

DISCOVERY OF NAUPLIUS-LIKE TRILOBITE LARVAE

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ABSTRACT. Phosphatized cybelinid trilobite larvae in an exceptional state of preservation have been obtained from early Ordovician limestones in northern Spitsbergen. A stage below the anaprotaspis is described, and termed the phaselus stage. There is a case for regarding the phaselus larva as homologous with the nauplius larva of extant Crustacea.

THIS paper describes some remarkably well-preserved trilobite larvae from Ordovician rocks in North Ny Friesland, Spitsbergen. The early growth stages of trilobites have been known for over a century, and the smallest of these stages—the protaspis—was so designated by Beecher (1895). Since that time many relatively complete ontogenetic series have been described, and great diversity of form even within the protaspis is now apparent. Recent summaries of ontogenies have been given by Whittington (1957, 1959) and Hu (1971). We describe here a growth stage that precedes the protaspis, and discuss the arguments for and against its homology with the crustacean nauplius stage. Our original intention was to describe the whole range of growth stages of trilobites from the Ordovician of Spitsbergen. Recent discussions concerning the relationships of the trilobites to other arthropods (Cisne 1974, 1975; Hessler and Newman 1975) have increased the importance of these early ontogenetic stages as criteria to be employed in phylogenetic arguments, and for this reason they are worthy of a separate note.

AGE, OCCURRENCE, AND PRESERVATION

Age

The protaspides and their smaller associates come from the Valhallfonna Formation, North Ny Friesland, Spitsbergen, stratigraphy and localities for which are given in Fortey and Bruton (1973). Two horizons yield the material figured here. The lower of these is within the Olenidsletta Member (Arenig) about 85 m from its base with a rich fauna including asaphid, nileid, raphiophorid, cybelinid and telephinid trilobites, many of which have been described by Fortey (1975*b*). Graptolites occur both above and below this horizon, which is deduced to correlate with Zone J of the Utah/Nevada zonal scheme (Ross 1951; Hintze 1953) and the North American (but not European) zone of *Didymograptus bifidus* (Fortey 1976, p. 271).

The upper occurrence is in limestones of the Profilbekken Member, 32 m from its base. This lies towards the base of a unit of Whiterock age (*Orthidiella* Zone), which is generally correlated with the earlier part of the Llanvirn Series of the standard European sequence.

Occurrence and Preservation

The larval stages are preserved in apatite, and they have been extracted from the enclosing limestones by solution in 10% acetic acid. From beds adjacent to the lower horizon Fortey and Whittaker (1976) obtained the enigmatic organism *Janospira*, which is preserved in a similar way. Neighbouring beds at both horizons have yielded great numbers of Radiolaria (Fortey and Holdsworth 1972) and Chitinozoa. There is thus an exceptionally prolific record of the planktonic components of the fauna at these parts of the sections—more than 100 trilobite larvae have been obtained from about 200 g of rock.

This high proportion of plankton fall-out and the mode of preservation can be explained by considering the environment of deposition of the Valhallfonna Formation. Both localities lie in those parts of the section characterized by the Nileid community type, based on the dominant kinds of trilobites (Fortey 1975a). This community type has been inferred as occupying an outer, but not outermost position on the early Ordovician continental shelf. Beyond it lay the Olenid community adapted to oxygen-poor sea bottom conditions, an environment that favoured the preservation of many graptolites. Ocean-going forms also included at least three trilobite genera: *Carolinites*, *Oopsites*, and *Opipeuter*, all three of which occur in unparalleled abundance in the Spitsbergen sections (Fortey 1976, p. 268). It is evident that the proto-Atlantic surface waters in the Spitsbergen area were highly productive, able to support great numbers of pelagic and planktonic organisms; in the latter we include the trilobite larvae. Such surface water productivity is characteristic of areas of oceanic upwelling at the edges of the continental slope, that is, near where the Spitsbergen rocks were inferred on independent grounds to have accumulated. The same site has been implicated in the formation of sedimentary phosphates (Hutchinson 1950)—phosphate from deep oceanic sources promotes a plankton bloom, is incorporated in larger organisms, and, with the death of such organisms, eventually into the sediment.

So a particular geographical position is consistent with the type and numbers of the fauna, and with saturation in calcium phosphate resulting in phosphatization of the fossils. This has implications in the search for other localities with similar preservation of larval forms.

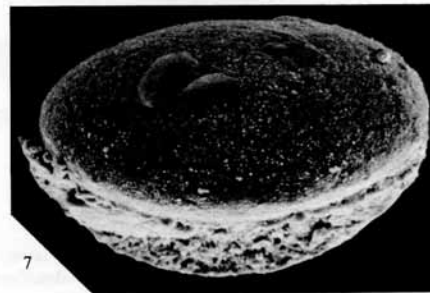
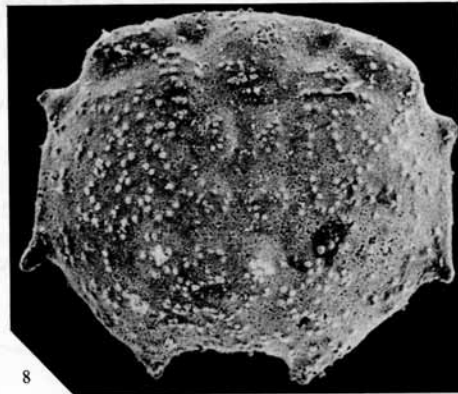
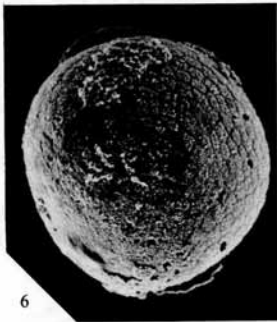
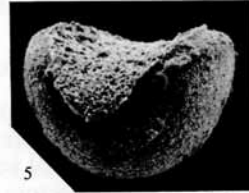
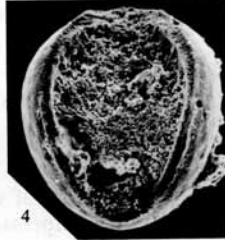
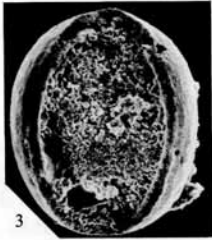
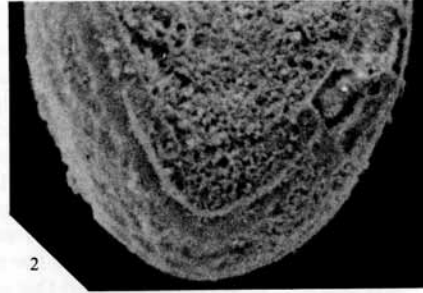
EXPLANATION OF PLATE 94

Cybelinid allied to *Cybelurus*.

Figs. 1, 5, 6. Profilbekken Member, Valhallfonna Formation; Ny Friesland, Spitsbergen. 1, dorsal view of phaselus larva to show cell polygons. SM A101335, $\times 135$. 5, view of 'posterior' of exfoliated phaselus larva to show protruding lip. SM A101336, $\times 150$. 6, dorsal view of internal mould to show internal expression of cell polygonation. SM A101337, $\times 150$.

Figs. 2-4, 7-9. Olenidsletta Member, Valhallfonna Formation; Ny Friesland, Spitsbergen. 2, ventral view of phaselus larva to show, marginal rim and 'doubleure'. SM A101330, $\times 360$. 3, ventral view of phaselus larva, slightly oblique. SM A101331, $\times 135$. The apparently backward projection anteromedially is an artifact of phosphatisation. 4, ventral view of phaselus larva. SM A101331, $\times 135$. 7, anaprotaspis. SM A101333, $\times 220$. 8, metaprotaspis. SM A101334, $\times 120$. 9, lateral view of phaselus larva. SM A101332, $\times 220$. L-protruding lip posteriorly.

All photographs taken on a stereoscan with variable apparent lighting directions.



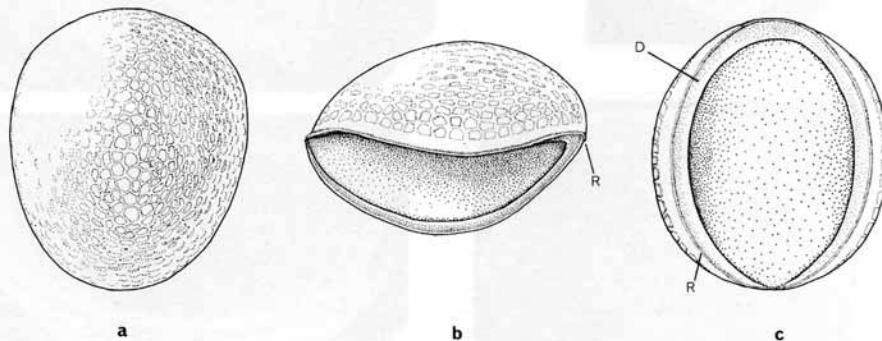
FORTEY and MORRIS, Trilobite larvae

Phosphatization varies within the samples. The interior of the fossils is invariably phosphate-filled and when no further replacement has occurred this results in internal mould replicas (e.g. Pl. 94, fig. 9). In the majority of cases the cuticle itself has been replaced, and these specimens have a characteristic white and glistening appearance. Exterior details are very well-preserved: for example, individual tubercles on metaprotaspides preserve pits in their tips, originally the sites of sensory hairs. This sort of detail could not survive on other than exterior surfaces. The polygonal sculpture pattern on the surface of some of the trilobite larvae is a similar feature (Pl. 94, fig. 1). On some examples the phosphate has been additionally plastered over the exterior of the carapace, and this subdues and conceals the surface features; such specimens can be misleading in interpretation of morphology. Corrosion of the surface is frequent (Pl. 94, fig. 8).

DESCRIPTION OF THE SMALLEST LARVAE

Minute oval body generally 200–250 μm long (text-fig. 2), deeply vaulted transversely and medially, less convex in anterior–posterior plane. Exterior surface covered with a fine pattern of raised polygonal ridges, the relief of which varies; this may be due to preservational factors as discussed above. Impression of same ridges visible on internal moulds (Pl. 94, figs. 6, 9) where they are marked by a network of smooth areas. Between these areas the polygons themselves include numbers of fine, raised phosphate tubercles which we interpret as filling bases of cuticular canals; they are on the right scale for pore canals (1–3 μm).

Elliptical ventral opening deflected upwards at both ends. Narrow rim separates doublure from dorsal surface (Pl. 94, fig. 2); rim not preserved on internal moulds. Outside rim and parallel to it a smooth bevelled area lacks dorsal reticulation. Doublure of width about 15 μm at mid length, slightly concave, and flexed at right angles to the adjacent dorsal body surface. Inner margin downward-turned and slightly thickened. At one end of phaselus doublure broader and flatter, at the other narrower; at narrow end ventral deflexion of the inner margin is greater. This



TEXT-FIG. 1. Restoration of the phaselus larva in *a*, dorsal, *b*, oblique ventral, and *c*, ventral views. D—doublure R—marginal rim.

produces a protruding lip which is especially apparent on internal moulds (Pl. 94, fig. 5), where cuticle evidently thickened.

So it is possible to distinguish anterior and posterior ends on the larvae from doublural characters, but problematic to decide which way round they are. When orientated symmetrically (which is difficult due to their extremely small size) the end with the flattened doublure is more obtusely rounded, and the maximum transverse width of the larva lies towards that end (Pl. 94, figs. 1, 4). Where there is a greater carapace width in trilobite larvae (or for that matter in crustacean nauplii) it lies anteriorly; tapering is posterior. For this reason we orientate our specimens with the flattened doublure anterior and the protruding 'lip' at the narrower posterior end (text-fig. 1). This orientation may be consistent with the nauplius interpretation (below).

INTERPRETATION

It must be emphasized that the argument for the carapaces just described being the smallest trilobite growth stage is independent of homology or otherwise with the nauplius stage of other arthropods. We regard their trilobite nature as probable, and their nauplius comparisons as a more speculative extension of the argument.

Note on terminology

The terms anaprotaspis, metaprotaspis, and paraprotaspis have been used for describing progressively larger stages within the larval ontogeny of trilobites. Paraprotaspis has been used especially by Hu (1971), and is unsatisfactory. Hu gives (1971, p. 52) length ranges for the paraprotaspis stage of 0.50–1.00 mm yet several of the illustrated forms ascribed to this stage Hu (1971, e.g. *Phaseolops*, pl. 23, figs. 4, 5; *Dytremacephalus*, pl. 16, fig. 7) are well below 0.50 mm in length and indeed approach the lower length limit of the metaprotaspis *sensu* Hu (0.35 mm). Furthermore some of the early growth stages attributed by Hu to the paraprotaspis stage are meraspis cranidia (see especially *Ptarmigania aurita* Resser; Hu 1971, pl. 10, figs. 11, 13). There is no satisfactory definition of paraprotaspis and its use by Hu is ambiguous to say the least. We do not employ it.

The division of the protaspis series into anaprotaspis and metaprotaspis stages is used here. Definitions by Whittington (1959) and Palmer (1962) stress the appearance of a posterior cephalic border on the protaspis shield, and thereby the distinct delineation of the protopygidium, as marking the beginning of the metaprotaspis stage of development. The anaprotaspis tends to be elusive in silicified preservation, or at least the coarseness of silicification obscures detail at this very small size (e.g. Ross 1951, pl. 82, figs. 1, 2). Phosphatization produces better preserved specimens. Numerous examples, invariably flattened-discoidal and quite well preserved in the rock have been illustrated by Hu (1971). At this stage the glabella may or may not be defined, but *regardless of glabellar definition, the forward limit of the glabella is marked by a pair of deep pits (anterior fossulae)*. These pits may be connected with the articulation of the proto-hypostoma (see below).

The smallest stages described above lack these pits, and have a different symmetry from any described anaprotaspis. More than their small size we regard this difference

as proving a distinction from the anaprotaspide stage. We term the smallest stage the phaselus stage (Latin: a kidney bean).

Trilobite nature of the phaselus stage

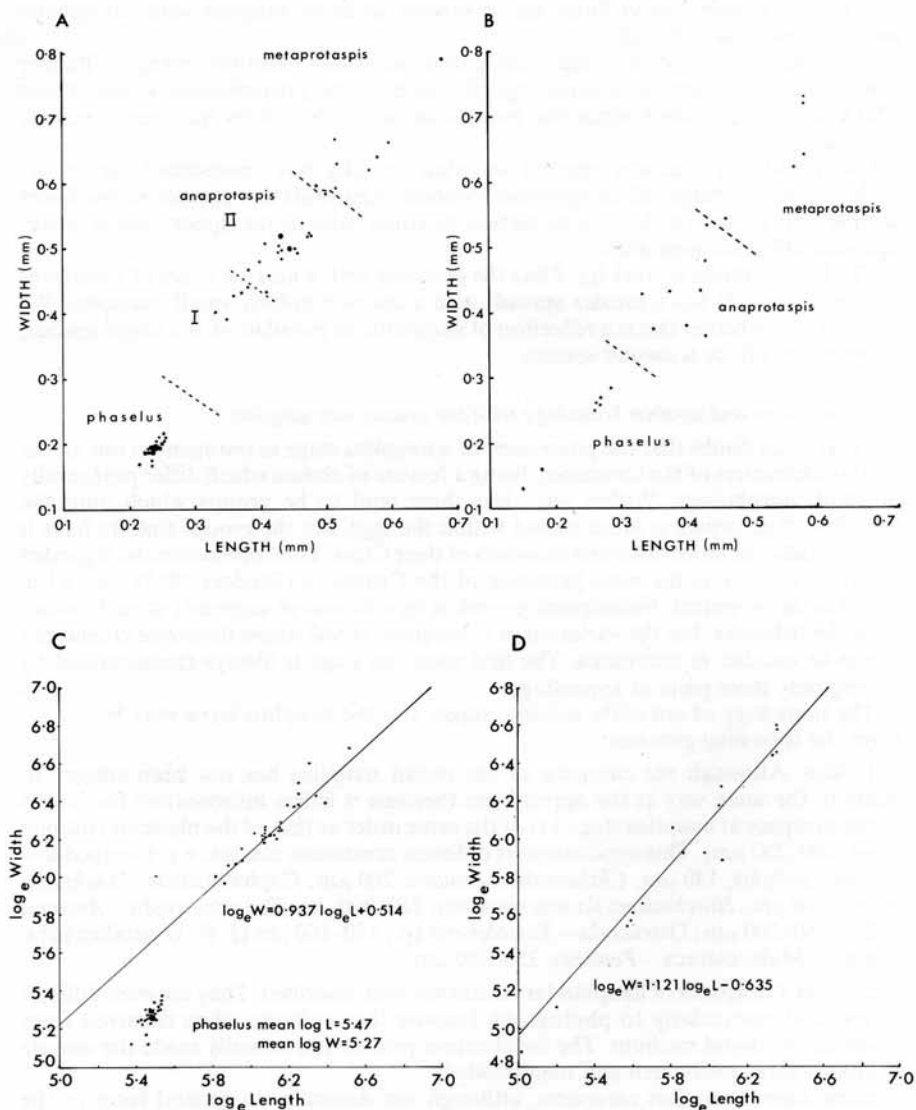
There are compelling reasons for our interpretation of the phaselus stage as a trilobite, which can be summarized as follows:

1. The raised network of ridges on a minute scale is a feature found in several examples of immature trilobites (e.g. *Paladin* see Miller 1975, fig. 11A). It is also common in many ostracodes, where it has been attributed to the external expression of epidermal cells (Dépêche 1974, p. 150); these are the 'cell polygons' of Miller (1976, p. 346). We note that the polygon pattern is visible on internal moulds (Pl. 94, fig. 6)—but not as ridges—in a manner similar to that figured by Dépêche (1974). Although ostracodes are present in the upper sample they are rare in the lower, where the phaselus stage is most abundant. The detailed morphology, and the growth pattern below, make ostracode affinities unlikely.

2. The doublure is a trilobite feature.

3. In the samples anaprotaspides and metaprotaspides of cybelinids, nileids, and raphiophorids occur. Of these, cybelinid protaspides are the most abundant, with an abundance of protaspides comparable to that of the phaselus larvae. The study is based on 43 phaselus stages and 44 protaspides (29 anaprotaspides, 15 metaprotaspides) of which 95% are well enough preserved for measurement. The cybelinid trilobites concerned are two species allied to *Cybelurus*, but not yet described. Length (sag.) and maximum transverse width (excluding spines) of phaselus larvae, anaprotaspides and metaprotaspides were measured using a vernier travelling microscope, which is accurate to $\pm 3 \mu\text{m}$. The graphs were constructed by S.F.M. using the separate data for upper and lower samples. A simple plot of length: width of the protaspides results in a progressive increase in size conforming to straight lines in the protaspis stage, and the phaselus larvae appear to lie close to their backward continuation, so that the phaseli are of the right order of magnitude to represent the previous growth stage. To test this more rigorously a log-log plot is given in text-figs. 2C, D, where the straight lines are a calculated best fit using linear regression. In the upper sample (text-fig. 2D) the phaseli lie within one standard deviation of the straight line, but in the lower sample (the larger) they clearly lie outside the line. This is a reflection of the fact that in the phaselus stage the length slightly exceeds the width, whereas protaspis width is greater than length. The phaselus stage is transversely more convex, and the point at which moulting takes place is presumably related to volume (rather than linear dimension), which is affected by the change in symmetry between phaselus and protaspis. For the upper sample the change is less and the conformation to a straight line correspondingly better. In terms of the ratios of the mean lengths of the various stages a slight discontinuity is also indicated between phaselus and protaspis for the lower sample: anaprotaspis I: phaselus = 1.53; anaprotaspis II: anaprotaspis I = 1.21; metaprotaspis: anaprotaspis II = 1.20.

We do not yet know whether the phaselus could lie at the origin of growth of other ontogenetic series in the samples, for which we have as yet only a few specimens. It is conceivable that different trilobites had similar phaselus stages. The answer to



TEXT-FIG. 2. Growth of phaselus-protaspis series. A, C, lower sample, Olenidsletta Member of the Valhallfonna Formation. B, D, upper sample from the Profilbekken Member of the Valhallfonna Formation. A, B, length/width plots showing how phaselus stage groups below protaspides. C, D, log-log plot of the same data, with regression lines derived from protaspide dimensions.

this will eventually derive from the discovery of more samples with phosphatic preservation of larval stages.

It is noteworthy that the anaprotaspis dimensions are like those given by Palmer (1962). There are several morphological stages in the post-phaselus development which will be described when the nomenclature of the adults has been formally established.

One possibility that was rejected was that the phaselus represented the (as yet undescribed) protaspis of an agnostid trilobite. Agnostids are present in the lower sample, but absent (with 30 m of section to either side) in the upper, which makes agnostid affinities improbable.

The lower sample on text-fig. 2 has the phaselus with a narrow range of variation; the upper sample has a greater spread, with some particularly small examples. We do not know whether this is a reflection of variability in population of a single species, a second moult, or a second species.

Arguments for and against homology with the crustacean nauplius

There is no doubt that the possession of a nauplius stage in ontogeny is one of the uniting characters of the Crustacea, being a feature of classes which differ profoundly in adult morphology. Within any class there tend to be groups which omit the nauplius stage (which is often passed within the egg), but the groups that do have it are generally the more primitive members of their Class. The Cephalocarida, regarded by some authors as the most primitive of the Crustacea (Sanders 1963), has a full nauplius development. Subsequent growth is by addition of segments at each instar, as in the trilobites, but the variation in subsequent larval stages from one crustacean group to another is enormous. The first nauplius stage is always characterized by having only *three* pairs of appendages.

The homology of our early trilobite stages and the nauplius larva may be argued from the following grounds:

1. *Size.* Although the carapace of the recent nauplius has not been subject to study in the same way as the appendages (because it is less informative) the length of the carapace at nauplius stage 1 is of the same order as that of the phaselus trilobite larva (200–250 μm). This applies across different crustacean classes: e.g. Cirripedia—*Balanus pallidus*, 140 μm , *Chthamalus aestuarii*, 200 μm ; Cephalocarida—*Ligitiella incisa*, 260 μm , *Hutchinsoniella macracantha*, 250–300 μm ; Branchiopoda—*Artemia salina*, 150–200 μm ; Ostracoda—*Xestoleberis* sp., 150–160 μm (J. E. Whittaker pers. comm.); Malacostraca—*Penaeus*, 250–300 μm .

2. *Form.* Carapaces of nauplius larvae are not well described. They are even difficult to see, and particularly to photograph because they collapse when removed from a supportive liquid medium. The fossilization process has actually made the minute trilobites more easily seen and manipulated.

Some recent nauplius carapaces, although not dissimilar in general form to the trilobite phaselus, are equipped with prominent paired spines (*Balanus*) which diminishes their resemblance to our material. However, the nauplius carapace of some species, for example of the genus *Ibla* (Cirripedia), are really very like the trilobite phaselus in size and proportions (Anderson 1973, p. 303; text-fig. 3a (dorsal

view)). Cell polygonation is drawn by Anderson; we have seen a similar pattern on nauplius carapaces of *Artemia* (Branchiopoda) (text-fig. 3b).

The appendages of the nauplius are sited beneath the carapace, but there is also a *postnaupliar region*—a fleshy lobe extending in many examples well beyond the posterior of the carapace (*Artemia*). This is unprovable on the phaselus, but it is worth remarking that the assumed posterior end of the carapace is strongly vaulted and that its edge there is thickened, and extended into a lip, features that would be consistent with posterior protrusion of a post-naupliar region, and its attachment to the posterior edge of the carapace.

A single median eye is characteristic of the nauplius stage, but (G. A. Boxshall pers. comm.) is not externally expressed on the carapace; certainly there is no external sign of an eye on the trilobite phaselus.



TEXT-FIG. 3. Carapaces of nauplii of the living crustaceans a, *Ibla quadrivalvis* (Cirripedia) and b, *Artemia salina* (Branchiopoda) $\times 150$ approx.

3. *Position in ontogeny and possible appendage number.* We have argued that the phaselus stage precedes the anaprotaspis in ontogeny. Ontogeny proceeds by regular addition of segments and presumably pairs of appendages through the protaspide stage of development, and it seems reasonable to suppose that the phaselus stage has one pair of appendages less than the anaprotaspis. Many anaprotaspides are not obviously divided into annulae, but the cybelinid described here is distinctly segmented. The smallest anaprotaspides are divided into four segments. The simplest assumption is that each segment represents a pair of appendages ventrally, totalling four pairs, the anterior fossulae here assumed to represent the hypostomal articulation. However, if one accepts that the transverse furrows themselves are the sites of appendage muscle attachment (e.g. Campbell 1975) three pairs are indicated medially. In this case the prominent anterior fossulae would also be interpreted as sites of muscle attachment for the antennae, following Harrington (1959, p. 96). Under this hypothesis the number of pairs of appendages still totals four; the antennae and three posterior pairs. The previous moult, the phaselus, would therefore have *three* pairs of appendages. This is the number for the crustacean nauplius. If the Spitsbergen examples can be duplicated elsewhere this may be the most compelling argument for the phaselus being a true nauplius. We may note that similar four-segment anaprotaspides have been figured by Hu (1971, e.g. *Missisquoia* text-fig. 51; *Dunderbergia* p. 92).

Contrary arguments. The main arguments which may be summoned against the nauplius affinities are:

1. The size of the larvae may be due simply to their being part of the plankton. Early larvae of other phyla (Branchiopoda, Echinodermata, Mollusca) are commonly in the range 150–300 μm , and it is not surprising to find the earliest larval stage of the trilobite in the same range.

2. At such a small size the carapace morphology is inevitably going to be simpler than is possible at a later ontogenetic stage. Any resemblance between phaselus and nauplius is coincidence, and merely a by-product of similarity in dimension.

The argument on size of the earliest larvae is reasonable, and does in fact add weight to the supposition that the phaselus is the early larval stage. The simplicity (or otherwise) of the phaselus morphology is a matter of taste. Furthermore, the argument for three pairs of appendages is independent of comparisons with recent nauplii. We believe that the lines of evidence favouring nauplius homology would otherwise stretch coincidence rather far. However, more examples of phaselus larvae in sequence with later ontogenetic series are needed before accepting the equivalence of nauplius and phaselus, and to establish how general this developmental stage is in the group as a whole.

SUMMARY

The earliest larval stage of the trilobite—the phaselus—differs in structure from the anaprotaspis which it precedes. The phaselus-protaspis transition is a fundamental one, analogous to changes from nauplius to zoea in the Malacostraca, or nauplius to cypris in Cirripedia. There is a case to be made for the homology of the phaselus with the nauplius of the Crustacea. If this is confirmed it may increase the likelihood of Crustacea and trilobites having a common ancestor.

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