The Carapace of the Branchiopod Crustacea

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SUMMARY

Notwithstanding suggestions to the contrary, the branchiopod carapace primitively originates as a fold that arises at the posterior margin of the head. This is generally from the maxillary segment but this region has sometimes been so modified during the radiation of the group that it is not always possible to be so precise. Fusion of any part of the carapace with the thorax is rare and does not negate the origin of the carapace fold. Although this has been denied, the Cambrian *Rehbachiella* displays the primitive pattern to perfection. In at least some notostracans there is a minor connection with the anterior part of the first thoracic segment which is interpreted as a secondary association. Notwithstanding differences in early ontogeny in the Spinicaudata and Laevicaudata, the carapace is clearly of maxillary origin and, although their ontogeny is again different, this is so also in the Anomopoda and Ctenopoda. In the Haplopoda the carapace lies topographically posteriorly on what appears to be a thorax made up of six fused segments. Nevertheless it is of anterior origin. To facilitate the efficient use of its grasping limbs and to enable the highly modified thoracic musculature to be anchored on the extremely thin cuticle, the thorax of *Leptodora* (the only extant haplopod) has elongated dorso-ventrally and rotated. This directs the limbs forward and has carried the carapace posteriorly, though it still lies in a morphologically anterior position. Developmental studies reveal that it originated from the maxillary segment. The most highly modified branchiopod carapaces are found in the Onychopoda. Here they form a specialized brood chamber, always provided with a nutrient-secreting Nährboden (or 'placenta'). Most specialized of all are those of the podonids where what Claus called an 'uterus' holds the eggs and developing young. These specialized structures are also derived from a classical carapace fold. There is no such thing as a 'secondary shield', a term that has been used instead of carapace in the Spinicaudata, Laevicaudata, Anomopoda, Ctenopoda, Haplopoda and Onychopoda. As no such character exists, to use its alleged common possession as a synapomorphy which unites all these disparate orders into one phyletic lineage has no meaning. The Anostraca lack a carapace, as did the Devonian Lipostraca, and there is nothing to indicate that they ever had one.

1. INTRODUCTION

The crustacean carapace has been the focus of discussions on such matters as whether it is a primitive feature of the group, from which region of the body it originates, and whether it consists of fused tergites. Recent contributions to such debates are those of Dahl (1983*a*, *b*) and Newman and Knight (1984) which concentrate on the Malacostraca, and Dahl (1991) and Walossek (1993) that embrace a wider range of taxa. This note considers the carapace of the Branchiopoda, about which there is evidently still considerable confusion though reliable information having a bearing on the points at issue has sometimes long been available in the older, neglected, literature.

The classical view of carapace formation is that of Calman (1909) which holds that it arises 'as a fold of the integument from the posterior margin of the cephalic region'. In many malacostracans the carapace is fused with some or all of the thoracic segments and Dahl (1991) has questioned whether it is then of cephalic origin. He has further claimed that in the branchiopod orders Notostraca, Spinicaudata and Laevicaudata it is also of thoracic origin and that this is probably so in the so-called 'Cladoceran' orders.

Although by 'posterior margin' it is generally assumed that the maxillary segment is implied, this is not specifically stated by Calman. Indeed in the Branchiopoda not only is segmentation in this region compressed and obscure but what are often regarded as thoracic elements, most notably the longitudinal trunk muscles, but sometimes the heart and other organs, penetrate the head whether or not a carapace is present, e.g. see Fryer (1974, fig. 6 for *Acantholeberis*; Anomopoda : 1983, fig. 42 for *Branchinecta*; Anostraca: 1988, figs. 66 and 67 for *Lepidurus*; Notostraca). This probably reflects the situation before tagmosis was firmly established and preserves echoes of a 'primary head' composed of the three naupliar segments, with which the maxillulary and maxillary segments, originally similar to those of the trunk and bearing similar appendages, only later combined to form the definitive crustacean head. Neither by gross examination nor by study of longitudinal sections is it always possible precisely to delimit head and thorax in branchiopods. The main point at issue, however, is whether the carapace is of cephalic or thoracic origin.

As a result of its marvellous preservation and its superb reconstruction by Walossek (1993) the Cambrian branchiopod *Rehbachiella* is known in remarkable detail from the earliest nauplius to what is almost certainly a sub-adult stage and provides valuable information on the ontogeny of the carapace in the earliest known branchiopod. The nauplius has a dorsal shield. As development proceeds this extends posteriorly. First it covers the next cephalic segment, remaining firmly fused to it. As it extends yet further a fold or duplicature develops at its posterior margin (though this is denied by Walossek : see below) so that the rudimentary carapace slightly overhangs the underlying segment without being attached to or fused with it. Initially the fold appears to arise in the maxillulary segment, but such details are naturally difficult to ascertain, and at all events in the oldest known stage the carapace is attached to the posterior margin of the head and covers the first seven thoracic segments but is not attached to them. Its lateral margins have flexed ventrally and it also extends anteriorly so that it covers the sides of the head and of such trunk segments as it overlies, and the basal portions of the limbs. This sequence is beautifully illustrated by Walossek (1993, figs. 6, 7, 15). The oldest known stage exemplifies with diagrammatic clarity the classical condition of the carapace arising from the posterior margin of the head, in this case unambiguously from the maxillary segment. Curiously Walossek says that neither this ontogenetic pattern nor the similar pattern displayed by the Cambrian *Bredocaris*, a putative maxillopodan, splendidly elucidated and beautifully illustrated by Müller and Walossek (1988), supports the classical belief, and he also categorically states that 'neither is there a fold appearing at any stage of growth'.

To take the last point first, there *must* be a fold. Otherwise the carapace could not grow. A carapace is always a two-walled structure, the outer wall generally with a robust (in some groups calcified) cuticle, the inner with a usually thinner cuticle. Each is lined by epidermis. Between the walls of living tissue is a space, continuous with the haemocoele, through which blood circulates. Spanned by fibrils, this is utilized by branchiopods for various purposes, such as respiration via the inner wall, and, in many cases, for housing the tubules of the maxillary glands. The only way in which such a two walled carapace can develop is via a fold.

Walossek emphasizes that the carapace of *Rehbachiella* is the product of progressive growth of the naupliar shield, as indeed it is, but this is not incompatible with the presence of a fold in post-naupliar instars. The naupliar shield increases in size before the fold develops, as it must if it is to continue to cover the dorsal surface of the early instars as they grow, but it cannot produce the carapace of older stages by this simple process. Although Walossek also says that the carapace does not 'belong exclusively to one of the head segments', it clearly develops from that of the maxillae. Furthermore, as demonstrated below, a carapace can originate from the maxillulary/maxillary region whether or not a dorsal shield is present.

The rest of the Branchiopoda can be considered under the different orders. No phyletic implications should be inferred from the sequence used.

2. THE SITUATION IN THE VARIOUS ORDERS

(*a*) *Anostraca*

There is no carapace in the Anostraca and no indication that such a structure was ever present. Important adult functions, such as locomotion and feeding, have clearly evolved in the absence of a carapace, of which there is also no trace at any stage of ontogeny.

That, as Walossek (1993) remarks, there is a shield in the anostracan nauplius is no indication of a former carapace. The 'headshield', designated in inverted commas to avoid any phyletic implications by Fryer (1983), is a functional necessity, being required to provide firm anchorage for the numerous dorsally inserting muscles that actuate the naupliar appendages responsible for locomotion and feeding (Fryer 1983, figs. 14–17 and 19).

(*b*) *Lipostraca*

The Devonian *Lepidocaris*, the only known representative of this order, had no carapace, nor as Scourfield (1940) showed, is there any sign of such in the few known post-naupliar stages.

(*c*) *Notostraca*

From a study of sections Dahl (1991) reported that in a 3 mm juvenile of *Triops cancriformis* the carapace is attached medially to the first and second trunk segments, more laterally only to the first, and that in adults of *T. namaquensis* (= *T. granarius*) it is attached to the posterior margin of the first and anterior margin of the second. However, he had earlier (Dahl 1983*a*) said that in the Notostraca 'a free carapace fold grows out from the posterior margin of the maxillary segment' and cites a paper then in press. There (Dahl 1983*b*), having said that a carapace is, by definition, a fold growing from the posterior border of the maxillary segment, adds 'it is to be found in its typical form in the Notostraca'. The statement is completely unambiguous. It is emphasized when he adds that the carapace is not, however, attached to the maxillary segment in all non-malacostracans, and says that in certain other branchiopods one, two, or more segments 'are fused to the head and the carapace fold is attached to the last of these segments'. This point will receive attention as we proceed.

I agree only in part with Dahl's (1991) findings. Longitudinal sections of *Lepidurus apus* show that trunk segment 2 has no connection with the carapace, as indeed can be seen by careful removal of the latter. The section of *T. granarius* shown in Dahl's fig. 9 is lateral to the mid line. What is labelled as segment 1 is in fact a cephalic extension of the dorsal longitudinal muscle, a more posterior trace of which can be seen at the level of segment 3. Segment 1 lies much further back than indicated, immediately anterior to the slightly longer segment 2. In *L. apus* the carapace arises in the vicinity of the maxillary/trunk segment 1 boundary: indeed segments 1 and 2 are so closely associated that the joint between them is difficult to discern over much of the lateral part of the trunk. While some of the dorsoventral muscles of segment 1 insert on the dorsal integument of the trunk adjacent to where the carapace fold arises, some anterior bundles insert on the carapace itself. The same is true in *T. cancriformis*. Pulling away of the carapace reveals the torn ends of these. No such torn ends are seen in other segments. Dahl's fig. 8 shows the close juxtaposition of segments 1 and 2. In some sections of *L. apus* the fold can be seen arising more anteriorly.

Dahl also presents two not very clear sections of a juvenile of *T. cancriformis* (L. c3 mm) and says that near the mid line the carapace is attached to trunk segments 1 and 2; more laterally only to segment 1. It is not clear from these photographs that there is any connection between the carapace and segment 2. My own, also not very good, longitudinal sections of a somewhat smaller individual revealed no such connection: the situation with respect to segment 1 is the same as prevails in the adult. (One's first impression that Dahl's trunk limb 1 is actually the maxillule, which is robust at this stage, is illusory: the section is too lateral to reveal the mouthparts. Ironically, had it been so, the labelling of trunk segment 2 in fig. 3, which is actually segment 3, would have been correct.)

While the situation might be interpreted as indicating that the carapace fold originates from the extreme anterior end of the thorax, it can equally be argued that it arises from the posterior end of the maxillary segment and that a few muscles from thoracic segment 1 have migrated into the head, presumably for functional reasons. Here the wide duct of the maxillary gland leaves the space between the lamellae of the carapace and descends toward its exit and requires considerable space. This requirement may have contributed to the migration of certain muscles.

A maxillary origin is indicated by Sars' (1896*b*) illustrations of *L. glacialis* (= *L. arcticus*). In plate 13, figs 1, 2, the trunk is exposed dorsally and laterally by removal of the carapace. No connection between the two is indicated. None of these observations supports the contention of Lang (1888), cited by Dahl (1991), that the carapace is attached to the anterior trunk segments. Thus, while other interpretations are possible, the most obvious conclusion is that the carapace fold of the Notostraca originates from the posterior end of the maxillary segment, though certain muscles from the anterior part of the first trunk segment now insert onto it in some species.

Contact between the carapace and thorax need not of course mean that the carapace fold is of thoracic origin. As Newman and Knight (1984) note with reference to the malacostracan cephalothorax, the carapace has simply become attached to the dorsum of the thorax. The same applies in branchiopods, though as we shall see, such association is unusual in this group.

(*d*) ***Kazacharthra***

Although kazacharthrans in an excellent state of preservation are now known, which clearly reveal trunk segmentation (McKenzie *et al.* 1991), it is not possible to ascertain whether any of these segments are fused to the carapace. Speculation is dangerous. The most that can be said is that in some cases, as seen for example in fig. 28 of McKenzie *et al.*, some at least of the thoracic segments are so distinct dorsally that, by analogy with the situation in the Notostraca, they appear to be free from the carapace.

(*e*) ***Spinicaudata***

As long ago as 1887 G. O. Sars, who is noted for the excellence of his illustrations, described the development of parthenogenetically produced individuals of *Cyclestheria hislopi*. His figures, especially lateral views of embryos at two stages (Plate 7, figs. 2–5), show the carapace arising from the posterior region of the head. Having achieved their definitive form, a juvenile male in the first, and a female in the third instar (Plate 8, figs. 1–4) clearly show the carapace attached by a pedicel anterior to the first trunk segments, and this is so also in the older females (Plate 2, figs. 1–2). There is no contact with any trunk segment.

Sars (1896*a*, *b*) also described the development of *Cyzicus packardi* (as *Estheria packardi*) and *Limnadia lenticularis*. Commenting on the former paper Dahl (1991) says that Sars 'found the earliest fold rudiments as small bulges in the anterior part of the trunk region of the third nauplius'. At this stage 'trunk' embraces all the post-mandibular region. So far as can be made out in the whole animal the carapace arises immediately behind the mandibles. By stage 6 (Plate 2, fig. 3) it is clearly seen to be attached to cephalic tissue dorsal to the maxillules and maxillae and has no connection with the thorax. Illustrations of the first, second and fourth adult instars (Plate 3, figs. 1–3) also clearly show the definitive carapace arising from a pedicel of cephalic origin and lacking any connection with the thorax. These illustrations do not show 'that the attachment of the bivalved dorsal folds lies at the posterior margin of the first trunk segment' as Dahl claims. Were such attachment to be the case it would seriously impair the efficiency of the adductor muscle, which is located in the head. Likewise the detailed illustrations of the development of *Limnadia* (Sars 1896*b*), and especially those of adult instars of various sizes (Plate 14, figs. 1, 4–6, Plate 2, fig. 1), show with great clarity that the carapace has no connection with any trunk segment. This is the case in other spinicaudatans.

Nowikoff (1905, figs. 2–9) illustrates the pedicel by which the carapace of *Limnadia* is attached. Dahl (1991) says that the presence here of a small muscle from the maxillary segment does not justify his referring to the entire muscle complex as maxillary, but this is not the only reason for so doing, and there is equally no reason for regarding the pedicel as thoracic because a branch from each dorsal longitudinal muscle extends

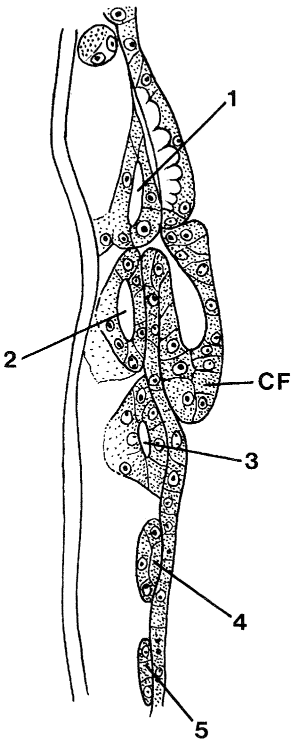

Figure 1. Horizontal section through the posterior part of the head and anterior part of the trunk at the level of the dorsal coelomic sacs (1–5) of a larva of *Estheria* (Spinicaudata) in which the carapace fold (CF) is developing. Coelomic sacs 1–5 or their precursors are apparent : cavities have not yet appeared in what will be sacs 4–5. The location of the carapace fold adjacent to the second coelomic sac shows that it originates in the maxillary region (Redrawn from Cannon 1922). Because of some ambiguity in the original paper, no scale is indicated.

into it, constitutes the main anchor of the carapace, and serves as a trunk adjuster. As noted above the anterior elements of the dorsal longitudinal muscle complex are cephalic. So too is the pedicel of *Limnadia*, and other spinicaudatans, and the carapace nowhere has any contact with the dorsal surface of the first trunk segment.

Although Cannon's (1922) study of the early development of a species of *Estheria* was not particularly concerned with the development of the carapace, it nevertheless provides detailed and unambiguous evidence of where it originates.

Paired rudiments of the carapace fold first appear at the level of the posterior limit of the first dorsal coelomic sac, which arises in the maxillulary segment but extends backwards to the posterior limits of the maxillary segment. While Cannon does not comment on this, it seems that this sac represents the fused dorsal coelomic sacs of the maxillulary and maxillary segments, and certainly the boundary between the head and first trunk segment lies between the first two sacs (p. 411 and text fig. 2*a*). One of these early lateral ectodermal folds is shown in transverse section in Cannon's fig. 9, somewhat later stages being illustrated in figs. 10–12. Figure 14 shows the fold, clearly near its origin, lateral to the maxillule, whose mesoderm separates early. It is in fact difficult to distinguish maxillulary and maxillary segments. Even such a landmark as the adductor muscle is not always helpful. Although generally regarded as maxillary, Cannon presents evidence that it belongs to the maxillulary segment and (p. 408) indeed suggests that the carapace fold may arise in that segment and that the dorsolateral ectoderm of the maxillary segment is practically absent. What is not in doubt is that the origin of the fold is cephalic. Other sections (see below) show that in fact it arises from the maxillary segment.

A more advanced stage (Cannon's fig. 17), shows, more posteriorly, the carapace overlying, but not fused with, the first trunk segment. A much simplified outline of fig. 18 is given by Dahl (1991, fig. 10) to support his belief that the carapace is here attached to the trunk, as superficially appears to be the case. However, in the original figure Cannon attempts 'to figure all the important features that occur in the thickness of the section' not just in one particular plane, and it is not possible to deduce from what is shown that the carapace is fused to any part of the segment. Its adductor muscle, which lies in the head, is partly seen. Furthermore, a slightly oblique section could show the carapace attached dorsally to the cephalic region yet cut the first trunk segment ventrally.

Cannon's fig. 22, redrawn here as fig. 1, is from a horizontal section of a larva in which a well developed rudiment of the carapace fold is present. The section passes through the dorsal coelomic sacs, whose locations serve as landmarks, the first being cephalic, the second in the trunk. The carapace fold clearly arises from the posterior margin of the head. This is the lateral extremity of the fold. As fig. 1 shows, although it is in contact with the first trunk segment it is independent of it. Anderson's (1967) study of larval development in *Limnadia stanleyana* confirms the cephalic origin of the carapace. In the third nauplius 'the body wall becomes pushed out dorsolaterally just behind the mandibular segment as paired carapace rudiments' and his fig. 4 shows such rudiments anterior to the just differentiating limb buds of the trunk. His fig. 6B is particularly informative. This longitudinal section shows the carapace rudiment arising at about the same level as does the maxilla ventrally, and clearly anterior to the first trunk limb bud.

Thus, notwithstanding Dahl's contrary view, and although Walossek (1993) says 'it remains open whether the shield grows from the maxillary segment or the anterior trunk region' in the Spinicaudata, its origin in the former location is clearly established. Walossek's uncertainty was due in part to his giving credence to the statements of Strenth and Sissom (1975) who looked at the development of *Eulimnadia texana*. This work is so inaccurate and misleading that a brief comment is necessary. Scant appreciation of morphology is apparent. For example, the labrum is referred to throughout as the labium. In their abstract the authors say that 'the first trunk segment enlarges and forms the valve of the carapace'. In the text, however, they say that 'the first pair of appendages of the trunk are modified into two distinct cup-shaped valves which are connected across the ventral [sic!] surface of the body' to form the carapace. They reiterate this by saying that the stage in question 'is characterized by the modification of the first trunk appendages to form the two valves of the carapace'. Of all suggested origins of the carapace this is the most bizarre. This paper should henceforth be ignored.

(*f*) *Laevicaudata*

The remarkable larva of *Lynceus* was competently described and illustrated by Grube as early as 1853 and has been illustrated by, among others, Gurney (1926) who clarified certain matters relevant to carapace formation. Notwithstanding its departure from the more usual branchiopod type, and a recent statement to the contrary (Walossek 1993), this is a true nauplius, hidden beneath a large, broad, dorsal shield. As Grube was aware, and as Gurney makes plain, this shield is only a larval feature. In the light of subsequent misunderstanding, Linder's (1945) statement that Gurney showed that the definitive carapace 'grows from the shield' is misleading. Gurney showed that the true carapace develops independently of the naupliar shield. This is of course also true of less conspicuous naupliar shields, which are replaced at each moult and only extend by the secretion of new cuticle beneath them. Not until the limb buds make their appearance, apparently in the second stage nauplius, is there any obvious sign of the definitive carapace, the incipient valves of which arise 'immediately behind the nuchal organ' (Gurney 1926), and therefore in the cephalic region. The carapace not only extends posteriorly beneath the naupliar shield but has an anterior fold that extends forward on either side of the head. After the moult to the first juvenile stage the definitive carapace completely covers the head as well as the trunk and its appendages.

As in the Spinicaudata the carapace is attached to the body via a pedicel. Accurate illustrations, such as those of *L. brachyurus* by Sars (1896*b*), show this to arise from the head and not from the trunk. An illustration of the dorsal musculature of this region by Hessler (1964) shows that, although elements of the dorsal longitudinal muscles extend into it, the pedicel lies anterior to the maxillary/trunk segment 1 boundary. Longitudinal muscles extend into the head in many branchiopods and are here no indicators of non-cephalic origin. It can be stated with confidence that the carapace of the Laevicaudata originates in the cephalic, and more specifically the maxillary, region and has no connection with the trunk.

(*g*) *Anomopoda*

Because the Anomopoda have lost the nauplius and develop directly to the definitive form either by parthenogenesis in the maternal brood pouch or in a resting egg, it is less easy to make direct observations on the development of the carapace than in forms with free-living nauplii. Furthermore, most species have yolky eggs, necessitated by the need to sustain development to the definitive stages when feeding begins. This makes it difficult to study sectioned material. Embryos of *Moina*, however, nourished by a Nähroboden ('placenta') are less obscured by yolk. Moreover adults of some anomopods present various complex situations in which, for example, in order to accommodate some of the large muscles that actuate the antennae and mandibles, the dorsal part of the head and the headshield extend posteriorly so as to lie further back than some of the anterior trunk limbs. The basic pattern of carapace development is not affected by these and other complications. Some species have a headshield: others lack such. Carapace formation is the same in both.

Among early investigations those of Grobben (1879) on *Moina* provide excellent information. His sections show that the carapace makes its first appearance in the embryo as a small swelling on each side as a result of duplicature of the dorsal integument in the maxillary region. This is shown in his fig. 47 – a transverse section. The early duplicature is also seen in the whole animal and shown, with cellular details, in fig. 35. Later the two dorsal duplicatures unite in the mid line so that the incipient carapace becomes free along its entire margin and has the form of an overhanging mantle.

An exactly similar process is seen in the development of the resting egg. Vollmer (1912) describes the appearance of the carapace as a duplicature on each side of the embryo, and its location can be fixed accurately from his transverse sections (figs. 22 and 23) of *Daphnia pulex*, which show an early stage of its formation at the level of the 'Nachenorgan' or dorsal organ.

Recent work by Kotov (1996 and in prep.) on whole embryos confirms the situation. Kotov's work, which has demonstrated the wide occurrence of the maxilla in the embryo of anomopods in which it is lacking in the adult, has incidentally cast light on the site of origin of the carapace whose location can be pin-pointed by reference to the rudimentary maxillules and maxillae. This is very clearly seen for example in an illustration of *Bosmina* (Kotov in prep.) which shows the carapace arising from the posterior region of the head.

In the Anomopoda there appears to be no convincing evidence that trunk segments ever contribute to the formation of the carapace, which seems always to arise in the maxillary region of the head.

(*h*) *Ctenopoda*

As in the Anomopoda the carapace of the Ctenopoda originates from the posterior region of the head. Its cephalic origin is apparent from longitudinal sections. In *Sida crystallina*, for example, although elements of the dorsal longitudinal muscles penetrate the head, as here do even the ovaries, the carapace arises anterior to any of the muscles of the first trunk segment and its appendages. Although it receives only brief mention, the cephalic origin of the carapace in the embryo of *Holopedium gibberum* is made apparent by Agar (1908).

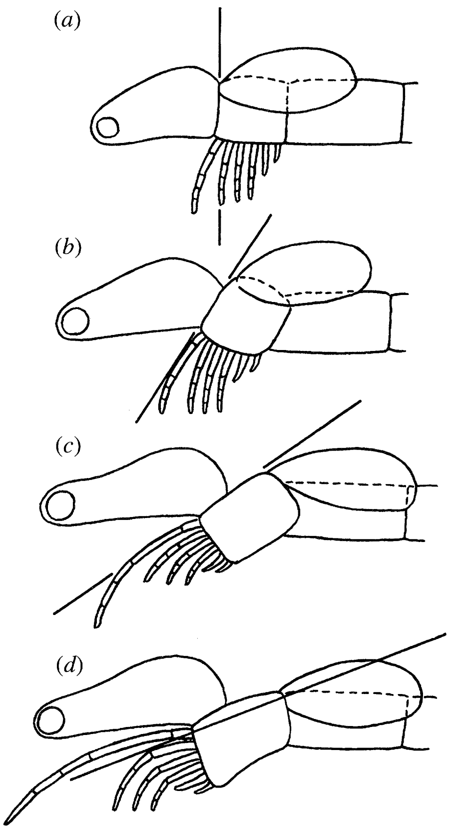

Figure 2. Evolutionary changes in the location of the carapace in the Haplopoda (diagrammatic). (*a*) An early haplopod with ventrally directed, relatively unspecialised thoracic limbs. (At this stage the thorax may have retained external signs of segmentation). The carapace arises from, and remains associated with, the maxillary segment. (*b*) The thorax begins to elongate in the dorso-ventral plane and to rotate, carrying the carapace posteriorly, as the limbs become more specialised for seizing and holding prey. (*c*) These processes continue and the abdomen shifts along the posterior margin of the thorax. (*d*) The modern *Leptodora*. The thorax, bearing highly specialised, forwardly-directed limbs, now inclines strongly posteriorly, the abdomen articulates with its morphologically dorsal surface, and the carapace lies physically remote from the head but is still attached in a morphologically antero-dorsal position.

(*i*) ***Haplopoda***

In the female of *Leptodora kindti*, the only representative of the Haplopoda, the carapace is reduced to a simple, more or less ovoid, brood sac, whose large ventral aperture fits neatly against the trunk thus preventing the escape of any eggs or embryos contained within. In the male it is reduced to a small, simple flap.

A striking feature of the carapace is its location. Topographically it lies remote from the head at what appears to be the posterior end of the thorax, which consists of six fused segments, and more posterior than any of the six pairs of trunk limbs. Not surprisingly this has been taken as indicating that it originates from a position well back on the trunk (e.g. Calman 1909, Dahl 1991). Appearances are, however, deceptive, which is why the position was described as being topographically at the posterior end of the thorax and posterior to the trunk limbs in publications having a bearing on classification and phylogeny (Fryer 1987*a*, *b*). The resolution of this anomalous situation is to be sought in the nature of the musculature of the 'thorax' which has never been properly described. This musculature, details of which are not needed here, is highly modified in order to meet the need to anchor various muscles on the extremely thin cuticle of this transparent and almost invisible predator. Its arrangement shows that the carapace arises near the morphologically anterior region of the 'thorax' dorsal to the first pair of trunk limbs. During the evolution of this remarkable animal, the thoracic region, which originally extended posteriorly from the head, (fig. 2*a*) has swung ventrally (forward) from its anterior ventral corner (figs. 2*b* and *c*), thus allowing the grasping appendages the better to seize prey detected by the large compound eye. Concomitant with this swing, the trunk limbs became more specialized for grasping and the 'thoracic' region began to extend in the morphologically dorso-ventral plane to accommodate changes in the musculature. As a result of these changes the carapace was carried dorsally and somewhat posteriorly (fig. 2*c*). As the depth of the 'thorax' gradually increased and the swing continued it was mechanically advantageous for the abdominal region gradually to shift dorsally along the margin of the 'thorax'. As a result it eventually came to articulate with what was originally, and morphologically still is, the dorsal surface of the 'thorax'. Thus the carapace, which remains attached to the anterior margin of the 'thorax', ultimately became located in a topographically posterior position and extends over the abdomen (fig. 2*d*). Throughout this process the heart, of necessity, kept pace with the swing of the thorax and maintained a topographically dorsal position.

Confirmation of this interpretation has long been available but the relevant publications have been largely forgotten. Sars (1873) not only discovered that the resting eggs of *Leptodora* hatch as nauplii but briefly described their subsequent development. As the primitive life cycle must have included a nauplius, direct development by parthenogenesis, such as takes place in the summer generations, is a later adaptation. Thus it is the former sequence that should in theory be the more informative about the primitive location of the carapace, though in fact both are illuminating. In the juvenile that follows the naupliar stages, which is illustrated by Sars, the thorax lies anterior-posterior, the developing limbs are ventral, and the rudimentary carapace arises just behind the mandibles, much as in the reconstructed ancestor shown in fig. 2*a*. The exact origin of the carapace cannot be ascertained by inspection. However, the work of Warren (1901) on the development of these early stages located it precisely. Although they are not particularly elegant, and suffered somewhat when they were redrawn by Gerschler (1911), Warren's illustrations are perfectly adequate and unambiguous.

Although the adult of *Leptodora* lacks both these appendages, as Samter (1900) had already shown, rudiments of the maxillules and maxillae make a fleeting appearance during the morphogenesis of the directly-developing generations, and this is so also during development from a nauplius. There is no trace of the carapace in the earliest nauplius. The first indication of its origin in an older nauplius is a dorso-lateral swelling which arises 'just behind the rudiment of the second maxilla' (= maxilla) and is shown in a transverse section by Warren (his fig. 3B) and, slightly more developed, in his fig. 3A. These swellings, which enclose the rudiment of the maxillary gland on each side, fuse to inaugurate the formation of the carapace, which can be seen in the entire nauplius and is shown in Warren's fig. 2. It arises as a typical carapace fold, shown in longitudinal section both near the mid line and more laterally in his figs. 4A and B where the minute rudiment of the maxilla unambiguously locates it as arising from the maxillary segment. As development proceeds the carapace is carried posteriorly to its adult location, taking with it on each side the maxillary gland, the end sac and an associated coil of which are tucked into its antero-lateral corner. No part of the gland occupies the dome of the carapace. Its duct, whose coils unravelled in the course of its migration, is voluminous near the carapace but narrows as it runs forward. The gland is illustrated by Weismann (1874, 1876) and Cannon & Manton (1927) and indicated *in situ* by Müller (1868*a*), Samter (1895), Gerschler (1911), the last two crudely, and Sebestyen (1931). Its duct traverses the full 'length' of the 'thorax' (actually passing ventrally from the morphologically dorsal side), enters the head (and is illustrated so doing from both dorsal and lateral aspects by Weismann, 1874), and, there being no maxilla, bends abruptly and opens on the wall of the head near the base of the antenna. The disposition of the maxillary gland, passing from the carapace to what can be defined no more precisely than the posterior region of the head, thus confirms the cephalic origin of the carapace.

The direct development of parthenogenetically produced young confirms the pattern of carapace migration and has long been known. Müller (1868*a*) gave simple sketches of the carapace at three stages of development. Clearer, larger, versions of these are given from the originals in an historical account of his numerous illustrations (Røen 1994). Müller (1868*b*) also gave illustrations of individuals at two stages of development that, while simple, show the carapace arising in the vicinity of the mandibles and later extending posteriorly.

Ironically, in his excellent account of *Leptodora* Weismann (1874) disputed Müller's findings and claimed that the carapace arises as a duplicature of the integument at the posterior end of the thorax. Moreover, in a postscript he reported some observations on the development of the spring generation and expressed his belief that these confirmed his opinion. However, he was led into error by the position of the heart which, he believed, would lie within the carapace duplicature if the latter arose anteriorly. This apparent geometrical incompatibility is resolved by the rotation of the thorax here described, during which process the heart retains a topographically dorsal location. According to Samter (1895), Weismann also found only relatively old stages in which of course the carapace had been carried posteriorly. Samter himself confirmed Müller's observations and illustrated the process more obviously, if rather crudely, at three stages of development.

As shown also in a photograph by Andrews (1948), at the time that a young *Leptodora* is released from the brood chamber its carapace arises well forward. At this stage the head is flexed ventrally and the trunk limbs are still aligned in an anterior to posterior row. Shortly thereafter the head extends anteriorly and the limbs assume the adult orientation.

Thus, notwithstanding its topographically posterior position, the carapace of *Leptodora* is of cephalic origin. The trunk limb (and carapace) – bearing tagma is clearly predominantly thoracic, but as it seems probable that some fragment of the maxillary segment has become incorporated in it, as of course has the carapace, it is best designated as the 'thorax' (using inverted commas).

(*j*) *Onychopoda*

The Onychopoda displays considerable morphological diversity and its members were, with justification, assigned to three families – Polyphemidae, Cercopagidae (orthography corrected to Cercopagididae by Martin & Cash-Clark 1995) and Podonidae – by Mordukhai-Boltovskoi (1968), largely on the basis of his work on the remarkable Ponto-Caspian fauna, whose cercopagidids and podonids have undergone much radiation. He had earlier erected subfamilies for the two latter groups (Mordukhai-Boltovskoi 1966). The diversity extends to the nature of the brood chamber. As in the Haplopoda, the onychopod trunk and its appendages are not protected by a carapace. Both have a dorsal brood pouch or chamber, but the resemblance is superficial, even when, as in the Cercopagididae, it is topographically as well as morphologically dorsal. In the other two families orientation of the trunk is such that eggs or young are carried in a backwardly projecting extension of the body.

In the Anomopoda, Ctenopoda and Haplopoda which, with scant justification, were for long united with the Onychopoda as the 'Cladocera', the carapace forms a brood chamber that is either open to the exterior or, as in *Moina*, simply sealed off so that the products of the Nährboden, whose secretions nourish the eggs and embryos, do not escape. The situation in the Onychopoda is more specialized and differs much within the order. Parallels can be drawn between the situation in *Moina* and in the Cercopagididae and Polyphemidae: the Podonidae is even more specialized. Our understanding of these systems owes much to the outstanding investigations of Carl Claus (1877), and to the penetrating observations of August Weismann (1877, 1879). Earlier observations of considerable merit were made by Müller (1868*a*), some of whose previously unpublished illustrations have been made available by Røen (1994).

In brief, in the Cercopagididae and Polyphemidae a carapace fold is formed in the usual manner. Its outer and inner lamellae lie close together and, initially, the

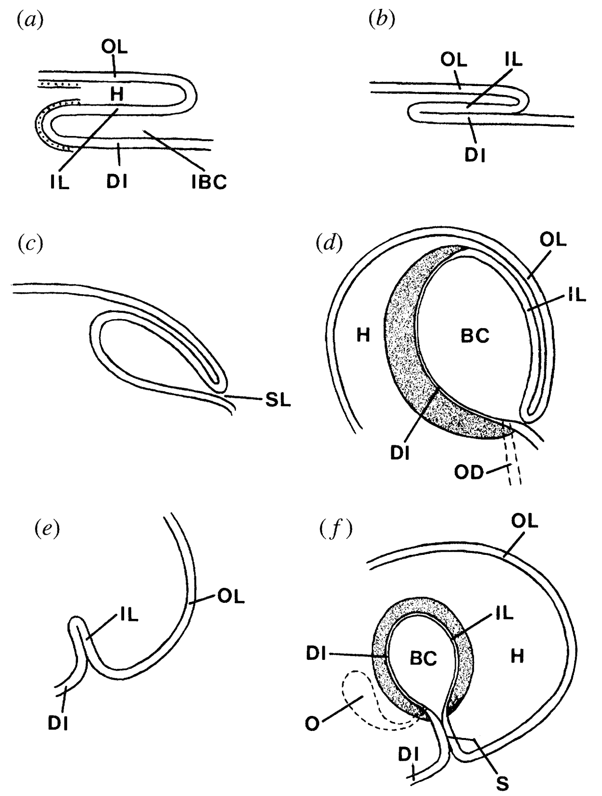

Figure 3. Diagrammatic representations of onychopod carapaces and their modifications. The epidermis, present throughout, is indicated in part only in (*a*). BC, brood chamber: DI, dorsal integument of thorax; H, haemocoele; IBC, incipient brood chamber; IL, inner lamella of carapace fold and derivatives; OL, outer lamella, likewise; OD, oviduct; O, ovary; S, stalk; SL, posterior slit. (*a*) The basic arrangement of the carapace fold (OL + IL) in branchiopod orders, indicating the location of the incipient brood chamber (IBC) in those groups in which such a receptacle is formed. In some of these cases the carapace also forms a bivalved protective device. (*b*) An early stage in the ontogeny of the brood chamber in cercopagidid onychopods. (*c*) A later stage in the same. The inner lamella of the carapace and the dorsal integument of the thorax have separated to form a chamber. (*d*) The basic nature of the brood chamber of the cercopagidid *Bythotrephes*. (*a*), (*c*) and (*d*) indicate in outline the evolutionary history of the simplest cercopagidid brood chamber. The location of the oviduct is also indicated. (*e*) and (*f*) Homologies and evolution of the podonid brood chamber. The fully formed chamber (BC), a nutrient secreting 'uterus' suspended in the haemocoele (H), is seen in (*f*). The location of the ovary is also indicated. Stippling in (*d*) and (*f*) indicates the nutrient-secreting Nährboden.

inner lamella becomes closely associated with the dorsal integument of the thorax (fig. 3*b*). The two latter, however, separate to produce a cavity which, save for a firmly secured narrow slit posteriorly (fig. 3*c*, SL), is completely closed. That part of this cavity which is derived from the dorsal integument of the thorax, and is therefore bathed by the blood of the haemocoele, becomes glandular (fig. 3*d*) and produces secretions that nourish the eggs, which are discharged into the chamber from the ovary, and the embryos to which they give rise. As the embryos develop they increase in size and the chamber expands, stretching the protective cuticle of the carapace lamellae. The entire structure takes on different shapes in different species – a bulbous dorsal swelling in *Bythotrephes*, long tubular arrangements that may incline forward in Ponto-Caspian species of *Cercopagis* and *Apagis*. In *Polyphemus*, because the morphologically dorsal surface is directed posteriorly, so is the swollen chamber.

The evolution of such a brood pouch from a simple dorsal chamber, such as occurs in most anomopods and ctenopods, is easy to envisage, and the oviduct would be directed towards it from the outset. The exact origin of the carapace fold is not always established, but in *Polyphemus* and some cercopagidids it clearly arises at the posterior extremity of the head, and doubtless does so in all cases.

The account of these elaborate structures given by Claus (1877) is supplemented by information provided by Weismann (1877, 1879) who presents various cytological and histological details, especially relating to the formation of resting eggs, which are also carried in the brood chamber. Weismann also demonstrates that a slit actually exists posteriorly and, particularly relevant in the present context, how a new carapace fold develops in preparation for the moult.

In the Podonidae the brood chamber complex also extends posteriorly. Here a very specialized condition prevails. The actual brood chamber, which Claus (1877) calls the uterus, takes the form of a sac, whose walls are entirely glandular, which is suspended in the haemocoele from a stalk. Claus interprets the sac as being derived from the inner lamella of the carapace and the dorsal integument of the thorax (as shown herein figs. 3*e*,*f*), which appears to be a logical development of the less specialised cercopagidid condition. It presupposes that the stalk is the remnant of a wide band of union such as exists in cercopagidids and polyphemids. The outer lamella of the carapace forms much of the capsule in which the 'uterus' is suspended. As the Nährboden of other branchiopods originates in the dorsal epidermis of the thorax, the entire secretory portion of the 'uterus' may be so derived in podonids, but this remains to be investigated. Additional cytological details are illustrated by Weismann (1879), showing especially the development of the 'uterus' in relation to the reception of a resting egg.

It is worth noting that, because it has not been understood, the nature of the podonid brood chamber is seldom evident from published illustrations. The same is generally true of references to hatching, moulting and the production of a new cuticle, further information on which is still required.

3. DISCUSSION AND CONCLUSIONS

Not all branchiopods have a carapace. Among those that do, although highly derived modifications are found in the Onychopoda, it always arises in the classical manner from the posterior region of the head, and does so as a fold that usually has no connection with the trunk. Minor secondary association, as in certain notostracans, in no way contradicts the basic pattern of development or its cephalic origin. Its apparently posterior position in the Haplopoda, represented only by *Leptodora*, is deceptive and is the result of profound morphological changes that have arisen in connection with a specialized way of life. It actually arises in the maxillary segment. The highly specialised brood chamber of cercopagidid and polyphemid onychopods has arisen as a result of intimate collaboration between the carapace fold and the dorsal integument of the trunk. That of podonids is an even more specialized development of the same process.

Like certain earlier authors, Martin & Cash-Clark (1995) incline to the view that the cercopagidids are the most derived onychopods. However, the modifications of the cercopagidid carapace/brood chamber complex, which shows more significant divergence from a primitive onychopod condition than do the attributes on which assessments have usually been based, reveal the Podonidae as undoubtedly the most derived onychopod family. With great perception Claus (1877) recognized this more than a century ago, even though at that time all onychopods were included in a single family. (Estimates of levels of divergence of course differ according to the criteria used : for example the eyes of polyphemids are particularly specialized).

Nauplii may have a dorsal shield, and it is sometimes true that, as Walossek (1993) says, 'the shields [= carapaces] of Crustacea are products of the progressive growth of the naupliar shield', though there are many exceptions, and this is not incompatible with the role of a carapace fold. Indeed there is no way in which a naupliar shield can develop into an adult carapace except via a dorsal fold, as outlined in this paper. Although Walossek says that neither the morphogenesis of recent crustacean shields (= carapaces) nor the ontogeny of *Rehbachiella* (nor of *Bredocaris*, currently assigned to the Maxillopoda) support the concept of a carapace fold growing from the rear of the head, and (p. 111) specifically refers to the 'simple growth' of the carapace of *Rehbachiella*, and says 'neither is there a fold appearing at any stage of growth', *Rehbachiella* in fact provides a perfect example of such development. 'Simple growth', whether in *Rehbachiella* or any other crustacean, cannot give rise to a carapace in the absence of a fold, whose existence Walossek denies. Although this may not be apparent from even such superbly preserved fossils as those of *Rehbachiella*, or indeed from simple inspection of developing extant microscopic crustaceans, where sections may be needed to reveal it, a fold must be present. To deny the existence of a fold and to refer to the 'simple growth' of a carapace is to misinterpret its two-walled nature, the manner of its development, and the way in which the cuticle is produced. There can be a simple dorsal shield in a nauplius, and this can increase in size as its bearer does so, but it cannot develop into a carapace by 'simple growth'.

The carapace of the Spinicaudata, Laevicaudata (where there is a large dorsal shield in the nauplius), Anomopoda, Ctenopoda, Haplopoda and Onychopoda, like that of *Rehbachiella*, develops, via a cephalic fold, in the classical manner of crustacean carapaces, and does so whether or not there is a nauplius lava, and whether or not the head has a headshield. New cuticle is always secreted beneath the old by the underlying epidermis and it matters not whether it is an expansive dorsal shield such as that of the larval *Lynceus*, or simply thin cuticle, that is replaced. The process is the same, and is repeated at each moult throughout life. There is no such thing as a 'secondary shield', by which term Walossek (1993, 1995) designated the carapace of these orders. He did not specifically define the term in 1993, but in 1995 said that members of these orders, which he regards as constituting a single taxon, 'develop a shield behind the original headshield... which originates from tergal outgrowths of the maxillary or first trunk somite'. He continued that 'this structure is clearly not homologous to the similarly large, bivalve head shields of other Crustacea'. I do not understand what the last sentence means, but what he refers to as tergal outgrowths are constituents of a carapace produced in the way that all crustacean carapaces are produced.

The concept of a 'secondary shield' is erroneous and is based on a misunderstanding of the processes involved in carapace formation. To use the alleged possession of such a 'shield' by all these orders as a synapomorphy which unites them into one group, for which Walossek uses the outmoded name Onychura, is to base this unity on a non-existent character. Nor is the carapace of these orders always bivalved, nor do they all have a nauplius as claimed. As do numerous other characters (Fryer 1987*a*, *b*) the attributes of the carapace and its derivatives, far from suggesting a close relationship of these orders, emphasize their differences; though all arose via a process that is not merely common to the whole of the Branchiopoda, but is universal in carapace-bearing Crustacea. The modifications of the onychopod carapace are indeed among the most divergent, not merely of the Branchiopoda, but of the Crustacea as a whole.

On a wider plane, there is no reason to restrict the name carapace to cases where all thoracic segments are fused to it (as in certain malacostracans) as Walossek suggests. Carapace is a long-established and much used name that refers to a clearly defined, usually readily recognized, structure whose nature and mode of origin are known. It should not be rejected, least of all on the basis of a misunderstanding.

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