRØYER, 1848 were collected from the Pacific Ocean east of Hokkaido, Japan at approximately 42°N 146°E.

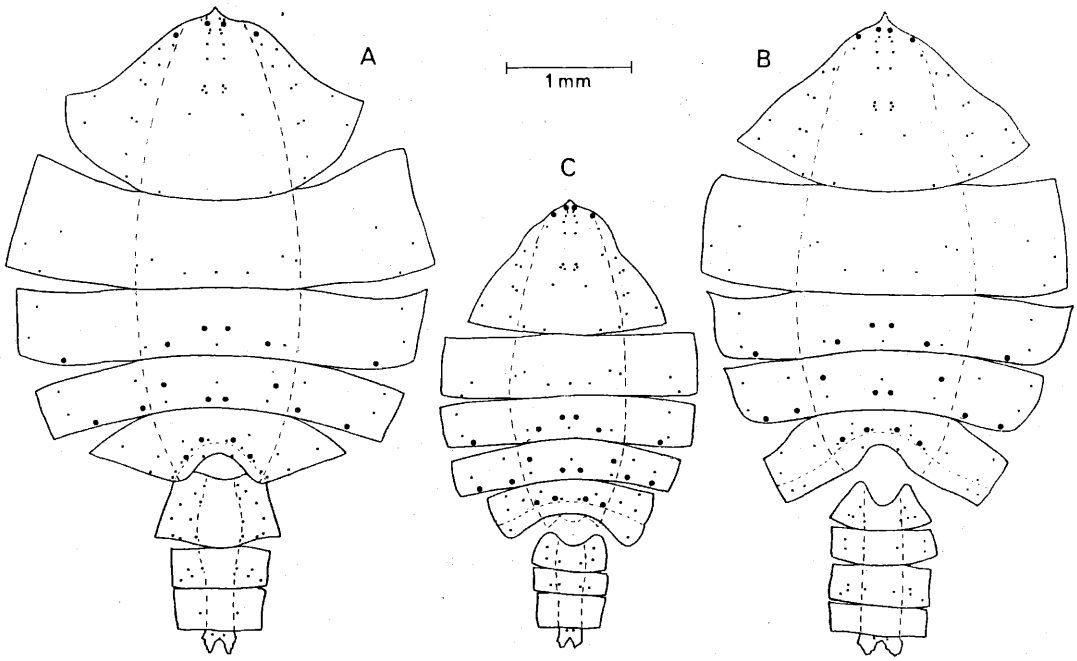

Fig. 1. *Pareuchaeta norvegica*, females. Distribution of pores in the treated integuments of A, adult, B, copepodid V, and C, copepodid IV.

The distribution of integumental organs is described by removing all soft tissues from the integument, and searching for holes or pores in the integument. To do this, five to ten copepods are placed in a test tube containing 20 m*l* of 10% aqueous potassium hydroxide at 80°–100°C for 24 hours. The specimens are then decanted into a Petri dish and washed with distilled water. The integuments are examined to ensure that all soft tissues have been digested by the potassium hydroxide. Integuments that are not clean are immersed for a further period in hot potassium hydroxide and re-washed in distilled water.

The clean integuments are then transferred to 70% ethanol for about 10 min before staining in a 1% solution of chlorazol black E in 70% ethanol. The time required for

staining varies but usually one minute is sufficient. Excess stain is removed by washing in 70% ethanol followed by distilled water.

The potassium hydroxide digests the soft parts of the animal including the tissues of

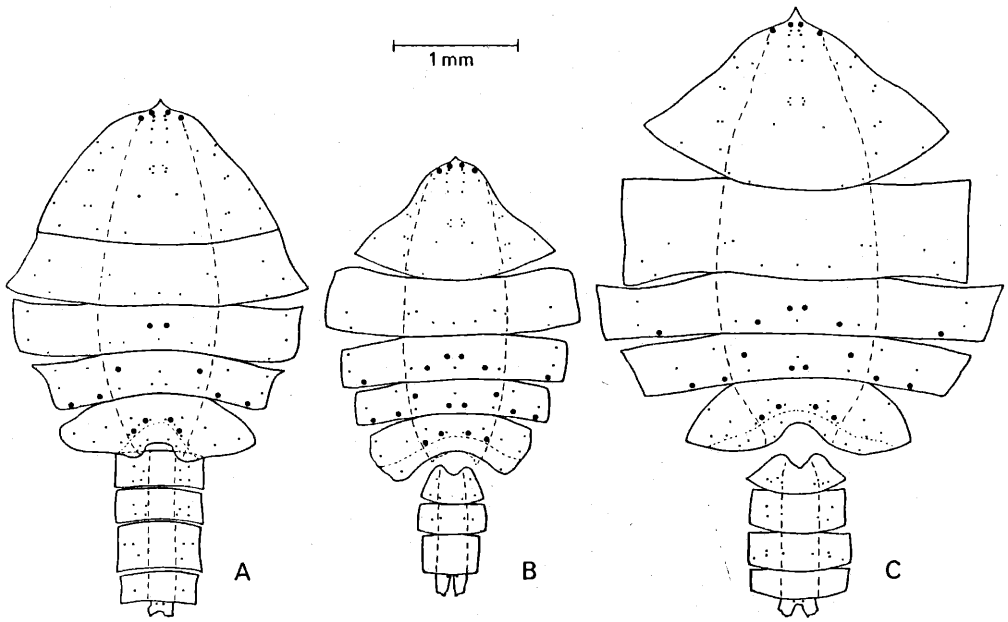

Fig. 2. *Pareuchaeta norvegica*, males, Distribution of pores in the treated integuments of A, adult, B, copepodid IV and C, copepodid V.

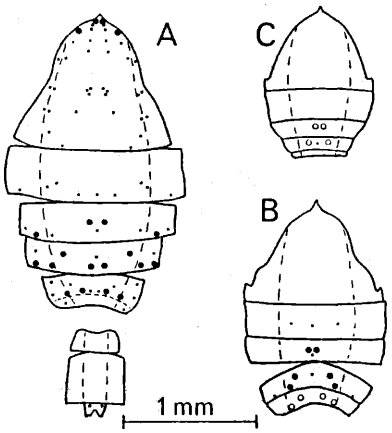

Fig. 3. *Pareuchaeta norvegica*. Distribution of pores in the treated integuments of A, copepodid III, B, copepodid II and C, copepodid I. Open circles represent sites of organs developing but no pore is yet present in the integument.

gland opening and the tissues of sensilla in the integument. Only holes or pores remain in the integument at the sites of these organs and these pores are seen as spots of light against the background of the black integument under the light microscope. The simplest method

of observing the pores is to mount the integument in polyvinyl lactophenol in the manner illustrated in Figures 1-5. This is done by carefully removing all appendages and ventral areas of integument and also separating the abdomen from the thorax. This leaves the tergal

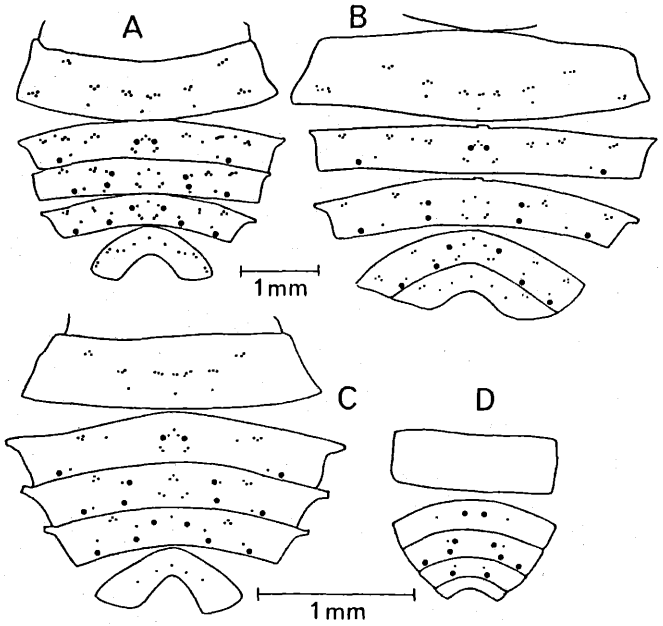

Fig. 4. *Calanus plumchrus.* Distribution of pores in the treated thoracic integuments of A, adult female, B, copepodid V, C, copepodid IV, and D, copepodid III.

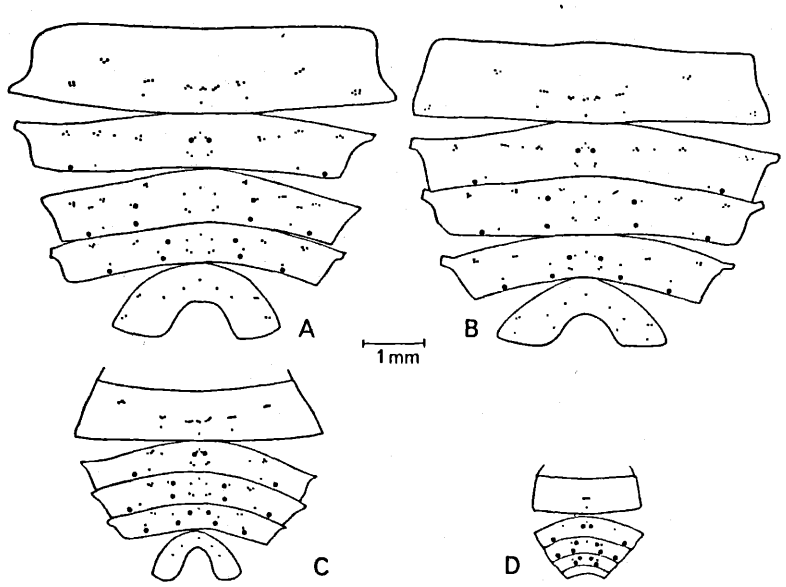

Fig. 5. *Calanus cristatus.* Distribution of pores in the treated thoracic integuments of A, adult female, B, copepodid V, C, copepodid IV and D, copepodid III.

(dorsal) and pleural (lateral) areas of the integument. The integument of the head and thorax is dissected into its individual parts or segments and each part is laid flat, outer surface upwards, in polyvinyl lactophenol on a microscope slide as shown in Figures 1-5. The abdominal integument has no structurally defined ventral region, such as is present in the head and thorax. The abdominal integument has, therefore, to be cut along the ventral mid-line and the individual segments mounted on the microscope slide as shown in Figures 1-3.

Results

The term "pore" throughout this paper refers strictly to the hole left in the integument after the soft tissues of the animal have been digested by the hot potassium hydroxide.

Pareuchaeta norvegica

The pattern of pores in the adults is peculiar to the species and is therefore a pore signature. The pore signature of the adult male and female are slightly different (Figures 1, 2). The female normally has two pairs of small pores immediately lateral to the base of the rostrum; these were not found in the male. The males have an extra small pore laterally in the posterior region of the head. The first thoracic segment is identical in both sexes. A small pore is substituted for a large pore in the lateral area of the median part of the second thoracic segment in the male. Similarly, in the third thoracic segment of the male a pair of small pores is substituted for the pair of large median pores of the females. The fused fourth and fifth segments show variability in the numbers of small pores present, or detected, near the posterior borders. Generally the males have one or two extra pairs of small pores in the fifth segment that do not seem to be present in the female. The first and second abdominal segments are fused in the female but the distribution of pores is the same as in the comparable segments of the male except that the female has a pair of pores, the male a single pore, laterally near the posterior margin of the second segment. The female has an extra pair of small pores in the third segment.

These sexual differences in pattern are primarily restricted to the adult stages. The substitution in the males in thoracic segments two or three of small pores for large pores is absent in the copepodid V (Figures 1, 2) when male and female are the same. Similarly the abdominal segments of male and female copepodid V are identical. The heads of male and female copepodid V are slightly different but this is because pores have not yet developed at a few sites.

The development of the individual pores or groups of pores can be traced back through the copepodid stages (Figures 1-3). A developmental stage of some of the larger pores is present in copepodids I and II; no pore as such appears to be present but the integument is thin in the region where a pore will be present in the subsequent stage (Figure 3). The development of the pores is shown quantitatively in Table 1. The second thoracic segment has its full complement of pores in the copepodid V, the first segment in copepodid IV or V while the head and the rest of the thoracic segments do not have complete patterns until copepodid V or the adult stage. The pattern in the abdomen and the sexual differences

are only completed in the adult.

Calanus species

The development of the adult pattern of integumental organs was examined in the thorax of two species of *Calanus*. Both species are large, *C. cristatus* being about 9 mm and *C. plumchrus* about 5 mm in length. It was difficult to stain the integuments of the copepodids of *C. plumchrus* successfully whereas the integuments of the copepodids of *C. cristatus* and *Pareuchaeta norvegica* stained darkly after a few seconds immersion in chlorazol black E. No reason for this difference in the staining properties of the species was evident.

TABLE 1. *Pareuchaeta norvegica*. NUMBERS OF PORES IN THE TREATED INTEGUMENTS OF THE HEAD, THORACIC SEGMENTS 1-5, AND THE ABDOMEN IN COPEPODID STAGES I-III AND FEMALE AND MALE COPEPODID STAGES IV-VI.

				Female			Male		
	CI	CII	CIII	CIV	CV	CVI	CIV	CV	CVI
Head	0	0	38	42	44	50	40	44	46
T1	0	3	9	11	13	13	13	13	13
T2	(2)	3	9	13	13	13	13	13	13
T3	1, (2)	7	11	15	17	17	15	15	17
T4	0	(4)	12	14	18	22	14	20	20
T5	0	0	2	2	6	2	2	8	6
Abd.	0	0	2	12	24	30	12	24	26
Total	1 (4)	13(4)	83	109	135	147	109	137	141

Numbers in parenthesis are sites where pores are developing but are not yet present.

TABLE 2. *Calanus* SPECIES. NUMBERS OF PORES IN THE TREATED INTEGUMENTS OF THORACIC SEGMENTS OF COPEPODID STAGES III-V AND ADULT FEMALES.

	C. plumchrus				*C. cristatus*			
	CIII	CIV	CV	CVI	CII	CIV	CV	CVI
T1	0	23	31	32	4	23	29	33
T2	4	21	33	35	7	21	33	33
T3	8	23	28	31	9	23	35	39
T4	4	17	27	27	6	15	27	27
T5	0	5	9	15	0	5	13	13
Total	16	89	128	140	26	87	137	145

The patterns of integumental organs in the adult female and copepodid stages III-V of *C. plumchrus* are shown in Figure 4 and comparable patterns of *C. cristatus* are shown in Figure 5. Again, the sequential development of the adult pattern can be traced through the successive copepodid stages. No pores could be found in the integuments of the copepodid stages I and II of either species. The sequential development of the pores is shown quantitatively in Table 2.

The adult patterns in each segment were not complete before the copepodid V and most segments did not develop the final pattern until the adult stage

Discussion

FLEMINGER (1973) states that in the genus *Eucalanus* the copepodid stages III to V all have the complete adult pattern of integumental organs on the head and thoracic segments but that the pattern on the abdomen is not completed until the adult stage. FLEMINGER and HULSEMANN (1977) direct attention to the specific differences that occur in the distributions and numbers of organs in the abdominal segments of north Atlantic species of the genus *Calanus* and discuss their probable roles in mating and speciation. Consequently, the inference is made that the abdominal patterns are especially important in the mating and evolution of species of copepods.

The situation described here is different. The copepodid stages I and II appear to have either none or very few integumental organs and these develop sequentially throughout the later copepodid stages. This is the normal pattern of ontogenetic development of a complex adult character in crustaceans. It suggests that the organs are primarily adult characters and that those on the head, thorax and abdomen probably act as a single complex system in the activities of the adults. This is further emphasized by the occurrence of sexual differences in the patterns on the head and thorax, as well as on the abdomen.

Specific differences in pore patterns also occur on all three regions of the body as instanced by FLEMINGER (1973) in species of the genus *Eucalanus*. Consequently, consideration of the abdomen in isolation, although obviously useful in the genus *Calanus*, omits equally important information from other regions of the body. Some of these organs are also probably involved in the sequence of events leading to successful mating between male and female. Similarly, organs in the head, thorax and abdomen are all probably involved in allowing one species to recognize its own members or, conversely those of another species.

Much further work on the distributions and types of organs and their histology in species combined with experimental observations on behaviour of the animals is required to gain an insight into the function of most of these organs. Some of the organs are thought to be hydrodynamic sensors monitoring water currents while some glands in certain families are luminescent glands (MAUCHLINE, 1977). There are, however, several other types of sensors, especially chemosensors, and glands of unknown function and it is these that are being discussed in the context of mating and species recognition.

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