

THE TRILOBITA AS A NATURAL GROUP

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(Received 17 June 1988)

It has been claimed that olenellids, long regarded as trilobites, are more closely related to chelicerates than to the rest of the trilobite clade (Lauterbach 1980). This was based on an interpretation of the homologies of segmental arrangement in the thorax, and of the thoracic axial spine. It is shown that there are more synapomorphies uniting accepted trilobites with the olenellids, than there are uniting olenellids with chelicerates. At least seven characters serve to define Trilobita as a natural, monophyletic group. These include the presence of a pygidium, the unique optical system, the presence of eye ridges, circum-ocular ecdysial sutures, and the construction of the hypostome. Olenelloids include the most primitive of the trilobites, retaining three (possibly four) primitive characters, including the permarginal suture, flange-like thoracic articulation and highly expressed segmentation on the larval cranidia. If facial sutures are primitively absent in the Trilobita there is no obvious olenelloid autapomorphy, and they may constitute a paraphyletic group.

KEY WORDS: Trilobita, chelicerates, olenelloids, phylogeny, classification

INTRODUCTION

Trilobites are among the most abundant fossils in the Palaeozoic, and thousands of species have been described over the last two centuries. That they constitute a natural group—a monophyletic group descended from a single ancestor—has been almost taken for granted. Yet the unique characters (autapomorphies) that might define such a clade Trilobita have not been determined. The diagnosis in the Treatise (Moore 1959) is largely a general description of a trilobite rather than an inventory of their distinguishing characters. This problem has been thrown into particular focus by Lauterbach (1980; 1983) in which the claim is made that the Olenellinae are more closely related to chelicerates than to Trilobita *sensu stricto*. By Olenellinae (or olenellines) Lauterbach (1980, p. 175) meant species of genera included in Olenellinae by Poulsen (in Moore 1959, p. 0192), and in Olenellidae by Bergström (1973, p. 312); we shall refer to them as “olenellids” in this paper (i.e. *Olenellus* and its close allies). According to Lauterbach such olenellids are not trilobites at all; their resemblances to true trilobites being one of symplesiomorphy only. Suggestions concerning the resemblances between trilobites and limuloids have a long tradition (Størmer 1944: Raw 1957), but the “splitting up” of the Trilobita as usually understood as not constituting a true clade is an idea that requires careful consideration. The purpose of this paper is to examine Lauterbach’s claims, and in so doing attempt to come to a better understanding of which characters serve to define the Trilobita. We shall informally term the larger group of Cambrian trilobites regarded as the suborder Olenellida (in Moore 1959, p. 0191) or the Order Olenellida (Bergström 1973, p. 284) as ‘olenelloids’. We shall not attempt to evaluate *Naraoia* and *Tegopelte* here. Both have

been regarded as uncalcified trilobites (Whittington 1977). Their proper discussion requires consideration of other 'trilobitomorphs' which is beyond the scope of this paper.

ARE OLENELLIDS TRILOBITES?

Cladograms afford an explicit way of expressing relationships and of showing the distribution of characters forming the basis of that assessment of relationships. Lauterbach's version of trilobite relationships was used by Ax (1984, 1987) as an example of phylogenetic reasoning in the Arthropoda. A modified version of Lauterbach's cladogram is reproduced here as Figure 1a. The problem centres on the relationships of the olenellids. The olenellids can be represented as they were by Lauterbach (1980, Figure 1) as the sister group of higher chelicerates. Lauterbach united Chelicerata + Olenellids + all other trilobites in the taxon Arachnata, a term which Ax (1984) found redundant. The alternative view of the relationships of the olenellids is that shown in Figure 1b, in which they form part of a natural group Trilobita. So what we are looking for to decide between these two theories of relationships are synapomorphies which may link olenellids with chelicerates on the one hand, or with accepted trilobites on the other. The usual procedure for deciding between such competing hypotheses is to favour that which has the greater number of synapomorphies supporting it (Wiley 1981). In the present context the two hypotheses of relationships shown in Figure 1 afford a relatively simple example of making a phylogenetic decision using cladistic treatment.

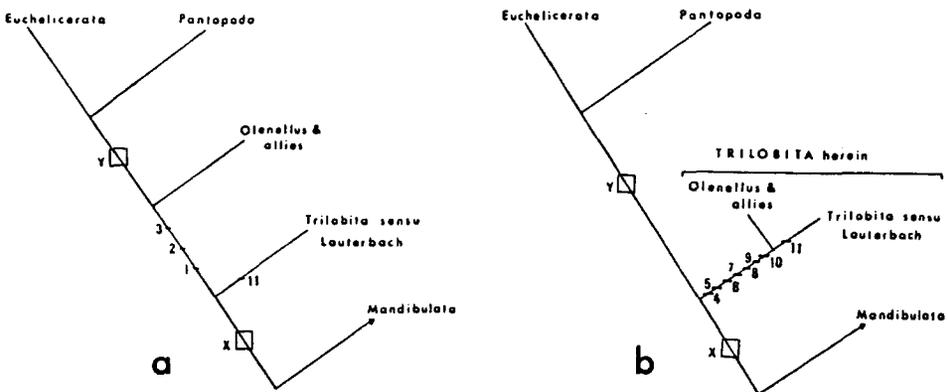


Figure 1 Competing cladograms of relationships of olenellids, Trilobita (in the sense used by Lauterbach, 1980, to exclude *Olenellus* and allies) and the rest of the Arachnata. a, left, Lauterbach's view, simplified from Lauterbach, 1980, p. 215, and Ax, 1987, figure 67, in which *Olenellus* and allied genera (here treated as a single taxon) are not considered part of the trilobite clade, supported by supposed synapomorphies 1–3, as discussed in the text. b, right, the alternative view, in which olenellids and the rest of the trilobites form a single clade, supported by synapomorphies 4–10, as described in the text. Under the Lauterbach hypothesis characters 4–10 would have to appear as homoplasous (i.e. independently derived) in olenellids and in other trilobites. Cladogram b is the more parsimonious, and is preferred. X, and Y comprise character complexes (see Ax 1987) serving to define the arachnate clade and the chelicerates respectively, and these are not critically discussed in this paper, even though some may be contentious. Character 11, "dorsal facial sutures developed" defines more derived Trilobita on this hypothesis.

For the moment we may accept the synapomorphies given by Lauterbach as linking olenellids and chelicerates as valid. In detail, there may be problems with these characters as we mention below. And for the sake of simplicity we may leave aside for the moment the question of whether olenelloids may be a paraphyletic group. For comparative purposes the most primitive living chelicerate is the merostome *Limulus* (Weygoldt and Paulus 1979).

Lauterbach listed essentially three synapomorphies to support his view that the olenellids were a sister group of higher chelicerates, as follows (Figure, 1a):

1. Long median spine on the 15th trunk (thoracic) segment; this is regarded as homologous with the terminal spine on merostomes, and the tail spine of eurypterids and scorpions.
2. The third thoracic segment is macroleural; in Lauterbach's view this means that the two anterior segments were destined to become part of the head (prosoma) in Chelicerata—the olenellids representing the intermediate character state in this regard.
3. Post-cephalic prothorax consists of fifteen segments, freely articulated. This was regarded by Lauterbach as homologous with the last two segments of the prosoma and the 13 of the opisthosoma of living Chelicerata.

In support of the trilobite relationships of olenellids we may list the following characters which may be regarded as synapomorphies between olenellids, other olenelloids and all other trilobites (Figures 1b, 2). Characters are discussed individually in the following section.

4. Presence of a pygidium. A pygidium is a posterior, dorso-ventrally flattened exoskeletal plate comprising more than one segment (it is not a telson).
5. Eyes with corneal surfaces composed of prismatic calcite lenses; the optical system (Towe 1973) utilising the orientation of the calcite lenses with the c-axis normal to the surface is apparently unique to the trilobites.
6. The presence of an eye ridge or palpebro-ocular ridges.
7. Calcium carbonate cuticle composed of inner fibrous and (usually) thin outer prismatic layer.
8. Rostral plate present.
9. Circum-ocular sutures in adult.
10. Hypostome with anterior wing which connects with anterior pit (or homologous point) in axial furrow.

If the characters listed above are valid synapomorphies it can be concluded that the trilobite relationships of olenellids (Hypothesis Figure 1b) is supported by the greater number. If Lauterbach's hypothesis were maintained characters 4–10 would have to appear in parallel in olenellids and in Trilobita (sensu Lauterbach), which is less parsimonious than the hypothesis of relationships in Figure 1b. The olenellids should be included within Trilobita—which is a natural group. This applies even if the synapomorphies listed by Lauterbach are valid, which they may not be.

DISCUSSION OF TRILOBITE CHARACTERS

Character 4: pygidium. It has been stated (Harrington, *in* Moore, 1959, p. 73) that the olenellid pygidium consisted of a single segment, and was not homologous with that of other trilobites. This is not so. Whittington (*in press*) has shown the presence of more

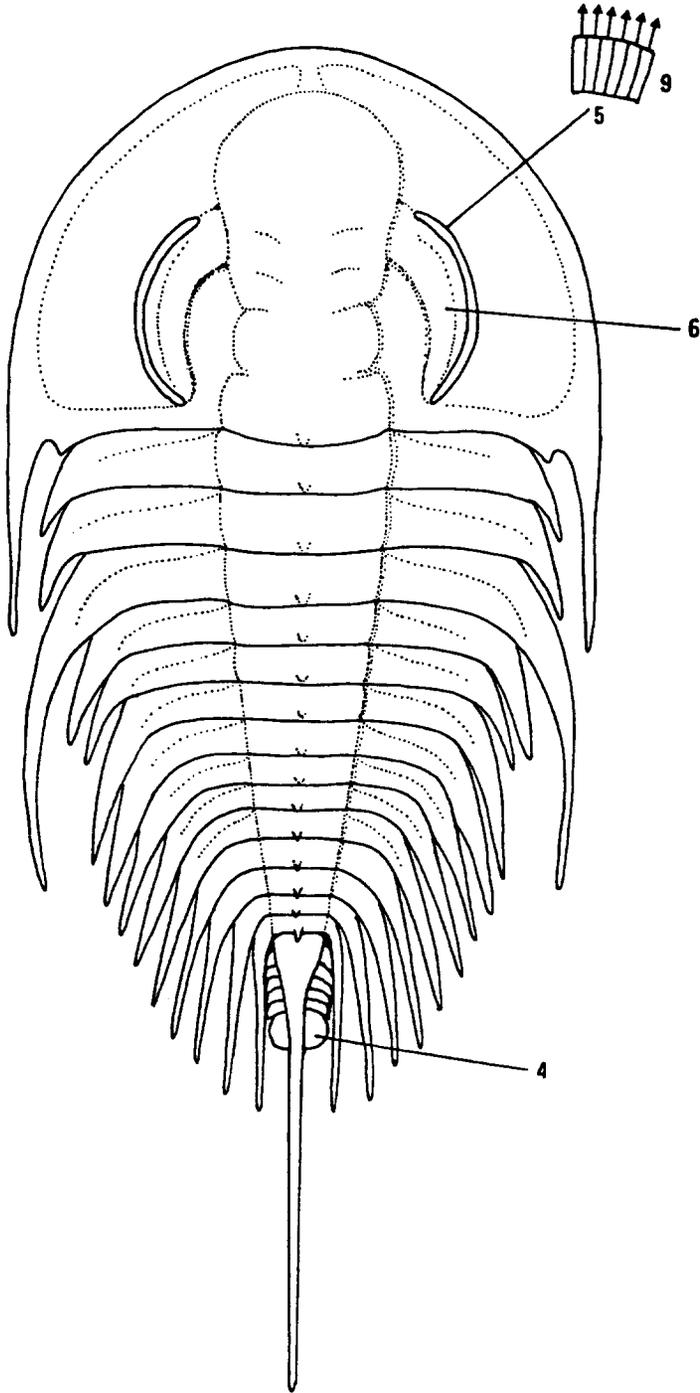


Figure 2 Dorsal view of *Olenellus thompsoni* (Hall) reconstructed after Whittington (in press) to show trilobite synapomorphies. Numbers as in text; 9 is enlargement of part of eye showing c axes of calcite crystals.

than one axial ring on this structure in a variety of olenelloids. The olenelloid pygidium is not fundamentally different in structure from the pygidia of many redlichoids (a variety of these were illustrated in Zhang *et al* 1980; Figure 56–60). These are pygidia, albeit small ones. It has long been known (Stubblefield 1926) that trilobites 'bud off' thoracic segments from the front of the pygidium during ontogeny, and the relative increase in size of the pygidium in many (not all) later trilobites is economically explained by the retention of unreleased segments. The olenelloid-redlichoid pygidium is primitive with regard to its few segments—but there is no reason to describe it as other than a pygidium.

Characters 5 & 9: eyes and circum-ocular sutures. These two characters have to be discussed together. The circum-ocular suture enabled the corneal surface of the eye to be moulted separately. It is thought to have been present on virtually all (exceptions are given below) Cambrian trilobites, belonging to many disparate groups (Clarkson 1975), and thus within the clade Trilobita its presence is primitive. It is lost on many advanced trilobites of Ordovician age or younger, which have the eye attached to the free cheek after moulting. It is certain that the loss of the circum-ocular suture happens polyphyletically. For example, it happens independently in at least three lineages of Asaphina, and in Olenina. Almost all post-Cambrian trilobites lack the circum-ocular sutures, but it is retained in the Calymenacea. One can conclude that the loss of the circum-ocular suture is an advanced character of low phylogenetic importance, but that the presence of this suture is a unifying character of Trilobita, not being found on

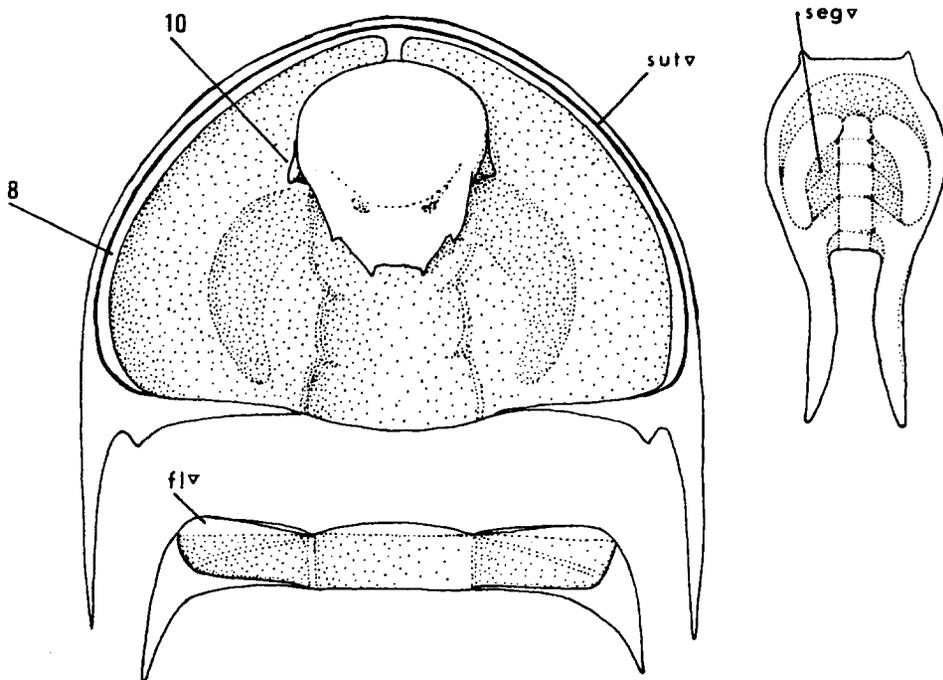


Figure 3 Ventral view of *Olenellus thompsoni* cephalic shield (left) to show trilobite synapomorphies, numbered as in text, and some retained primitive characters of olenelloids (triangles); fl—articulating flange, sut—permarginal suture. Right, small cephalic shield of *Olenellus* after Palmer 1957, showing retained segmentation of interocular cheeks (seg.).

other arthropods. Wherever trilobite eyes are known they have lenses composed of calcium carbonate with the c-axes perpendicular to the surface, an optical system peculiar to the trilobites (Towe 1973). That eyes of such a type are found on the many post-Cambrian trilobites which have lost the circum-ocular suture is an indication that it is the common eye structure for the trilobites as a whole. There are occasional Cambrian examples where the circum-ocular suture has also been lost, for example in a few late Cambrian Olenidae (Clarkson 1973) or early Cambrian eodiscids (Jell 1975) in which the visual surface is apparently of the usual kind. Eyes have been described in immature olenellids only (Kiaer 1917; Clarkson 1973; Palmer and Halley 1979, pl. 1, Figure 12), and it is believed that the circum-ocular suture was present in the adult. It does seem possible that the secondary fusion of the eye to the free cheek was an originally juvenile character which was displaced into the adult growth stages. There seems to be no good reason to suppose that the visual system of the olenelloids differed from that of other trilobites, but investigation of this matter is hampered by lack of material. Both the visual system and the circum-ocular suture appear to be good characters supporting monophyly of the Trilobita. Many trilobites became blind, but this is always a secondary feature, as it is in arthropods as a whole.

Character 6. Eye ridge and palpebro-ocular ridge. In many Cambrian and younger trilobites an eye ridge extends from the eye lobe forward and inward to the axial furrow; this ridge arises from the anterior edge of the palpebral lobe, the raised portion of the eye lobe adaxial to the suture. In some olenelloids the eye ridge is divided longitudinally by a furrow, continuous with the palpebral furrow, into anterior and posterior palpebro-ocular ridges. These structures appear to be homologous in all trilobites. The eye ridge may become effaced in many derived trilobites, however, and, as was discussed with the loss of the circum-ocular suture, one can show that this loss is polyphyletic, and not of great taxonomic weight. Some trilobite groups (such as odontopleurids) retain the eye ridge throughout a history of several hundred million years. Other derived trilobites (e.g. primitive trinucleids) may retain the eye ridge while losing the palpebral lobe; others again may lose the eye ridge while retaining the palpebral lobe (e.g. lichids). Hence we prefer to describe this character in terms of both its components.

Character 7. Cuticle structure. The high carbonate content of the trilobite cuticle is unusual in the clade comprising trilobites and chelicerates, although similar calcification is developed convergently in the decapods and ostracodes. However, the trilobites differ from the decapods in not having postoral ventral calcified plates. The division of the trilobite cuticle into a fibrous endocuticle and prismatic exocuticle is described from many different trilobite groups, and the prismatic outer layer has been reported in one species of olenelloid by Teigler and Towe (1975). This slim evidence suggests that the olenelloid cuticle was like that of other trilobites. Certain olenellids have a coarse polygonal surface structure which is not present on other olenelloid taxa, nor apparently on redlichiids; this may define a clade within the olenelloids.

Character 8. Rostral plate present. This is perhaps the most disputable of the trilobite characters listed linking olenelloids and "higher" trilobites. A wide rostral plate is present in olenelloids, which lack dorsal ecdysial sutures. A rostral plate is present in redlichioids (which have dorsal ecdysial sutures) and in the great group currently classified in Ptychopariida. It is present in the primitive phacopide *Gyrometopus* (Jaanusson 1975), and in Proetida, a general occurrence suggesting that it is a trilobite character. It is lost in those forms with fused free cheeks (Olenidae, Raphiophoridae, Cyclopygidae etc.) and in those having a median suture (Asaphina, sensu Fortey and Chatterton 1988). So far as we know these latter are derived from other trilobites in which the rostral plate was present, that is, they are secondarily

modified from the rostrate condition. What is perhaps more doubtful is whether the rostral plate is different from ventral structures on chelicerates. A permarginal suture is believed to be primitive in this group, and this is most closely approached in the olenellids. There are a variety of cephalic doublural structures described in eurypterids (Størmer 1934, Figure 11). The "general" type, as in *Hughmilleria*, has a median plate (epistoma), which it might be contended was homologous with the rostral plate of trilobites; however, it is flanked by two other suturally bounded plates (see Figure 4B, antelateral shields of Størmer) which are certainly not obviously homologous with any known trilobite structure. The ventral organisation of such eurypterids may be different enough from that of the generalised trilobite pattern to suggest that the trilobite rostral plate is an autapomorphy of the group.

Character 10. Hypostomal wings. Whittington (1988) has claimed that the presence of the anterior wing on trilobite hypostomes, and its engagement with anterior pit or fossula in the axial furrow (or with the same point in the axial furrow in effaced forms) is homologous in all trilobites, including olenelloids.

LAUTERBACH'S CHARACTERS

Even if those characters given by Lauterbach (1980) as uniting olenellids and chelicerates were correct, they are fewer than those which unite trilobites and all olenelloids. However, his characters can be criticised on several counts, and have been by Whittington (in press). In effect they depend on the interpretation of the position of olenellids within a transformation series running from the "ground-plan arthropod", which is a theoretical construct and not a real animal, towards crown-group chelicerates. The homologies depend on the theory. Thus it is not as obvious as has been claimed that the two segments in front of the macropleural one in olenellids are destined to become part of the cephalic shield of higher chelicerates—it only seems obvious if the particular course of phylogenesis proposed by Lauterbach is accepted as axiomatic. The first two of Lauterbach's trilobite/chelicerate synapomorphies as listed above deserve some comment here. The third, concerning the division between prothorax and opisthothorax, and the nature of the so-called telosoma, has been discussed by Whittington (in press).

1. The long median spine on the fifteenth segment. A special significance is attached to the presence of the spine on this segment, because of its claimed homology with the posterior spine in chelicerates. Yet the spine seems no different from those of other trilobites, in which it appears to be an unusually labile character. It is absent in many olenelloid taxa. Although present in *Olenellus thompsoni* (Figure 2), for example, it is absent in *Olenellus (Olenelloides)*, a taxon which is now regarded as different from *Olenellus* only at subgeneric level (McNamara 1978). In other accepted monophyletic trilobite families an axial spine may be present in some taxa, absent in others (Remopleurididae, Olenidae, Aulacopleuridae are examples). Nor is there any noticeable propensity for the axial spines in such families to be present on the fifteenth axial ring. In remopleuridids a long axial spine may be developed on the eighth thoracic segment in *Pseudokainella*, and some *Remopleurides* species; among olenids an axial spine may be present on the thirteenth (*Balnibarbi*), twelfth (*Bienvillia shinetonensis*), or eleventh (*Leptoplastus*) thoracic segment; in certain aulacopleurids the sixth segment may carry a median spine. Öpik (1958) illustrates median spines on the fourth and the twelfth thoracic segments of *Redlichia forresti*. None of this disproves

Lauterbach's homology (it could be claimed that only those olenellids with a spine on the fifteenth thoracic segment were chelicerate sister taxa), but it does seem unwise to place much emphasis on a character which appears so variable among contemporary arthropods. It seems to be a character carrying little burden, in the sense of Riedl (1975).

2. Third macropleural segment, and homology of anterior two thoracic segments with posterior cephalic segments of chelicerates. This character depends very much on Lauterbach's interpretation of the sequence of events leading to chelicerates. It is of course possible that the chelicerate prosoma was reached by a process of 'cephalisation' accruing segments therein, but it remains to be demonstrated that the olenellids were the correct candidates for an intermediate stage in this process. Whittington (in press) has pointed out that macropleural segments are developed in other trilobites on segments other than the third. In paradoxidids those species with macropleural segments have the second segment enlarged, but in the young forms the first *two* segments are both enlarged, the first becoming progressively reduced through ontogeny (Šnajdr 1958). Those favouring trilobite relationships of olenelloids would tend to regard this character as another variable character within the group to which exceptional significance cannot be attached.

In summary it can be stated that the Trilobita is a monophyletic group, and should include the olenellids and olenelloids.

OLENELLOIDS AS THE MOST PRIMITIVE TRILOBITES

The view that olenelloids were primitive was based in part on a stratigraphical argument, because olenelloids are the earliest trilobites recovered from some continuous rock sections spanning the latest Precambrian to early Cambrian, in North America, Siberia and Morocco. However, in the "redlichiid faunal realm" (Richter and Richter 1941; Cowie 1971), which includes China and Australia, redlichioids are found in early Cambrian rocks, and olenelloids are absent. In at least one section in Morocco (Sdzuy 1978) olenelloids and redlichioids co-occur in the earliest Cambrian. There is thus no stratigraphical evidence as to which is the more primitive group. Hence morphological evidence must be used in seeking to decide whether olenelloids are the most primitive trilobites, or a derived group within the clade. The answer to this question depends to some extent on the answer to the broader question of the relationships of the Trilobita within Arthropoda as a whole, because this allows us to judge which characters are likely to be retained primitive ones in the olenelloids as compared with other trilobites. The broader questions of trilobite relationships are not within the scope of the present paper. However, a series of cladistic analyses, using a matrix of more than forty characters and a computer program which produces the most parsimonious tree(s) (PAUP) have been prepared by D.E.G. Briggs and R.A.F. (Briggs and Fortey in press). These indicate that trilobites and chelicerates are part of a larger clade, which also includes several of the more enigmatic early Palaeozoic (mostly Cambrian) arthropods such as aglaspidids, and *Alalcomenaeus*, *Habelia* and *Naraoia* among the Burgess Shale fauna. This is in general agreement with Lauterbach (1983) in his suggestion of trilobite/chelicerate monophyly, although there are differences in the synapomorphies used. We use this larger clade in seeking to determine primitive retained characters, and also consider whether such characters may be regarded as primitive, by comparison with redlichioids and other trilobites. These characters are discussed below; others, such as the possession of genal spines, are not included because they are present in both olenelloids and higher trilobites, and also in some

members of the chelicerate sister group. The characters of interest are those particularly retained by olenelloids.

- A. Retention of per-marginal suture. Both limuloids and eurypterids moulted by way of a suture running around the margin of the cephalic shield (Henriksen 1932; Figure 4). The rostral suture of olenelloids is also long and marginal (see *Holmia* in Whittington 1988, Figure 3 herein), and in this respect the olenelloids retain the primitive condition. In other Cambrian trilobites the only part of the suture which is marginal is the rostral suture (Figure 4C), the rest of the cephalic structure being attached to the free cheeks, and sharply divided from the rostral plate by connective sutures. It should be noted that some highly advanced trilobites (raphiophorids, trinucleids) also have marginal sutures, but the phylogenetic relationships of these groups show that this is secondarily acquired (the ancestors of such forms having normal dorsal ecdysial sutures) along with other specialised characters like the loss of dorsal sutures and the loss or reduction of the eyes.
- B. Flange-like thoracic articulation. Whittington (in press) has shown that the inner portion of the pleura in *Olenellus* and other olenelloids articulated by an anterior flange which underlies the preceding pleura. The flanges act to guide the pleurae in the probably limited capacity for enrolment. A similar thoracic structure may be present in at least some redlichoids, but in most other trilobites the inner portion of the pleura is horizontal, and the edges of these pleurae act as a hinge during enrolment. However, olenelloid-like thoracic articulation is present in a range of Cambrian arthropods which are undoubtedly primitive, and which may form part of the sister group of the trilobites + chelicerates: *Aglaspis*, *Sidneyia*, *Alalcomenaeus*, *Leanchoilia*, *Molaria*. It seems reasonable to assert that the presence of this kind of overlapping thoracic structure is a primitive character retained by olenelloids, some redlichoids and few other Trilobita.
- C. Expressed segmentation on larval cranidia. Well-preserved, silicified ontogenetic sequences of olenellids (Palmer 1957; Palmer and Halley 1979) show that the early meraspid cranidia have a clearly defined pleuroccipital segment, and that the interocular cheek also shows clear signs of segmentation (see Figure 3). In ontogenies of redlichoids (e.g. Zhang *et al.* 1980 Pl. 35 Figures 1–4) and “higher” trilobites such segmentation is not so expressed. If this follows the general rule in arthropods (or indeed trilobites, see Lane and Thomas 1983) that expressed segmentation is primitive and its suppression a derived character, then the olenelloids are primitive with regard to this character also.

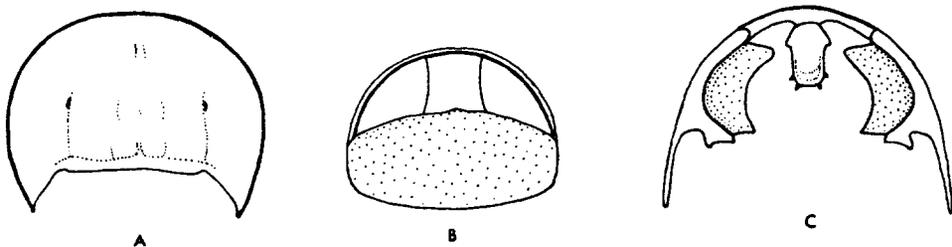


Figure 4 Ecdysial sutures in *Limulus* (A, dorsal) after Henriksen 1932; a eurypterid, *Pterygotus* after Størmer 1934 (B, ventral); and in a primitive member of the non-olenellid Trilobita, *Redlichia*, after Whittington 1988, ventral view of cheeks, doublure and hypostome. Heavy line shows proportion of marginal suture. Compare A and B with text-figure 3. The redlichiid shows a shorter marginal section.

D. Lack of dorsal ecdysial sutures. This character has been given such importance that it has tended to dominate discussion of olenelloid status and affinities. We find the evidence for the importance of the lack of sutures somewhat equivocal. Lauterbach (1980) and Bergström (1973) have claimed that dorsal sutures on olenelloids were primitively absent, but another school of thought regards their absence as secondary (Hupé 1953), having "ankylosed" (Moore *in* Moore, 1959). Such secondary loss is well-known among highly derived trilobites such as brachymetopids (Devonian-Carboniferous). Regardless of such cases of secondary loss, Lauterbach (1980) is surely correct in identifying the presence of dorsal ecdysial sutures as an important derived character for defining the majority of trilobites (his clade Eutrilibita + Emuellida)—the way these sutures are developed is unique within the arthropods. However, unlike Lauterbach, it is not regarded as a necessary condition for the recognition of the Trilobita as a clade, which is supported by the additional synapomorphies discussed previously. It is because the sister groups of the trilobites did not have dorsal ecdysial sutures that we consider their absence in olenelloids to be most probably primitive.

In support of this opinion two arguments may be listed which perhaps favour primitive absence rather than derived loss:

1. Nobody has yet discovered an intermediate olenelloid population including individuals displaying both ankylosed and non-ankylosed dorsal sutures, but there is no reason why such a dithyrial population should not have existed if the loss were secondary. For example the Ordovician dimeropygid *Ischyrotoma anataphra* apparently included some individuals in which the sutures were functional, others in which they were not (Fortey 1979, Pl. 36, Figures 1, 3). Other relevant examples include closely related species with and without functional sutures, as in certain Odontopleuridae (Chatterton and Perry 1983). In these younger trilobites the course of the sutures is visible and it may be that those with fused sutures were individuals between moults, the sutures becoming functional only at exuviation. In the olenelloids there is no trace of dorsal sutures at any stage of growth.
2. The earliest supposed trilobite growth stage is the phaselus reported by Fortey and Morris (1978). Although not everywhere accepted as trilobite (e.g. by Schram 1986), phaseli of three other kinds have now been found in association with trilobite growth stages (B.D.E. Chatterton 1988, written comm.), which means that they are almost certainly correctly associated. They lack dorsal ecdysial sutures. Hence during ontogeny there is a change from lacking dorsal sutures to having them—which would support the polarity of this character during the course of the evolution of the group.

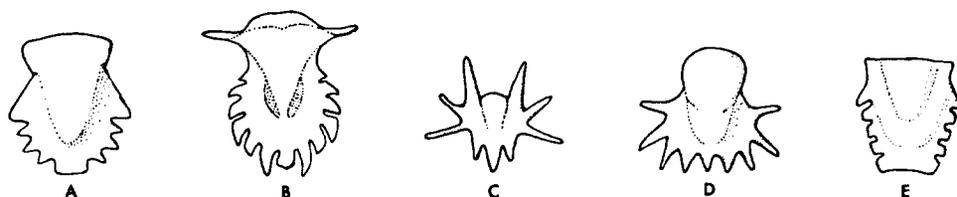


Figure 5 Larval hypostomes of representatives of various trilobite orders, including olenelloids, showing general occurrence of spinose margins. A, ptychoparioid *Spencella*; B, olenellid *Olenellus*; C, asaphine *Isotelus*; D, phacopide *Gravalymene*; E, lichide *Acanthopyge*. A,C after Fortey and Chatterton 1988; B after Palmer 1957; D,E after Chatterton 1971. Not to scale $\times 20$ – $\times 40$.

On balance these arguments favour the primitive lack of dorsal sutures in olenellids (Bergström 1973) rather than their subsequent loss, but the evidence is scarcely compelling. This character can be added to the three above to make a reasonable case for the olenellids being the most primitive of trilobites. However, if the lack of dorsal sutures is indeed primitive in the olenelloids this means that this cannot be an autapomorphy defining the group; indeed, we cannot find any other character which could be considered autapomorphic for the group. Olenelloids may, therefore, prove to be a paraphyletic group, as Lauterbach suggested. This would also account for the many different ways in which they have been classified, as Whittington (in press) summarised.

SOME ADDITIONAL CHARACTERS WHICH MAY PROVE RELEVANT TO THE DEFINITION OF TRILOBITA

Four more characters should be mentioned which may prove useful in amplifying the preceding arguments, but which at the moment are not without ambiguity.

1. *Absence of calcified protaspis in olenelloids.* No protaspis has been described for an olenelloid. Given the other primitive characters of the group it seems very likely that this is a matter of the protaspis stage not having been calcified, rather than being absent (by means of accelerated development in the egg, for example). A fully developed step-by-step ontogeny is invariably characteristic of the more primitive members of arthropodan groups. Calcification of the protaspis might be a derived character linking "higher" trilobites. However, absence of a calcified protaspis is not unique to olenelloids among trilobites, because none has been described for an agnostid either. However, agnostids are among the most specialised of trilobites, and it cannot be assumed that the absence of a protaspis in the agnostids is a symplesiomorphy shared with olenelloids. The answer to this will depend on whether a protaspis can be discovered for the eodiscids, which are the most primitive members of the agnostoid clade. For the moment it seems wiser not to add this character to a list of primitive olenelloid features.
2. *Cephalic appendages.* Thanks to recent descriptions of the appendages of *Olenoides* (Whittington 1975), *Triarthrus* (Whittington and Almond 1987) and *Agnostus* (Müller and Walossek 1987) we know more about the trilobite appendages than in the past, but there are still very few species for which limbs are described. Little is known about the appendages of olenelloids, but it is proven that they had antennae (Dunbar 1925). This is of some importance, because loss of antennae was claimed by Lauterbach (1980) as a synapomorphy of chelicerates. Their presence would be a symplesiomorphy of trilobites + "Crustacea" on this view. The recent descriptions confirm the presence of antennae + 3 pairs of limbs beneath the trilobite cephalic shield, and this might be claimed as a trilobite character were it not for the description by Bergström and Brassel (1984) of a Devonian *Rhenops* species with antennae + 4 pairs of cephalic appendages. These authors stress that there is a "lack of phylogenetic and systematic significance of the segmental arrangement in the arthropod head". It is probably better to remain on the side of caution and not use cephalic appendage number in the definition of Trilobita until we know the limbs of more species. The structure of the limbs of the various trilobites described show some autapomorphies (especially the agnostid) for each taxon, but not any one synapomorphy to differentiate them from the limbs of all other arthropods.

3. *Spinose larval hypostoma*. This character was introduced by Lauterbach (1983:234) as one of his supposed synapomorphies between trilobites and chelicerates. However, taking the view of trilobite monophyly advocated here it is considered equally possible to regard the character as another trilobite autapomorphy. The spinose margin of the olenelloid hypostome has been known for some time (Palmer 1957). It is surprising to find that Lauterbach claims that the larval hypostomes of non-olenellid trilobites are not well known. In fact larval hypostomes have now been described for a very wide range of trilobite families (Figure 5) from the Cambrian to the Devonian (Chatterton 1971). These include representatives of nearly all the major groups, including Asaphina (see Fortey and Chatterton 1988), Ptychopariida, Odontopleurida, Lichida, Illaenina (= Scutelluina, sensu Lane and Thomas 1983). Spinose hypostomal margins are general. If this feature is not known from chelicerates (which according to Lauterbach it is not) it may be reasonable to regard it as another synapomorphy between olenelloids and "eutrilobites", and hence an additional autapomorphy of Trilobita, as understood in this paper. We do not do so in the list given above, because so little is known about ontogeny of the labrum of stratigraphically early merostomes and eurypterids that it remains uncertain whether the labral plate of these groups had a spinose margin at an early growth stage. It is possible that the character was a primitive one for the trilobite + chelicerate clade. Given the other characters shared between olenelloids and other trilobites this is less plausible than regarding a larval spinose hypostomal margin as another distinctive trilobite character.

4. *Terrace ridges on doublure*. Many trilobites have a distinctive pattern of concentrically arranged terrace ridges on the ventral surface of the doublure (Miller 1975). They have been claimed (e.g. Schmalfuss 1981) as related to the function of gripping the sediment during feeding, but other functions must have been involved in some kinds of trilobites (Fortey 1986). Terrace ridges are present on olenelloids (Whittington in press), in all other primitive trilobite groups, and in many derived ones: ptychoparioids, redlichoids, corynexochoids, proetoids, Asaphina, Lichida. Their loss is secondary, and happens only in a few groups, but is consistent within those groups: Phacopida and Odontopleurida. Their presence is thus another probable synapomorphy between olenelloids and other trilobites. Our reason for not including this character in the list of trilobite characters above is that we do not know whether the presence of such ridges may be proved on other arthropods (e.g. primitive limuloids) for which the information is not yet adequate—such ridges may characterise a larger clade than Trilobita.

CONCLUSIONS

1. Lauterbach's contention that some olenelloids and the rest of the trilobites belong in different clades is disproved. The trilobites are a monophyletic group, which includes olenelloids.
2. This is supported by seven (possibly nine) synapomorphies between olenelloids and the rest of the Trilobita, which provide the defining characters for the group.
3. Olenelloids are the most primitive trilobites known because they retain three, and probably four, primitive characters; they may be a paraphyletic group.

Acknowledgements

Our thanks particularly to A.W.A. Rushton and D.E.G. Briggs for much helpful discussion; H.B.W. is indebted to the Leverhulme Trust for their support.

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