

# On the Distribution of the Crustacean Dorsal Organ

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## Abstract

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An oval, dorsal organ, variously bearing four minute pits around a central pore and/or encircled by a cuticular border, has been reported for the cephalic region of various groups of living and fossil crustaceans. Although varying somewhat in location and in size, the organ appears basically uniform in organization in at least two of the major crustacean taxa: Branchiopoda (especially Laevicaudata) and Malacostraca (Decapoda and Syncarida). Little is known about its ultrastructure and function in various groups, and it is likely that the term 'dorsal organ' also has been applied to several nonhomologous structures. In particular, the *embryonic* dorsal organ, reviewed recently by Fioroni (Fioroni, P. 1980.—*Zoologische Jahrbücher (Anatomie)* 104: 425–465) and apparently functioning in nutrition and ecdysis, is not the topic of this paper; that organ is similar in name and location only and appears in embryonic unirami-ans, chelicerates, and crustaceans. The function of the dorsal organ in branchiopods is in ion regulation, possibly a secondary modification of the original function in marine crustaceans, which is unknown. In larval decapods, the organ probably functions as a chemo- or mechano-receptor. We review the known occurrence of the crustacean dorsal organ, describe the similarities and differences in structure in various taxa, and review the competing hypotheses concerning its function. Phylogenetic implications are discussed.

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## Introduction

While attending a symposium on decapod Crustacea hosted by the Zoological Society of London (Fincham & Rainbow 1988), we realized that a striking similarity exists in the external organization of a cuticular organ—herein referred to as the dorsal organ—that appears in two very different and only distantly related groups of Crustacea, the Malacostraca and Branchiopoda. Independently, this organ, or at least one very similar to it, was described by Müller & Walossek (1988) in an exquisitely preserved Upper Cambrian taxon showing maxillopodan affinities. A subsequent search of the literature has revealed that many other crustacean groups, and some non-crustacean arthropods, have a similar organ, either as adults or as larvae, but that the literature on these organs, although rather extensive, is scattered.

The various structures and organs found on the head of crustaceans differ greatly among taxa. In fact, the term 'dorsal organ' seems rather imprecise, the name having been given to a variety of structures that may not be homologous. The organ to which we refer is located in the anterior region of the head and is small, oval, and may bear four small bumps or pits that more or less surround a central pore. It is usually slightly elevated relative to the surrounding cuticle, and may be surrounded by a cuticular border.

Special mention should be made of a large body of literature dealing with a different structure, an embryonic

organ that unfortunately has also been given the name 'dorsal organ'. This embryonic structure, which apparently aids in the processes of nutrition and ecdysis in several different arthropod groups, including insects, chelicerates, and crustaceans, was reviewed by Fioroni (1980). It is particularly well known in the Peracarida; reviews and discussions can be found in the works of Strömberg (1965, 1967, 1972) on isopod embryology and Meschenmoser (1989) on amphipods.

The purpose of this paper is to review the occurrence of the cuticular (non-embryonic) dorsal organ in the Crustacea, describe the organ in some detail as it appears in the Decapoda and Branchiopoda, discuss homologous and non-homologous structures in similar locations in a variety of taxa, and alert other workers in the field as to the possible presence of such organs in other taxa.

## Materials and Methods

We examined living and freshly preserved material of various Branchiopoda (Anostraca, Notostraca, Conchostraca, Cladocera) and decapod Malacostraca (including the Caridea, Brachyura, and Nephropoidea). Data on fossil taxa were kindly supplied by D. Walossek. Crustacea were collected in the field or borrowed from museum or private collections. Scanning electron microscopy preparation generally followed the outline given by Felgenhauer (1987). Original illustrations were made with a Wild M5APO stereoscope with camera lucida; other illustrations were taken from the literature as indicated in the text and figure legends.

## General Description of the Dorsal Organ

### External morphology

The dorsal organ discussed in this paper has a characteristic location and external morphology. It is located on the midline of the anterior head region, often just posterior to the eyes but occasionally further back on the carapace (e.g. see Decapoda, below). The organ consists of an oval region usually demarcated from the surrounding cuticle by a thin cuticular border. The shape may be slightly flattened on one side or otherwise distorted, but most often it is oval and is slightly elevated with respect to the surrounding cuticle; in spinicaudatan branchiopods it is even borne on a stalk. Within the cuticular borders four small bumps or pits are found that in decapod larvae and in syncarids (but not in branchiopods) bear minute papilliform projections in their central depression. A fifth structure, which in some eumalacostracans takes the form of a pore, is found more or less centered within the square formed by the four peripheral bumps. In other Crustacea this 4 + 1 arrangement of pores/pits is not seen; again, we stress that homology is not proven and the interpretation is open to question.

### Internal morphology

A detailed knowledge of the internal structure of this organ is at present confined to the larval stages of the Decapoda (see Laverack & Barrientos 1985) and to several Branchiopoda (e.g. Rieder *et al.* 1984, for Conchostraca (Spinicaudata); Criel 1991, for *Artemia*; Dejdur 1931, for 'cladocerans').

The study by Laverack & Barrientos on decapods showed that the central pit is the opening of a single-cell gland, while the four surrounding depressions are composed of two sensory cells, each carrying a double cilium that branches peripherally to end in a highly modified cuticle (Laverack & Barrientos 1985; Laverack 1988, 1990). This arrangement suggests that the organ of larval decapods is either a chemoreceptor, with branched endings within a porous cuticular region, or that it is a baroreceptor responding to change in hydrostatic pressure (see Laverack 1988, 1990).

In branchiopods the internal structure is different. A summary of our knowledge of the ultrastructure of this organ in *Artemia* was given by Criel (1991, pp. 180–182), based mostly on the work of Copeland (1966, 1967), Freeman (1989), Hootman & Conte (1975), Kikuchi (1972), and Lowry & Conte (1985), and we quote her below:

The ultrastructure is similar to that of the branchial gills of the adult described by Copeland (1966, 1967). As in the gills, dark and light cells were found initially (Conte *et al.* 1972; Kikuchi 1972). Later, improved techniques only revealed one cell type (Hootman & Conte 1975; Lowry & Conte 1985) in which an apical, a central, and a basal zone can be discerned. The apical plasmalemma is infolded into irregular loops which are in contact with the cuticle. A major ultrastructural characteristic which suggests a salt secretory role is the smooth tubular network which fills the central cytoplasmic zone. Sinusoids from this labyrinth open directly into the hemocoel on the basal and lateral cell surfaces. Kikuchi (1972) has shown that

the extent of this network, both in the neck organ and in the gills, is related to the salinity of the culture medium. The most abundant organelles are mitochondria. They often form aggregations in intimate contact with the tubular membranes reminiscent of mitochondrial pumps (Copeland 1966, 1967).  $\text{Na}^+\text{K}^-\text{ATPase}$  is found on the apical and baso-lateral cell boundaries. An unusual feature of the neck organ epithelium is the absence of a basal lamina. Scanning electron microscopy of the organ in young nauplii (Hootman *et al.* 1972) shows continued development of the gland by growth and enlargement of the epithelium from a flat cap-like structure into a hemispherical dome having deep channels through the epithelium and covered by a thin cuticular film.

Rieder *et al.* (1984) described a slightly different structure in their study of the spinicaudatan *Limnadia lenticularis*. For this species, Rieder *et al.* examined in detail the external and internal structure of the organ and described five different cell types in the organ's epithelium. A central cell, containing many mitochondria and ribosomes and having well-developed microvilli, is surrounded by a ring of two other cell types, which have fewer organelles. Unlike *Artemia*, *Limnadia* has four nerve fibers that extend through the epithelium to the overlying cuticle (Rieder *et al.* 1984), although there is no external indication of four sensory pits as seen in decapod larvae and syncarids. Based on the ultrastructure of these cell types, Rieder *et al.* suggested that the organ functions in the regulation of chloride ions. The structure is apparently the same in the family Leptestheriidae, although it has not been illustrated (see Rieder *et al.* 1984).

## Known Distribution in the Crustacea

### Branchiopoda

The dorsal organ is best known in the Branchiopoda, where it has been variously termed a salt gland, dorsal organ, Nackenorgan or nuchal organ (neck organ). The organ has been most thoroughly described for larval anostracans, because it is primarily a larval organ and because of the amount of attention lavished on the developmental biology of the genus *Artemia* (e.g., see Criel 1991). The structure is also known from notostracans, conchostracans (both Spinicaudata and Laevicaudata), and many species of 'cladocerans' (now split into four orders; see Fryer 1987). Only in the Laevicaudata does the organ display the 4 + 1 arrangement (Martin & Belk 1988), and no central pore is known in any group. The list of examples below is not meant to be exhaustive.

*Anostraca.* The dorsal organ in anostracans has been known since at least 1851, when Leydig described it in larval stages of *Branchipus stagnalis* and *Artemia salina*. Subsequent workers have also mentioned or described this structure in adults and in larvae (Fig. 1A), some including excellent illustrations (e.g. Claus 1873; Sars 1896). Sars illustrated for *Branchinecta paludosa* (pl. VII, fig. 2) an oval area on the head of a mature male; he labeled this oval area 'c' (reproduced here as Figs 1B, C). Unfortunately, in the corresponding legend, Sars stated 'Lettering as in fig. 1,' which did not contain the structure

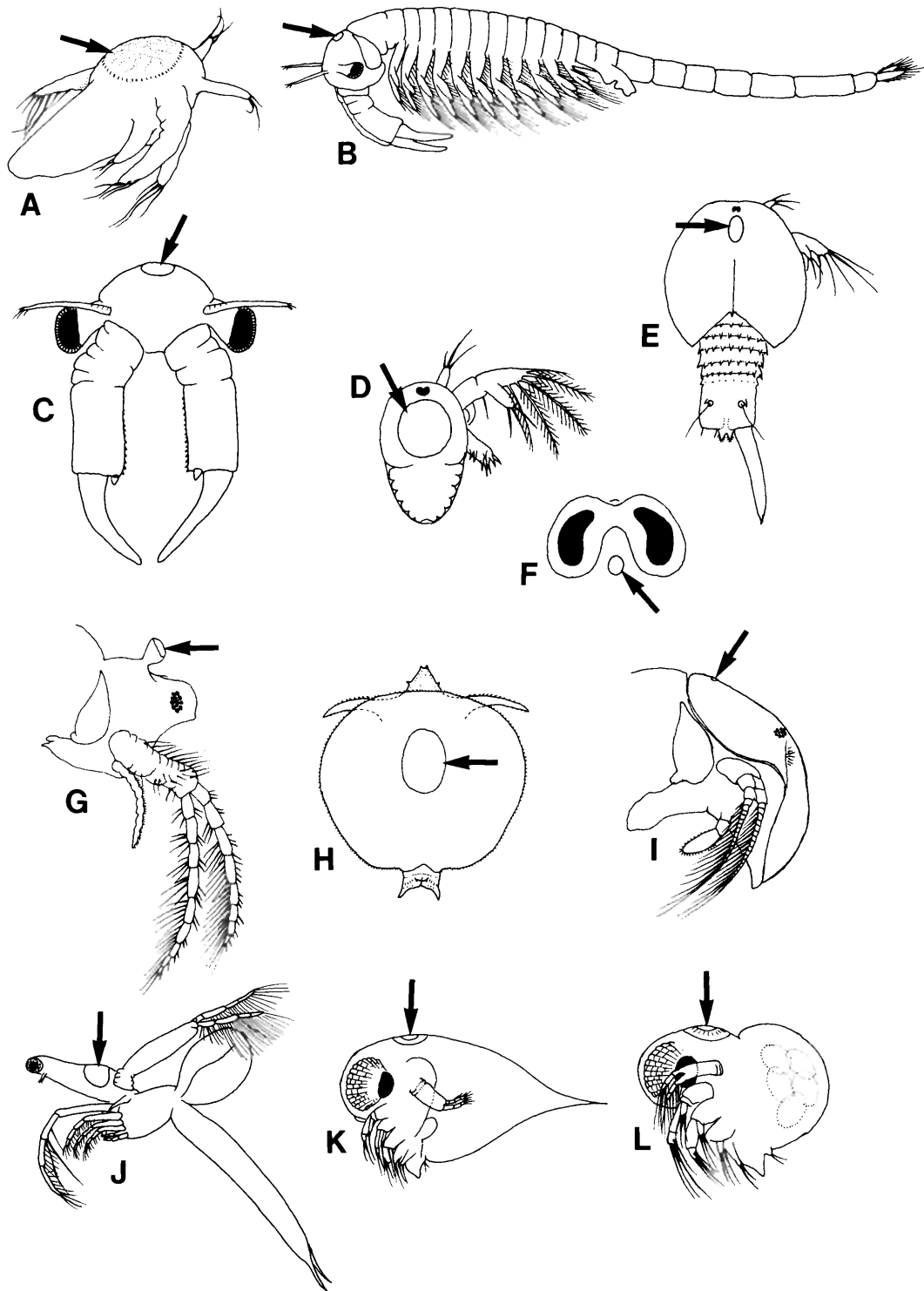


Fig. 1. Illustrations from the literature of dorsal organs (arrows) in the Branchiopoda.—A. Nauplius of *Artemia*.—B. Adult *Branchinecta paludosa*.—C. Frontal view of head of *B. paludosa*.—D. Hatching larva (metanauplius) stage of *Triops cancriformis*.—E. Later ('neonatal') stage of *Leptidurus arcticus*.—F. Dorsal view of eyes and organ in adult notostracan (*T. cancriformis*).—G. Lateral view of head of adult limnadiid clam shrimp (*Spinicaudata*).—H. Dorsal view of heilophore larval stage of *Lynceus* (*Laevicaudata*).—I. Lateral view of head of adult lynceid.—J. *Leptodora kindtii* (*Haplopoda*).—K. Female *Evadne spinifera*.—L. Female *Pleopis polyphemoides* (both *Onychopoda*). (A From photograph in Schrehardt 1986; B, C after Sars 1896; D–F after Longhurst 1955; G, I after Martin 1988; H after Gurney 1926; J after Calman 1909 (from Lilljeborg 1901); K, L after Smirnov & Timms 1983.)

or the letter 'c', and the structure is not mentioned in the corresponding text. The structure is easily observed in other anostracan genera (e.g. see Fig. 3A, *Streptocephalus*). Its location suggests that it is similar in origin and function to the dorsal organ of the Conchostraca and Notostraca, but it seems to lack the 4 + 1 arrangement seen in laevicaudatan (lynceid) conchostra-

cans and in larval decapods. The morphology and ontogeny of the dorsal organ in *Artemia* were recently reviewed by Criel (1991, p. 180), who described it, based on earlier work by Conte *et al.* (1972), Hootman & Conte (1975), and Hootman *et al.* (1972), as 'a dome-like gland situated atop the cephalothorax [*sic*; actually head only] of the larva, composed of 50 to 60 cuboidal epithelial

cells, much larger than the surrounding epidermal cells, having a large nucleus with two to five prominent nucleoli, a diffuse membranous cytoplasm, yolk platelets, and other storage products'. Furthermore, Criel (1991) states that the ultrastructure is similar to that of the branchial gills of the adult *Artemia* as described by Copeland (1966, 1967) (see above, under Internal Morphology).

The organ is particularly obvious in early developmental stages (Fig. 1A), as can be seen in recent SEM studies by Schrehardt (1986, 1987, especially 1987, fig. 3) and Go *et al.* (1990, figs 4f, 5a, 7c). Several workers have assumed that this organ occurs exclusively in larval anostracans and disappears by the adult stage, but at least externally, and in a reduced state, the organ can be seen in adult males and females of some species (Figs 1B, C, 3A).

The Upper Cambrian *Rehbachella kinnekullensis* from the Orsten fauna of Sweden (see Walossek this issue) has been suggested to be close to the anostracan lineage of the Branchiopoda (Walossek 1992). Early developmental stages of this species bear a conspicuous plate-like area on the head-shield (Fig. 3E). Walossek (1992) describes two pairs of pits or pores on this plate, one on its surface and one on the posterior plate margin, and discusses the similarity of the organ in Upper Cambrian and Recent crustaceans.

*Notostraca.* Claus (1873) and Sars (1896) were among the first to describe this organ in notostracans. For *Lepidurus glacialis*, Sars (1896) illustrated (pl. XI, fig. 6 and pl. XIII, figs 1, 2, 8) a large oval structure that he labeled 'x'. The shape of the oval is slightly different from that seen in the Anostraca, but both are flattened to some degree on the posterior border. Sars defined 'x' as the 'post-orbital tubercle'. The 4 + 1 arrangement of pits and pores is not seen; rather, as in anostracans, the area within the cuticular borders is more or less uniformly wrinkled. This conspicuous structure has been noted by most subsequent workers, such as Longhurst (1955), who illustrated the organ in larvae and adults of both notostracan genera and commented on variations in its shape (Figs 1D–F). Thiery (1987, fig. 108) also has illustrated variations in the shape of this organ, which he refers to as the 'organe nuchal', in *Triops granarius*. As is the case with anostracans, the organ is much larger (relative to the shield size) in larval forms (Figs 1D, E). Henry (1948) illustrated this organ in *Triops* (as *Apus*) and figured a nerve supplying it.

*Conchostraca (Spinicaudata and Laevicaudata).* For the Conchostraca, Sars (1896) illustrated two genera, *Limnadia* and *Lynceus* (the latter as *Limnetis*). In *Limnadia*, there is a projection of the head region that Sars labeled 'af' and termed the 'affixing organ' (Sars 1896, pl. XV, fig. 2); Sars noted (1896, p. 89) that this organ 'is usually interpreted as an organ of attachment'. It is found also on all other genera in the Limnadiidae (Figs 1G, 3B), although in the genus *Imnadia* it is not borne on a stalk. Virtually all descriptions of limnadiids illustrate this stalked organ, as it is diagnostic of the family Limnadiidae. Straskraba (1965, p. 268), who discussed the organ, noting that it was referred to as the 'Haftorgan' by earlier

German workers (whom he does not cite), felt that the organ 'cannot have a prehensile function since the head is fully hidden between the shells'. Rieder *et al.* (1984), referring to the organ as the 'Nackenorgan' (neck organ), noted that the organ is seen also in the family Leptestheriidae (*Leptestheria dahalacensis*) but is not borne on a peduncle in the Leptestheriidae. Rieder *et al.* described the organ in *Limnadia lenticularis* and in *Leptestheria* and, based on the ultrastructure of the various internal cell types, suggested that the organ functions in the regulation of chloride ions.

In the family Lynceidae, which Fryer (1987) and Martin & Belk (1988) have shown differs significantly from other 'conchostracan' families in a number of morphological features, Sars (1896) also illustrated a dorsal organ. In *Lynceus*, this organ, which is not borne on a peduncle, was labeled by Sars 'x' (pl. XIX, fig. 11) and defined in the legend, obviously tentatively, as 'affixing organ (?)'. Martin & Belk (1988) illustrated in more detail the dorsal organ in the genera *Lynceus* and *Paralimnetis*, and it has been illustrated in lynceid larval stages as well (Figs 1H, I). The organ is as described earlier (see External Morphology), although the peripheral bumps do not bear central 'pimples' and the fifth (median) bump does not appear to be a pore, and is apparently lacking in *Paralimnetis* (Figs 3C, D). Internal anatomy of the organ in lynceids has not been described.

*Cladocera.* The four orders that now comprise the former Cladocera (see Fryer 1987) all have some species that bear a dorsal organ. The organ is rather well known in 'larval' daphniids (order Anomopoda), and the details were given in a SEM examination by Halcrow (1982) for *Daphnia magna*. In the Haplozoa, *Leptodora kindtii* (the sole member of the order) was illustrated by Lilljeborg (1901, figure repeated in Calman 1909, p. 34) as having a dorsal oval or saddle-shaped structure located posteriorly to the eye, closer to and between the bases of the second antenna (Fig. 1J). Halcrow (1985) examined the internal structure of this organ in *Leptodora* and noted that in gross morphology it was similar to the organ in 'other branchiopods examined to date'. Halcrow suggested that its function is in ion transport, and not respiratory as had been suggested earlier (e.g. Sebestyen 1931). The marine genera *Evadne* and *Podon* (Onychopoda) and some related genera also bear a dorsal organ (Figs 1K, L), which earlier was assigned a respiratory function (Mordukhai-Boltovskoi 1968) or a glandular function (Monoyer & Bussers 1978), but in these genera the organ has since been shown to function in ion transport (see Potts & Durning 1980). The cuticular border in both genera is obvious, but there are no apparent pits, pores, or bumps.

#### Maxillopoda

Literature referring to maxillopodan 'dorsal organs' is still limited. There are several cephalic specializations among the Copepoda, but it is unclear if any of these are homologous to the dorsal organ. Cuticular specializations such as the 'cephalic dorsal hump' described by Nishida (1989)

for male calanoids lie in the same general area of the head-shield, and are roughly similar in organization, but beyond this nothing more can be said. Por & Hadel (1986, fig. 38) provide SEM photographs of an oval structure, which they call the dorsal organ, on the cephalothorax of the copepod *Attheyella (Attheyella) jureiae*. The structure is oval, bordered by a cuticular ring, and appears remarkably similar to the branchiopod (laevicaudatan) condition, although no pits or pores can be discerned from the low magnification photograph. However, in the same paper, Por & Hadel (1986, fig. 43) describe a 'shallow, tongue-shaped' dorsal organ on the cephalothorax of a female *A. (Canthosella) vera*, and in that SEM view, which is slightly higher in magnification, at least two pits toward the anterior end of the field are clearly visible. Por & Hadel (1986) cite Kiefer (1967) as having provided the first descriptions of this dorsal organ in this group of copepods. A similar structure was described by Coull & Grant (1981, fig. 1D) for *Heteropsyllus nunni*, a unique encysting marine copepod. Coull & Grant suggested that this 'oblong platelike structure' on the middorsal surface of the cephalothorax might be the site of cyst formation, as it was known to them to occur only in two other copepod species, both freshwater encysting harpacticoids, and had been described previously as a cyst-forming gland. Dibbern & Arlt (1989) described an oval to slightly triangular organ, which they called a dorsal nuchal organ, in naupliar stages of the harpacticoid *Mesochra aestuarii* (their figs 2B–7B), but presented only line drawings without ultrastructural details.

Facetotectan larvae bear a dorsal 'cuticular window' in the approximate location of the dorsal organ (Fig. 2A). This 'window' is so named because the cuticle is thin and transparent; since it is probably associated with the underlying naupliar eye it may not be homologous to the structure we are discussing. There is no evidence of a 4 + 1 pit/pore arrangement, although we have not seen SEM photographs of this region. Finally, in the Upper Cambrian fossil *Bredocaris admirabilis*, a species that shows affinities, particularly in the developmental pattern, to taxa of the 'thecostracan line' of the Maxillopoda, Müller & Walossek (1988) described 'a group of four pores' on a plate-like structure on the apex of the cephalic shield for all developmental stages (Figs 2B, C, 3F, G). Their SEM figures (1988, pl. 3, fig. 2, pl. 10, fig. 1) show these four pits clearly, and the similarity to the branchiopod condition, and less so to the larval decapod condition, is obvious. The Upper Cambrian Skaracarida, assigned to the copepodan line of the Maxillopoda, clearly lack a comparable structure (Müller & Walossek 1985).

#### *Malacostraca*

*Hoplocarida*. We have not examined under the SEM any species of Stomatopoda. However, Hansen (1921) stated that the organ has figured in several taxonomic descriptions where it had been termed the 'dorsal pit'. Hansen found the organ in adults of species of *Squilla*, *Pseudosquilla*, *Odontodactylus*, *Gonodactylus*, and (tentatively) *Lysiosquilla*. For *Pseudosquilla ciliata* he

described the organ as 'a nearly circular, very conspicuous and somewhat deep depression with two or three tiny pits on the flat or a little convex bottom, situated a little in front of the middle of the carapace and somewhat in front of the mandibles'. Hansen was unable to find the organ in any larval stages.

*Phyllocarida*. Although we have not examined any members of the Nebaliacea, it is perhaps worthwhile to note that Sars (1896), who was undoubtedly attuned to the presence of this organ as he described it in the same paper for other groups, shows, in his equally detailed illustrations of *Nebalia*, no such organ. However, Hansen (1921) saw something on the carapace of *Nebalia bipes* that might have been such an organ: 'In turning the animal a little to and fro so that the light changes on the smooth, shining dorsal surface of the head it is generally possible to perceive a faint vestige of a median protuberance situated not inconsiderably behind the base of the moveable rostral plate' (Hansen 1921, p. 70). Finally, Mauchline (1977) described both anterior and posterior dorsal organs on the carapace of *Nebaliopsis typica*, and these are almost certainly homologous to the anterior and posterior dorsal organs seen in decapod larvae (see below). Mauchline (1977, p. 982) states that the organs 'each consist of two pairs of pores and larger central areas', and he illustrates (1977, fig. 5) a slightly modified 4 + 1 pore pattern for both the anterior and the posterior dorsal organ (reproduced in our Fig. 2D).

#### *Eumalacostraca*

*Peracarida*. We mention the peracarids first among the eumalacostracans because of a curious and perhaps meaningful coincidence: the *embryonic* dorsal organ is best known for the peracarids, having been found in isopods, amphipods, and tanaidaceans, but there are few records of adults or post-embryonic developmental stages with a cuticular dorsal organ of the type we describe herein. An exception might be the Isopoda, where Hansen (1921) noted a median tubercle 'on the surface of the head near the posterior margin' in *Bathynomus* and *Cirolana*, and possibly in the Mysidacea. Hansen (1921) tentatively described some possibly homologous structures in the correct location for several mysidacean genera, and his description for the genus *Boreomysis* is certainly fairly close to our general description of the cuticular dorsal organ: '... a little oval, rounded and very distinct protuberance with one to three minute pits'. Mauchline (1977) also described what might be the cuticular dorsal organ on the posterior margin of the cephalon in the mysids *Eucopia sculpticauda* and *Katerythroops oceanae*; both figures (1977, figs 7, 8B) show a cluster of four pores on the midline of the cephalon (see our Fig. 2E).

The *embryonic* dorsal organ, which we feel is not homologous, was reviewed by Fioroni (1980), and detailed observations on the nature and function of this organ in peracarids are found in the works of Strömberg (1965, 1967, 1972) on isopod embryology and Meschenmoser (1989) on amphipods. The embryonic organ apparently

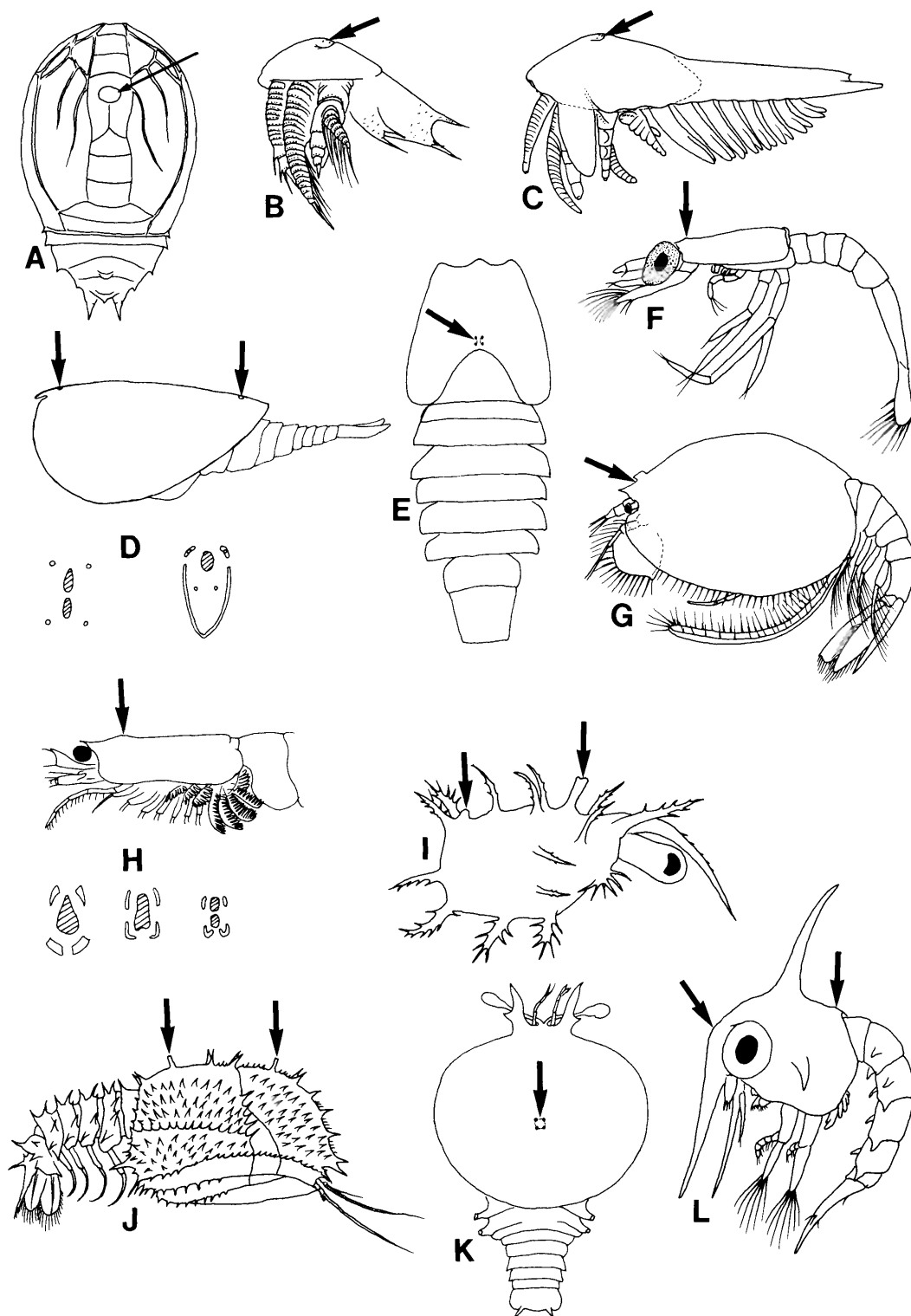


Fig. 2. Illustrations from the literature of dorsal organs (arrows) in the Maxillopoda and Malacostraca.—A. Faciotectan larva, lighter arrow indicating improbable homology with other dorsal organs.—B, C. First instar and later stages of the Upper Cambrian maxillopod *Bredocaris admirabilis*.—D. The nebaliacean *Nebaliopsis typica*, lower figures are drawings of ultrastructure of anterior and posterior organs, dorsal view.—E. Dorsal view of somites of the mysid *Eucopia sculpticauda*.—F. Early larval stage of amphionidacean.—G. Adult amphionidacean.—H. Schematic illustration of a euphausiid showing area where organ is located, lower figures are indicative of variations in ultrastructure.—I. Carapace of larval penacid shrimp, *Solenocera*.—J. 'Eryonichus' larva of polychelid lobster.—K. Unidentified phyllosome larva (*Palinura*).—L. Schematic crab zoea showing locations where organs are typically found in brachyuran larvae. (A after Ito 1986; B, C after Muller & Walossek 1988; D, E, H, K from Mauchline 1977; F, G after Heegaard 1969; I, J after Gurney 1942 (from Bouvier 1917); L after Martin 1984.)

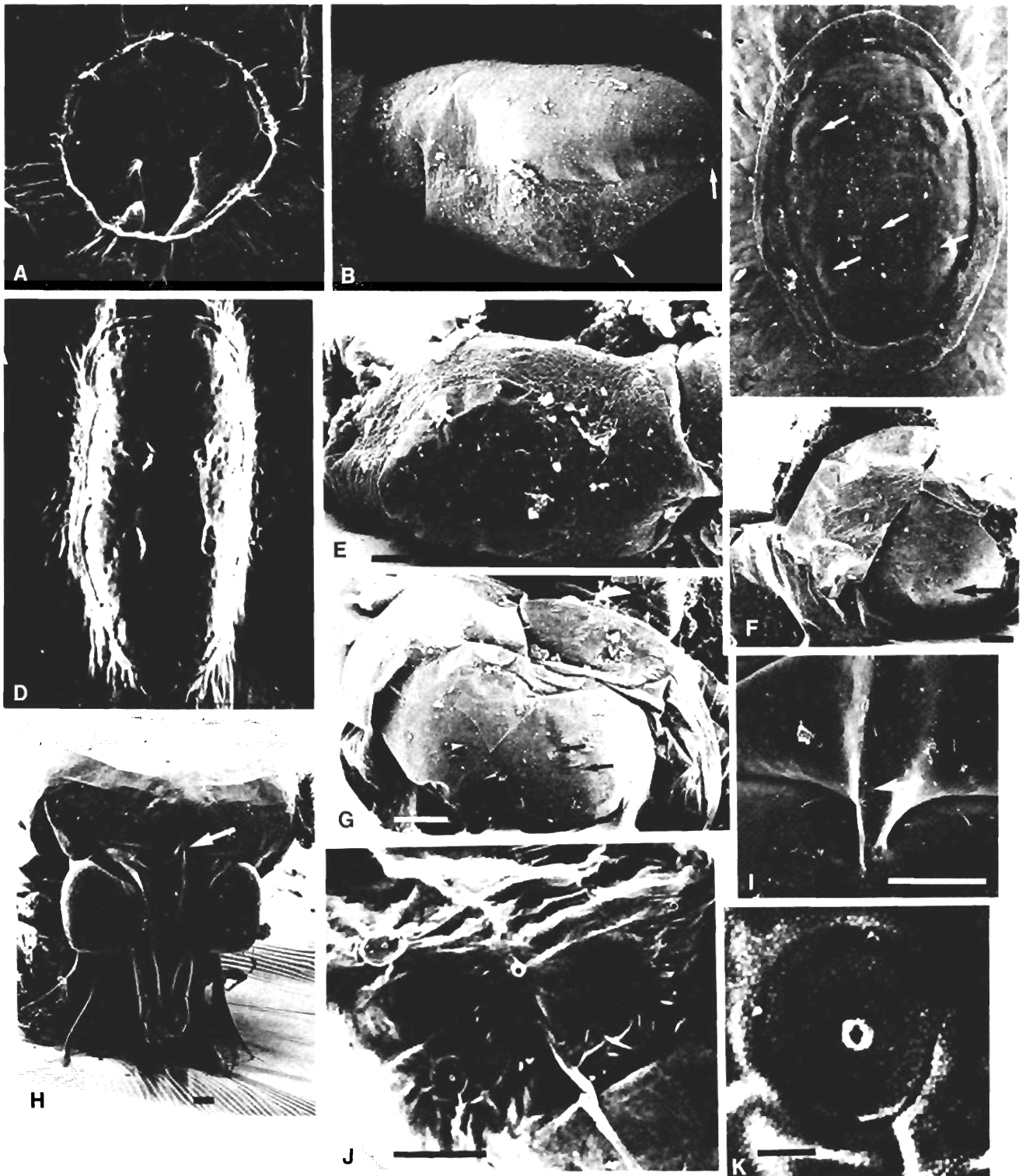


Fig. 3. SEM photographs of various dorsal organs in the Branchiopoda, Maxillopoda, and Decapoda.—A. Dorsal view of head of adult *Streptocephalus sealii* (Anostraca).—B. Lateral view of pedunculate organ in a limnadiid clam shrimp (Spinicaudata).—C. Fronto-dorsal view of head region in the laevicaudatan *Lynceus*.—D. Same view of a species of *Paralimnietis* (also Laevicaudata).—E. Dorsal plate on apex of cephalic shield in early developmental stage of Upper Cambrian *Rehbachella kinnekullensis* (Branchiopoda, probably anostracan affinity) (scale bar = 10  $\mu$ m).—F. Area bearing four pores or pits on apex of adult cephalic shield in Upper Cambrian maxillopod *Bredocaris admirabilis* (scale bar = 30  $\mu$ m).—G. Another specimen of *Bredocaris* showing four small pits (black arrows) on apex of cephalic shield (scale bar = 30  $\mu$ m).—H. Anterior view of zoea II of *Porcellana* sp. (Decapoda, Anomura) (scale bar = 100  $\mu$ m).—I. Higher magnification of area between eyes in H (scale bar = 100  $\mu$ m).—J. Dorsal organ in zoea larva of *Sesarma* (Decapoda, Brachyura) (scale bar = 10  $\mu$ m).—K. Higher magnification of one of the peripheral 'plate pits' seen in J (scale bar = 1  $\mu$ m). (A, B are original; C, D from Martin & Belk 1988; E from Walossek 1992; F, G from Müller & Walossek 1988; H–K from Laverack 1988.)

plays a role in supplying nutrition to the developing embryo and also aids in ecdysis (Fioroni 1980). Strömberg (1972) suggests a role in secretion of some as yet unidentified product, although Meschenmoser (1989) notes that in the terrestrial amphipod *Orchestia*, which might have some of the same osmotic problems facing freshwater branchiopods, there is good evidence for ion transport. Whatever the function of the embryonic dorsal organ, it is, in our estimation, a different structure from the cuticular dorsal organ that is the topic of this paper.

*Syncarida*. In his 1909 handbook, Calman (1909, p. 164, based on his earlier work) described the organ on the carapace of an adult *Anaspides tasmaniae* as follows: 'On the dorsal surface, in front of the cervical groove, is a pigmented area with a circular central spot surrounded by four minute pits. The significance of this structure is quite unknown, but it might be comparable to an obscure "dorsal organ," apparently glandular in nature, occupying a similar position in certain other Malacostraca.' There can be little doubt that the organ figured by Siewing (1959, in H. G. Bronns, p. 57, figs A, B) is the same structure that Calman described and that we described earlier under External Morphology. Siewing's figure, actually a photograph taken through a microscope, clearly shows four small bumps centered around a central larger pit, nearly identical to the condition described for decapod larvae. Unfortunately the magnification of the photograph is too high to discern if a cuticular border defines and demarcates the structure from the surrounding carapace cuticle. Hansen (1921) noted the presence of a dorsal organ in *Paranaspides lacustris* and stated that it was more reduced than in *Anaspides*; Hansen also noted that the pits on the dorsal organ vary, with anywhere from three to five pits on the three specimens available to Hansen at the time.

*Amphionidacea*. Heegaard (1969) illustrated a dorsal organ in nearly all developmental stages of the Amphionidacea, and assumed that the anterior spine in the adults is a manifestation of this larval organ as well. According to Heegaard (1969, p. 11), 'Throughout its larval life *Amphion* has a vestigial anterior dorsal organ, which in the older stages develops an anteriorly pointing spine.' We have reproduced Heegaard's figs 1 and 111 and in our Figs 2F, G. Thus the situation is similar to what is known for caridean shrimps (see below).

*Euphausiacea*. A dorsal organ in euphausiids apparently was first observed by Giesbrecht (1913, not seen, as cited in Hansen 1921), who noted the structure in larvae and adults. Hansen (1921) observed in some genera (*Thysanopoda*, *Bentheophausia*, *Meganyctiphanes*, and *Nematobrachion*) an area that differed from the surrounding cuticle, but he could not be certain as to its detailed structure. Mauchline (1977) described a dorsal organ in several euphausiid genera, illustrating (1977, fig. 10) the arrangement in eight genera, some of which are reproduced in our Fig. 2H. His general description is as follows: 'The compound organ occurs in a groove on the top of this (dorsal anterior carapace) keel. It consists of a number of anterior pairs of pores, the number dependent upon the species. There are then two pairs of larger structures that

are digested by the potassium hydroxide and leave the peculiar geometrically shaped holes found in *Thysanopoda acutifrons* or the elongated pores found in the other species;' he later stated 'The anterior pairs of pores and the thin central area can be seen quite clearly' (1977, p. 987). The homology to the 4 + 1 dorsal organ of decapods, syncarids, and branchiopods seems very probable.

#### Decapoda

*Dendrobranchiata*. Several records of a dorsal organ in larval and adult decapods were reviewed by Hansen, who noted (1921, p. 74) that 'The dorsal organ is found in adults of most species of the Penaeidae inspected by me, and in all genera and species of the Sergestidae excepting *Lucifer*.' Hansen (1921) specifically discussed the occurrence of a dorsal organ in adults of some species in the penaeid genera *Aristeus*, *Solenocera* (an illustration of which appeared in Gurney 1942, p. 111; see our Fig. 2I) and *Penaeus*. For *Penaeus* he notes its presence in larvae as well. In the Sergestidae Hansen noted its presence in adults of species in the genera *Petalidium*, *Sicyonella*, *Acetes*, and in adults and larvae of *Sergestes*; in the latter genus Mauchline (1977, p. 989 and fig. 11) notes that a 'dorsal median compound organ, probably analogous to that of the euphausiids, is present on the carapace of this species (*S. arcticus*) and *S. robustus* and *S. mollis*.'

*Caridea*. Laverack & Crombie (1988) stated that it is found in all stages, including the adult, in the shrimps *Crangon crangon*, *Thorulus cranchii* (their figs 6A, B, developmental stage not given), and *Pandalus montagui* (their figs 4, 5, 70–80 mm range). For *C. crangon*, their figs 1A, B (developmental stage not given), and 2A, B (a 15 mm specimen), show the organ clearly. Laverack & Crombie (1988) also show the organ in a larger (60 mm) animal (their fig. 3); the smallest specimen they examined was 10 mm. A recent review (Laverack 1990) of this organ in *Crangon crangon* includes more detailed observations on ultrastructure. The organ is therein described as having a central glandular cell 'possessing a brush-border microvillous lumen suggestive of an ion regulating cell'. For the 'sensory cells' of the four peripheral pits, a short ciliary body is described. The outlying pits, which lie in an area of very thin (0.21  $\mu$ ) cuticle, are shown to have dendrites extending into the central projection of each (Laverack 1990). There is as yet no known connection between the central glandular cell and the adjacent sensory cells. Hansen (1921) had reviewed previously the presence of the organ in the caridean genera *Acanthephyra*, *Nematocarcinus*, *Ephyrina*, *Pasiphaea*, *Spirontocaris*, *Bythocaris*, *Alpheus*, and *Palaemon*. Hansen did not provide any illustrations, but his description of the organ was more or less the same for all caridean genera: 'an area marked off by a circular depression very near the base of the first dorsal spine' (from his account of *Spirontocaris*). In several genera Hansen describes the presence of pits in the circular area. Mauchline (1977) mentions the presence of this organ in several of the above genera, and additionally notes its presence in the genera *Parapasiphaea*, *Hymenodora*, *Systemaspis*, *Oplophorus*, *Meningodora*, *Notostomus*, *Pandalus*, and *Bentheogennema*.



*Astacidea*. According to Gurney (1942), Bouvier (1917, pl. i, fig. 2) illustrated a dorsal organ in *Nephropsis atlantica*. Laverack & Barrientos (1985) and Laverack (1988) mentioned the presence of the organ (no illustrations) in larvae of *Homarus* and *Nephrops* (Nephropidae).

*Palinura*. Gurney (1942, fig. 27A) reproduced one of Bouvier's figures of an eryoneic larva with two dorsal organs, one anterior to the cervical groove and one closer to the posterior border of the carapace (our Fig. 2J). Gurney describes the organ as having the form of a 'long slender papilla' (1942, p. 111). Gurney (1942, p. 112) also cites Terao (1919) as having described three dorsal organs in *Panulirus*, but Terao's paper dealt only with the embryology; the three dorsal organs are actually the one embryonic dorsal organ (located medially) and paired lateral organs found in a number of malacostracan species during embryological development. The presence of the dorsal organ in larval *Palinura* was reported (no illustration) by Laverack & Barrientos (1985) and by Laverack (1988), and Mauchline (1977) described it in an unidentified phyllosoma larva: 'A compound organ consisting of two pairs of pores, each 6  $\mu\text{m}$  in diameter, is present in the middorsal region of the carapace . . .' (our Fig. 2K).

*Anomura*. According to Barrientos & Laverack (1986), the dorsal organ occurs in larvae of *Porcellana longicornis* and *P. platycheles* in all zoeal stages. Their fig. 3B showed the organ in a first stage zoea of *P. platycheles*. Laverack (1988, fig. 6) provided SEM photographs of the organ in a first zoeal stage of an unspecified species of *Porcellana*; these photographs are reproduced here as Figs 3H, I.

*Brachyura*. Pohle & Telford (1981) described a 'cuticular organ complex' on the midline of the carapace in larval stages of the pinnotherid crab *Dissodactylus crinitichelis*. Their description, and their excellent SEM photographs (their figs 5K, L, M), agree closely with other descriptions of this organ in larval decapods (see above). Pohle & Telford describe the complex as follows: 'A peculiar, previously undescribed organ complex was found frontally, in the center of the carapace, about midway between the eyes and dorsal spine in all zoeal stages. It consists of a central pore, surrounded by four equidistant ring-like cuticular elevations which bear a nipple-like structure in the center' (Pohle & Telford 1981, p. 746). Interestingly, they also found a similar structure just behind the dorsal spine; both organs were found in the same location on the megalopa and first crab stages as well. This finding of two dorsal organs in brachyuran larvae is reminiscent of earlier reports (e.g. see Hansen 1921 and Gurney 1942) of paired median dorsal organs in shrimp and eryonoid lobsters. Many students of zoeal morphology have illustrated, without discussion of what it might be, a protuberance on the posterior carapace that is probably this second organ (e.g. see Martin & Truesdale 1989 for the Dorippidae). The dorsal organ in larvae of *Sesarma (Aratus) elegans* was illustrated by way of SEM photographs by Laverack (1988, figs 7A, B, zoea II); in that species not only is there a central pore but

the peripheral 'plate pits' bear apertures as well (Figs 3J, K). It is interesting to note that in *Sesarma*, as in *Dissodactylus*, the cuticular border demarcating the organ from the surrounding carapace is lacking. Barrientos & Laverack (1986) noted the presence (no figures) of the organ in zoeal stages of *Carcinus maenas*; juveniles were not found to have it. Furthermore, they illustrated the organ in the megalopa stage of *Hyas cornutatus* (their fig. 1A), and the zoeal stages were said to have it also.

### Function of the Dorsal Organ

Criel (1991) discusses early hypotheses for function of the organ in *Artemia*, such as adhesion (e.g. Spangenberg 1875) and glandular secretions (Claus 1886). Weisz (1947) and Benesch (1969) considered the organ in anostracans as nothing more than a site for anchoring of the antennal and mandibular muscles, while Dejdjar (1931) suggested (based on reducing properties indicated by selective staining) a respiratory function in 'cladocerans'. Most of the above beliefs were challenged by Croghan's (1958) work on ionic and osmotic regulation in *Artemia*. The structure in larval anostracans and some cladocerans (mostly anomopods) is now demonstrated widely to function in salt or chloride regulation, and so it is most often referred to as a salt-secreting organ (e.g. Conte *et al.* 1972, 1973; Kikuchi 1972; Hootman *et al.* 1972; Criel 1991). This function is also supported by 'micropuncture studies' (Russler & Mangos 1978) and by the finding of  $\text{Na}^+\text{K}^+$  activated ATPase in the organ (Conte *et al.* 1977; Criel 1991). Horridge (1965) illustrated in the Notostraca a nerve cord extending to the dorsal organ (1965, p. 1168, fig. 21.1 [after Henry 1948]), possibly suggestive of a sensory role. Adhesion has also been suggested in various cladocerans and conchostracans, as has respiration. Adhesion does occur in some cladocerans, e.g. *Sida*, but the details of the attachment mechanism, and thus the role of the dorsal organ, are unknown. Because the present habitat of most branchiopods is in fresh or saline inland waters, we assume that the currently accepted function in branchiopods—ion transport—is derived from the original use in marine branchiopods (e.g. the Cambrian *Rehbachella*, see Walossek 1992). The function in other marine crustaceans is insufficiently understood, although, as mentioned in the section on decapods earlier, it has been suggested that the zoeal dorsal organ plays a role in chemo- or baroreception (Laverack & Barrientos 1985; Laverack 1987) and that the central pore is glandular in nature (Laverack & Crombie 1985; Laverack 1988, 1990). Laverack (1990) reviewed recently evidence for chemoreception, mechanoreception, and baroreception in the caridean *Crangon crangon*.

### Discussion

The most pressing questions about the dorsal organ discussed here concern homology. Three hypotheses that

should be tested are (1) that all dorsal organs (including the embryonic ones) are homologous; (2) that none of the structures mentioned in this article is homologous; and (3) that some of the organs (for example only those showing a clear 4 + 1 pit/pore arrangement) are homologous, with other structures arising convergently. Promising areas of investigation include the syncarids, which have a dorsal organ nearly identical to that seen in larval decapods, and also the non-anostracan branchiopods, to ascertain the extent to which adaptation to similar environments (freshwater ephemeral ponds) might have resulted in convergence in structure and function. A comparison of freshwater vs marine isopods and amphipods might also answer questions about the need for such an organ in all freshwater crustaceans, and an examination of larval stages in many taxa would probably repay study.

There is a question concerning the *embryonic* dorsal organ, described previously in embryonic states of many taxa (see Anderson 1973) and reviewed recently by Fioroni (1980). The embryonic dorsal organ appears in crustaceans (including pentastomids [Osche 1963; Fioroni 1980], which were suggested to be crustaceans on the basis of sperm morphology [Wingstrand 1972] and rRNA [Abele *et al.* 1989]), insects, tardigrades, onychophorans, and chelicerates (Fioroni 1980). According to Fioroni (1980) and several other workers, this embryonic structure is transitory, disappearing long before maturity, and functions in supplying nutrients to the developing embryo and in the process of ecdysis. That this embryonic structure appears in many arthropod groups, including crustaceans, may not be surprising; such an organ may be necessitated by the need to supply nutrients to an externally shelled animal within the egg membrane. In other words it may be a convergent character that has arisen independently among arthropods. Although we do not think it likely that the embryonic dorsal organ is homologous with the external feature discussed in this paper, the embryonic dorsal organ is located in approximately the same area (dorsal surface, posterior to eye region, along midline), and one possibility is that the cuticular organ we describe here is, in some taxa, merely a remnant of the embryonic structure.

Hansen (1921, p. 67), in his review of this structure in the Malacostraca, considered the two structures equal: '... it must be the so-called dorsal organ known in embryos of Crustacea of most orders, but unknown in almost all adult Malacostraca and in larvae of the same sub-class'. Meschenmoser (1989) even attributes some ion transport function—the presumed function in larval and some adult branchiopods—to the embryonic dorsal organ in the amphipod *Orchestia*. But we think it is unlikely that the cuticular dorsal organs discussed here are only remnants of an embryonic organ, as the organ is clearly functional in larval and adult branchiopods in several species and in larval decapods. We have assumed in this paper that this embryonic feature is not homologous with the cuticular dorsal organ, but we point out that the two structures do occur in the same region of the head.

Second, there are problems with serial homology in decapods. Specifically, is the second (posterior carapace) dorsal organ truly the same organ as has been described for the anterior region by so many workers? Early work-

ers, such as Hansen (1921), considered all of these structures homologous. As far as we know there have been no ultrastructural studies on the posterior larval dorsal organ in decapods, although Pohle & Telford (1981) state that the appearance of the two organs is the same. Before attempting to answer these questions we need more information at the ultrastructural level.

Questions concerning phylogeny must also await more detailed information. Variations of the 4 + 1 arrangement, such as the apparent absence of any pits and pores in most branchiopods, may indicate loss or modification, but just as easily these differences may mean that we are talking about different, non-homologous structures. We do not yet know the full distribution of this organ in the Crustacea, and we are unsure as to homologies both within and without the Crustacea. A similar 'dorsal tubercle' has been noted in several non-crustacean arthropods, including trilobites (see discussion in Barrientos & Laverack 1986 and in Müller & Walossek 1987). Are any of these structures indeed homologous to the crustacean dorsal organ, as suggested by Barrientos & Laverack (1986)? If so, arguments for polyphyly or paraphyly of major arthropod taxa are weakened.

As noted previously, the head of an arthropod is where sensory structures would be expected to occur, and it should not come as a surprise if several such organs, similar in external appearance because of physical constraints of the arthropod head, have arisen independently. But if the organs have arisen independently within the Crustacea, it is surprising that there is such apparent similarity in the details of this organ (the 4 + 1 arrangement of pits and pores) in the Syncarida (Siewing 1959), in at least some Branchiopoda (e.g. *Lynceus*, see Martin & Belk 1988, although it lacks a central pore), and in larval Decapoda (e.g. Pohle & Telford 1981, Barrientos & Laverack 1985), and that similar (but not identical) organs exist in Upper Cambrian fossils with maxillopod and branchiopod affinities.

We have seen little evidence of the dorsal organ in the peracarids (recalling that this is different from the embryonic dorsal organ so well known for that group), and nothing in the hoplocarids (but see Hansen 1921) or in the ostracodes (where it would be obscured by the dorsal hinge). In the Remipedia, one of us (JWM) has seen a specimen of the genus *Lasionectes* that was sputter coated in preparation for SEM work; there is a small bump on the midline in the appropriate area, but we have not been able to examine this specimen under SEM. It is absent in at least some species that have been subjected to SEM analysis (D. Felder, personal communication). There is no report of such an organ in the literature on remipedes. No mention is made of such an organ in the detailed work on cephalocarids by Sanders (1963), but nearly all of his illustrations were of the ventral aspect. Therefore it may be possible that it exists in larval stages but was overlooked. It is apparently absent in adults or, if present, it has never been described (R. Hessler, personal communication). Indeed, the main purpose of this note is to inspire specialists with access to a variety of taxa to search for this organ. We hope that this review will facilitate the detailed functional approach necessary to answer these questions.

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## Note Added in Proof

Subsequent to the time this paper was submitted, a more thorough review of the dorsal organ in the Branchiopoda has been completed, and is scheduled to appear at about the same time as this issue: Martin, J. W. 1992. Ch. 3. Branchiopoda. In F. W. Harrison (ed.): *Microscopic anatomy of invertebrates*, Vol. 9: *Crustacea*, pp. 26–227. Wiley Liss, New York.

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