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TRILOBITE MONOPHYLY REVISITED

LARS RAMSKÖLD[1] and GREGORY D. EDGECOMBE[2]

[1]Department of Palaeozoology, Swedish Museum of Natural History, Box 50007, S-10405 Stockholm, Sweden; [2]Department of Invertebrates, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024-5192, USA

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Fortey's and Whittington's recent refutation of Lauterbach's hypothesis of a paraphyletic Trilobita is supported. However, much of the character evidence raised by Fortey and Whittington to substantiate the monophyly of the Trilobita (including, *inter alia*, "Olenellinae" and Agnostoidea) is ambiguous. Of seven proposed synapomorphies, only one (dorsal cuticle calcification) may be maintained at that node after testing within a cladistic framework. The other six characters are either constrained by calcification or define nodes up or down the cladogram. As positioned by Fortey's and Whittington's characters, Agnostoidea could be regarded either as the most primitive trilobites, or as being outside that clade. Lauterbach's support for an "olenelline"-chelicerate clade is found to include interdependent characters which are reduced here to two testable derived similarities. Only one of these may conform to general criteria indicative of homology, such as detailed similarity and topology. It is, however, rejected on the basis of parsimony. We emphasize that resolution of the chelicerate-"olenelline"-trilobite three-taxon problem must be based on recognition of homologies among each of these taxa. Nectaspida are excluded from Trilobita as defined by cuticle calcification, but as ingroup "Arachnata" (*sensu* Lauterbach) they are important for determining character generality in this clade.

KEY WORDS: Trilobites, chelicerates, olenellines, agnostids, Nectaspida, phylogeny, monophyly, character analysis.

INTRODUCTION

Lauterbach's (1980, 1983, 1989) repeatedly proposed paraphyly of Trilobita as traditionally delimited was first rejected by Ahlberg *et al.* (1986:40) as "a curiosity". They stated that Lauterbach's main character, the presence of fifteen "prothoracic" (*sensu* Lauterbach) segments in *Olenellus*, was a simple miscount for fourteen. Lauterbach, however, explicity stated (e.g., 1983:217) that the spine-bearing fifteenth segment was the last of the "prothorax" (which is otherwise usually taken to include only the fourteen segments anterior to the spine-bearing one). The basis for Ahlberg *et al.*'s statement is that in Lauterbach's figure of "*Paedumias*" *robsonensis* the thoracic axial spine is (erroneously) drawn as if situated on the fourteenth segment. Thus Lauterbach's claim stood essentially unopposed until a fuller response was offered by Fortey and Whittington (1989) (it should be noted that several non-trilobite workers have accepted Lauterbach's hypothesis and used it to exemplify paraphyly, e.g. Ax, 1985, and in procedures for classifying fossil taxa; Weygoldt, 1986). Another response to Lauterbach's proposals was recently published by Hahn (1989); this and the simultaneously published reply by Lauterbach (1989) are dealt with separately below.

Correspondence should be addressed to Lars Ramsköld at the above address.

Fortey and Whittington (1989) aimed at examining Lauterbach's claims and finding character support for Trilobita as conceived by them. Our intent here is twofold: first, to examine the evidential basis for each competing hypothesis (monophyly versus paraphyly of Trilobita inclusive of "olenellines") and evaluate the characters used, and second, to explore the methodological basis for Fortey's and Whittington's (1989) claims of trilobite monophyly. To a limited extent we also propose alternative hypotheses or characters. Following Lauterbach's provocative introduction of phylogenetic systematics into research of higher trilobite taxonomy, Fortey's and Whittington's study is regarded as a further step towards a more phylogenetically defined Trilobita. We propose that future studies building on Fortey's and Whittington's work must be based on character analysis evaluating possible homology among structures not only in each group of the three-taxon problem of concern (i.e., Chelicerata, "Olenellinae", and Trilobita *sensu* Lauterbach), but also of other taxa that are ingroups in this context, of which there are several. This is necessary since, in our view, the question of trilobite monophyly has perhaps overemphasized the Olenellinae, while the ingroup status of agnostids (but not eodiscids) remains to be character-supported.

Systematic Terminology

In a study dealing with alternative definitions of taxa, a consistent use of names of higher taxa is obviously essential. We use "olenellines" in the sense of Lauterbach (1983) rather than "olenelloids" *sensu* Whittington (1989) for ease of referral to Lauterbach's (1980, 1983) discussions, which did not specify the position of olenelloids outside the Olenellinae, though he later (1989) also removed these from the Trilobita. For this reason, and because of the uncertainty of Fortey's and Whittington's (1989) use of Trilobita (where Nectaspida seem to be excluded) we use Trilobita sensu Lauterbach rather than Trilobita in any conventional sense. This use does not indicate any preferred hypothesis. The Nectaspida Raymond, 1920 (informally called "nectaspids" below) is used in a wider sense than in its original definition, and is here taken to include *Naraoia* Walcott, 1912, *Tegopelte* Simonetta and Delle Cave, 1975, *Maritimella* Repina and Okuneva, 1969 (but see Robison 1984:2 for remarks) and *Liwia* Dzik and Lendzion, 1988. The monophyly of this group has not been tested. Agnostoidea (informal "agnostids") and Eodiscoidea ("eodiscids") are treated as separate groups following Walossek and Müller (1990).

THE COMPETING HYPOTHESES

Fortey and Whittington (1989) contrast cladograms depicting Lauterbach's (1983) phylogenetic hypothesis and the traditionally accepted topology defended in their paper (their Figure 1). Lauterbach's cladogram unites "Olenellinae" and Chelicerata by three alleged synapomorphies. Fortey's and Whittington's cladogram groups "olenellines" with Trilobita (*sensu* Lauterbach), and this clade is supported by seven characters proposed to be apomorphic. Parsimony is cited by Fortey and Whittington as a criterion for favoring the latter hypothesis, predicting the monophyly of Trilobita as conventionally grouped. Fortey and Whittington suggest that Lauterbach's hypothesis would be less favored even if his diagnostic characters were "correct". We take this to mean "descriptively correct" rather than "evolutionary true".

Character Analysis

A necessary prerequisite for any phylogenetic statement is that character state distributions are considered for each of at least three taxa (four if characters are polarized via the "outgroup method"). In this instance, the relevant taxa are Chelicerata, "Olenellinae", and Trilobita *sensu* Lauterbach (plus non-arachnate outgroups). For the majority of the proposed synapomorphies, Fortey and Whittington present character information for only two of the three taxa concerned. In their list of trilobite synapomorphies, possible homologues in Chelicerata are not evaluated for characters 5 (eye structure), 6 (eye ridge and palpebro-ocular ridge), and 10 (hypostomal anterior wing articulation). Regarding character 4 (pygidium), it is simply stated that it is not a telson (of chelicerates). Without documenting the absence of possible homologues in Chelicerata we do not see how these characters have an evidential basis for diagnosing Trilobita. It is also unfortunate that Fortey's and Whittington's discussion largely excludes the non-calcified Nectaspida Raymond, 1920, since members of this group have elsewhere been referred to the Trilobita by Whittington (1977, 1985), a view accepted by several workers (e.g. Robinson, 1984; Zhang and Hou, 1985).

Fortey's and Whittington's discussions of Lauterbach's characters, although useful, could have been made more valuable by the use of a stringent methodology. In their effort to refute the status of these similarities as synapomorphies, they present evidence from Lauterbach's outgroup (i.e., his Trilobita) but not for his ingroup taxa (i.e., chelicerates and "olenellines"). It is argued that lability of these features in trilobites (*sensu* Lauterbach) precludes their utility as diagnostic features for major groupings. This reasoning is akin to that advocated by proponents of compatibility (clique) methods, where a character deemed homoplasious in one occurrence is dismissed as homoplasious in all occurrences, and data are thus discarded. For example, the presence of an axial spine on the fifteenth post-cephalic segment (used by Lauterbach to group "olenellines" with Chelicerata) is rejected by Fortey and Whittington because in accepted monophyletic trilobite families an axial spine may be present in some taxa, and absent in others. They cite examples of a "similar" spine occurring on different thoracic segments in a number of different trilobite groups. As acknowledged by Fortey and Whittington, this does not disprove Lauterbach's conjecture of homology. Without reference to the proposed homologous conditions in ingroup taxa, evidence from the outgroup is irrelevant, and Lauterbach's claim remains standing unopposed.

Fortey's and Whittington's refutation of Lauterbach's second synapomorphy is also based singularly on outgroup evidence. The presence of macropleural thoracic segments in variable positions in the outgroup is forwarded as evidence weakening Lauterbach's claim that the anterior two "prothoracic" segments of "olenellines" are homologous with the two posterior prosomal segments of Chelicerata.

The arguments of Fortey and Whittington regarding axial spines and macropleural segments were independently forwarded by Hahn (1989). As recognized by Lauterbach (1989) in his reply, these arguments are not relevant. We would suggest that an alternative method could be used in attempts to refute Lauterbach's homology conjecture (see character 2 below).

DISCUSSION OF CHARACTERS (numbered as by Fortey and Whittington).

In evaluating the status of characters, homology of structure must first be rendered plausible by presenting supportive evidence. That is, discussion on any structures must be on the basis that a hypothesis on homology of these structures can be proposed. Since homology, defined as continuity of information (Van Valen, 1982), can rarely, if ever, be tested in fossil taxa, homology must be proposed on the minimum basis of indications such as similarity of structure, morphogenesis (ontogenic development), and topological relation. Even when characters pass more refined tests such as those of Patterson (1982), the concept of homology can only be framed in terms of mutually or cumulatively supportive indications.

A. Characters of Lauterbach (1983)

Character 1. Following Walcott 1910, Lauterbach suggested the homology between the spine of the fifteenth thoracic segment in "olenellines" with the terminal spine of chelicerates. He further drew the conclusion that the telson of chelicerates therefore must be of an original segmental origin. Whittington (1989) stated that Walcott's "idea was derived from imperfect specimens, which lacked the posterior thoracic segments and pygidium", and he described and figured specimens showing these posterior areas. One of Lauterbach's examples was the proposed "telosoma" ("post-pygidial abdomen") of *Triarthrus* (see Cisne 1975, 1981). This has since been convincingly shown by Whittington and Almond (1987) not to exist, a fact that Lauterbach (1989) has recently accepted. We have no new evidence that may dispute Lauterbach's claim, but suggest that such evidence should be sought in detailed character analysis within the taxa concerned.

Character 2. Lauterbach proposed the homology of the macropleural third segment in "olenellines" with the first opisthosomal segment in chelicerates. This was proposed not because of any observed similarity between these respective segments, but largely as a corollary to the suggested homology of the two anterior segments of "olenellines" with the two posterior prosomal segments in chelicerates. In our view, however, topological position alone is not a sufficient criterion for homology but must be supported by similarity of structure or other indications. In this case, structure may provide contrary evidence, in that the first opisthosomal segment (segment VII) in xiphosurids is reduced rather than macropleural. Nor has (derived) structural similarity of any other kind been observed. Embryological evidence indicates that the opisthosomal somite VII is borne as the chilaria and is not expressed dorsally in extant taxa. This is consistent with the circumstance that some Paleozoic xiphosurids have a greatly reduced first opisthosomal tergite (Seldon and Siveter, 1987). In the oldest and most primitive chelicerate, *Sanctacaris* Briggs and Collins, 1988, the first opisthosomal segment is slightly smaller than the succeding ones, but is structurally similar. We regard this evidence, weak though it may be, as contradicting Lauterbach's transformation series for the origin of the chelicerate prosoma from an "olenelline" morphology.

More serious objections come from the actual morphology of "olenellines". Macropleurality in "olenellines" was inferred by Lauterbach (1980, 1983, 1989) to be associated with modification of appendages of the macropleural segment and blockage of the "ventral food groove". This speculation is unsupported by known or, regarding feeding procedure, by observable data. On the contrary, morphological evidence (see below) indicates that the appendages of the macropleural segment were in exactly the same position relative to anterior and posterior appendage pairs as appendages in other parts of the thorax. Lauterbach has made a common error, seeing differences but not similarities.

The laterally strongly exsagittally widened pleural area of the macropleural segment in "olenellines" tapers adaxially to become equally wide at the axial furrow as are adjacent segments. The sagittal and exsagittal width of the axial ring, below which lies the "ventral food groove", is identical to that of adjacent segments. We have measured these widths in *Olenellus thompsoni, O. vermontanus, O. robsonensis,* and *Wanneria walcottanus* (all figured by Whittington, 1989), without finding any difference between macropleural and adjacent segments. Even in the Biceratopsinae, olenelloids with an extremely enlarged macropleural third segment, this segment is of the same exsagittal width at the axial furrows and in the axial ring as are adjacent segments (e.g., *Biceratops* Pack and Gayle, 1971; *Peachella* Walcott, 1910; see Stitt and Clark, 1984, Figure 2; *Bristolia* Harrington, 1956; see Resser, 1928, pl. 2, Figure 1; Riccio, 1952, pl. 5, Figure 5, pl. 6). Also in olenellids lacking a macropleural segment, e.g. *Nevadia* (see Whittington, 1989) the exsagittal widths are undifferentiated.

The appendages were joined by musculature to various exoskeletal areas, foremost the apodemes, situated ventrally below the axial furrow (see reconstructions by Cisne, 1975, 1981; Campbell, 1975; Whittington and Almond, 1987). The coxae extended adaxially below the axis (rhachis), forming between their inner gnathobases the inferred "ventral food groove", along which food particles are assumed to have been transported anteriorly to the mouth. Since the exsagittal lengths of the axial rings as well as the distances between the attachment sites (the apodemes) for the coxae are identical through the anterior part of the thorax, the rotational movement and muscular work needed for this function would be equal in these appendage pairs, including that of the macropleural segment. We regard this morphological evidence—equal segmental widths adaxially regardless of whether or not macropleurality is present—as indicating a functional constraint. This constraint may well have been the necessity of a functioning "ventral food groove" throughout the thorax.

We regard Lauterbach's "hypothesis" of food blockage as contrary to morphological evidence, and as refuted.

Character 3. Lauterbach's third character was the homology of the fifteen segments of the post-cephalic "prothorax" in "Olenellinae" with the last two segments of the prosoma and the thirteen of the opisthosoma of the Chelicerata. Although this character is only referred to by Fortey and Whittington (1989) as already refuted by Whittington (1989), it is a corollary of Lauterbach's characters 1 and 2. Hence it is not an independent character.

B. Characters of Fortey and Whittington (1989)

Character 4. The first of Fortey's and Whittington's proposed synapomorphies for trilobites is the presence of a pygidium. The presence of a pygidium is also one of Lauterbach's proposed apomorphies for his Trilobita. Lauterbach, however, regarded the pygidium as a non-terminal tergite (incorporating a more or less reduced "telosoma").

Unfortunately, Fortey and Whittington excluded Nectaspida from their discussion and further did not consider Agnostoidea or Eodiscoidea. However, we believe that any phylogenetic speculation concerning Trilobita must include these groups in assessing character generality. For example, if the presence of a pygidium is an apomorphy for Trilobita, then Nectaspida must be assigned to this group. Alternatively, the presence of a pygidium could indeed prove to be a synapomorphy for trilobites if it was demonstrated that the "pygidium" of nectaspids is not homologus with that of dorsally calcified trilobites. It should be noted that on the basis of at least five of Fortey's and Whittington's further six characters, in particular character 7 (see below), Nectaspida is excluded from their Trilobita (see remarks under each character below). Nectaspids such as *Liwia* Dzik and Lendzion, 1988 have a thoracopygidial tagmosis of typical trilobite appearance, suggesting that the pygidium is apomorphic at a phylogenetic level broader than that of dorsal calcification (character 7).

Fortey and Whittington further regard the small size of the pygidium of "olenellines" as primitive for Trilobita. In Agnostoidea, Eodiscoidea, and Nectaspida the pygidium is, on the contrary, unusually large. It should be noted that the trilobite ingroup status of Agnostoidea has recently been questioned (Walossek and Müller, 1990), while eodiscids are universally accepted as trilobites. A small pygidium may well be plesiomorphic for "olenellines" + Trilobita (sensu Lauterbach), but may be ambiguous for a trilobite grouping which includes agnostids. It is conceivable, in theory, that a large pygidium indicates the primitive condition of a clade of dorsally calcified trilobites + Nectaspida (see Figure 1). If so, then the small pygidium of "olenellines" would be most parsimoniously interpreted as derived. The latter polarization is contrary to that of Fortey and Whittington, and the choice between the two is dependent on whether Eodiscoidea and Agnostoidea have a paedomorphic origin from "normal polymerids" (with small pygidia in adults) or if their large pygidia reflect a plesiomorphic condition. Only if we, following convention, assume the former to be the case, the presence of a small pygidium may be proposed as an apomorphy for Trilobita (as defined by dorsal calcification).

A related point of interest is that the definition of the pygidium as a terminal tagma composed of more than one segment cannot always be upheld. In pygidia of "olenellines" such as *Olenellus*, *Wanneria*, *Nevadia*, and *Elliptocephala*, all beautifully illustrated by Whittington (1989), we fail to see evidence for more than one segment (plus a possible, fused, rudimentary "telson"-like area between the posteriorly flexed pleural areas of this segment). This circumstance may not be of great importance, and we are inclined to interpret it as an apomorphy for olenellines. Other olenellid genera such as *Holmiella* and *Schmidtiellus* have multisegmented pygidia (Fritz, 1972; Bergström, 1973b; Ahlberg *et al.*, 1986).

A "true" pygidium is the result of the retention of unreleased ("fused") segments in a posterior body region, and the absence of a (multisegmented) pygidium would merely indicate that all segments have been released. Polarization of this character may be dependent of which phylogenetic level is considered. It is generally accepted that the absence of a pygidium is primitive for arthropods as a group, and outgroup polarization from numerous taxa (see Briggs and Fortey, 1989 for cladogram showing these taxa) does give absence of pygidium as primitive for "Arachnata". On the other hand, using trilobite ontogeny to polarize this character, the "complete release condition" may be regarded as the apomorphic condition with regard to taxa possessing a pygidium. This would apply to olenelloids with one-segmented pygidia ("olenellines"). If (and this is highly debatable) Nectaspida is regarded as the sister group to a clade including Olenelloidea, Eodiscoidea and more derived trilobites (whether or not Agnostoidea is included does not affect the reasoning), then in this grouping the presence of a pygidium would be plesiomorphic for dorsally calcified trilobites. The condition in olenellines would thus be apomorphic, and the ontogenetic polarization would be supported. At the present state of knowledge either of the two polarizations can be supported, and we refrain from a choice here.

Postembryonic development in chelicerates is epimorphic (hatching in juveniles without addition of further segments). Early ontogeny is not known for primitive fossil xiphosurids (Synziphosurina) possessing articulated opisthosomal tergites. This lack of information precludes a search for a developmental homologue in these taxa of the transitory pygidium of trilobites.

Character 5. The calcified lens structure of the trilobite eye and the orientation of the optical axis was regarded by Fortey and Whittington as an independent character. The mineralogy and the optical axis are two characters that are obligately coupled in trilobites (Towe, 1973; Clarkson, 1973a, 1973b). In other arthropods the lenses are usually unmineralized, and only a few crustaceans possess calcite in the corneal lenses. This calcite is, however, composed of randomly oriented crystals (Towe, 1973 and references therein). The orientation of the optical axis in "olenellines" is unknown, but their lenses are definitely calcified, and we agree with Fortey and Whittington (1989) who state that there is no reason to assume that the optical axis is different from that of other trilobites. It is unknown to what extent this feature is coupled with the presence of a calcified dorsal cuticle, and can be treated as an independent apomorphic character. Some support of its apomorphic character is given by undescribed Chinese Cambrian aglaspidid material showing a calcified exoskeleton, but in which the visual surfaces apparently are phosphatic (J. Dalingwater and D. J. Siveter, pers. comm.).

Evidence for eyes in Nectaspida is very weak (see Whittington, 1985) and they most probably did not possess eyes in the dorsal exoskeleton, and thus lacked calcified lenses. Also Agnostoidea lacked dorsal eyes (evidence for "ocular" structures in *Oculagnostus* Ahlberg, 1988 is ambiguous and needs confirmation).

Character 6. This character was the presence of an eye ridge or palpebro-ocular ridges. Fortey and Whittington cite the invariance of this character in certain long-ranging taxa (e.g. odontopleurids) as support for its diagnostic value. On the other hand, in some diverse and long-ranging groups (e.g., encrinurids) presence and absence of the eye ridge are distributed sporadically. Both distribution patterns are irrelevant, since the stability or not of a character for long periods of time can not be the basis for its polarization.

It may be noted that the structure and topological relations of these features in primitive Trilobita (*sensu* Fortey and Whittington) are similar to those of primitive xiphosurids, for which the ophthalmic ridge anterior to the eyes is the corresponding (possibly homologous) feature (see, e.g., Bergström, 1975, Figure 1). In addition, there are similarities between the metagenal ridge (Bergström, 1973a = intergenal ridge of McNamara, 1978) of olenelloids to the "ophthalmic ridge" posterior to the eyes of xiphosurids. The posterior extension of the ridge into an intergenal spine is observed in olenelloids, in particular in early ontogenetic stages, as well as in many xiphosurids (Selden and Siveter, 1987, Figure 1). In both groups there is a genal spine outside the intergenal spine. These similarities may or may not be homologous, and must be investigated in further detail. Should these structures in xiphosurids prove to be homologous with those in olenellids, then they cannot be autopomorphic for Trilobita. As noted by Lauterbach (1989), eye ridges are not present in blind forms, and for secondarily blind advanced Trilobita (e.g., phacopids and proetids) we know this to be a secondary loss. Whether due to primary absence or secondary loss, this character is not applicable to Nectaspida (nor to Agnostoidea), so that the relationships of these groups cannot be evaluated on this criterion.

Character 7. Fortey and Whittington cite calcification of the dorsal cuticle ("exoskeleton") as apomorphic for Trilobita. However, both *Naraoia* and *Tegopelte* have been described as non-calcified ("soft-bodied") trilobites by Whittington (1977, 1985), and no statement to the contrary has, to our knowledge, been published. Due to this contradiction, we feel that any discussion of the character status of calcification must include these taxa. However, we regard this character as the best supported of those presented, and uphold Fortey's and Whittington's claim that dorsal calcification may be apomorphic for the Trilobita as defined by them. As a corollary, we suggest that Nectaspida cannot be retained as trilobites without broadening the inclusiveness of the Trilobita (Figure 1). Unfortunately, a calcified dorsal cuticle is in itself not a unique apomorphy for the Trilobita, but is present also in several other groups. Calcification in, e.g., aglaspidids and ostracods certainly represent developments parallel to that in Trilobita. This presence precludes dorsal calcification from being used alone for diagnosing Trilobita. In the absence of other supporting characters, we are thus reluctant to regard node 3 of Figure 1, which is singularly based on this character, as the basal node of Trilobita.

Character 8. The trilobite rostral plate was regarded by Fortey and Whittington as their weakest character supporting the monophyly of Trilobita. We agree, since if the ecdysial suture itself is regarded as homologous between "olenellines" and Trilobita (*sensu* Lauterbach), then the alleged rostral plate of "olenellines" cannot be homologous with the rostral plate of Trilobita (*sensu* Lauterbach). The so called rostral plate of "olenellines" includes ventrolateral cephalic parts which are included in the free cheek of trilobites possessing dorsal ecdysial sutures, as well as including the median ventral component which constitutes the rostral plate in the latter taxa. The true rostral plate can only be defined by the presence of connective sutures. This, in turn, is an apparent correlate of dorsal ecdysial sutures and the presence of free cheeks. We therefore regard the rostral plate as apomorphic for more derived trilobites (Figure 1), although the condition in Eodiscoidea is unknown.

No positive evidence for a rostral plate in Eodiscoidea has been forwarded, and Jell (1975a) regarded it as absent or uncalcified, while Whittington (1988a) left the question open. From the shape of the tapering, possibly pointed anterior tip of the free cheek border in eodiscids (e.g., Jell, 1975a, pl. 27, Figure 9) it is certain that any connective suture must have been very short, i.e., the rostral plate must have been very narrow. A narrow, doublural strip of appropriate appearance is present in well preserved, articulated specimens of the eodiscid *Pagetia triaena* (Jell, 1975a, pl. 21, Figs 3 and 8). We do not propose that this feature is a rostral plate, but suggest that any search for such a plate should look for a similar, very narrow structure, rather than the inferred very wide rostral structure hypothesized by Jell (1975a) and Whittington (1988a).

"Olenellines" primitively possess a submarginal suture and a horse-shoe shaped ventral plate. Comparable structures were described in an agnostid by Hunt (1966), although we agree with the doubts forwarded by Müller and Walossek (1987:20) on the interpretation of the structures. As noted by Fortey and Whittington (1989, Figure 4), an olenelloid type of marginal suture is present in primitive chelicerates such as xiphosurids and eurypterids.

Character 9. As indicated by Fortey and Whittington, a circumocular suture is primitively present in Trilobita (*sensu* Lauterbach), including eodiscids (Jell, 1975a, b). Little is known regarding visual structures in Nectaspida, although they appear to be absent in *Naraoia* (Whittington, 1977; Zhang and Hou, 1985; personal examination), and are poorly developed or possibly absent in *Tegopelte* (Whittington, 1985). The positive evidence indicating the presence of a functional

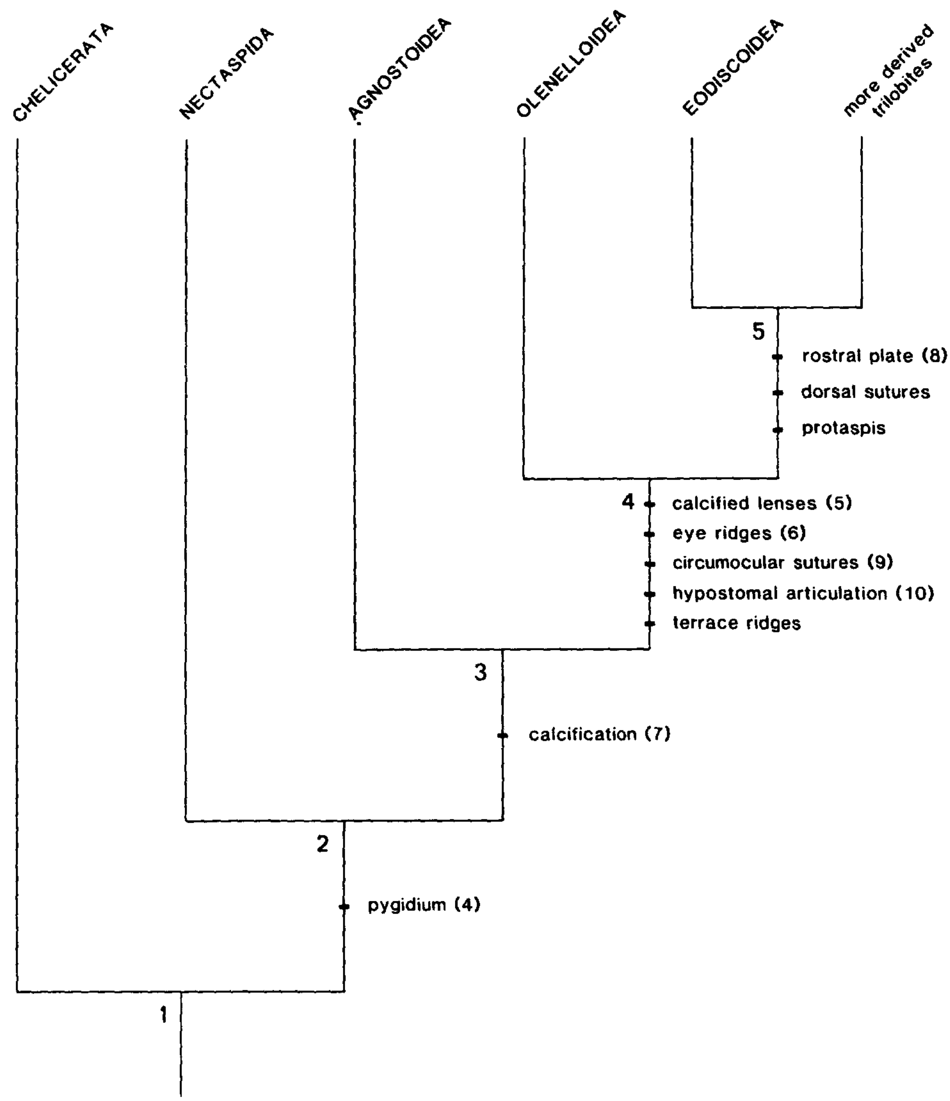

Figure 1. Cladogram showing the most parsimonous topology yielded by the characters of Fortey and Whittington (1989). Taxa are those of Fortey and Whittington with Nectaspida added and Agnostoidea and Eodiscoidea treated separately. Characters are numbered as by Fortey and Whittington ("calcification" is calcification of the dorsal cuticle, "dorsal sutures" are dorsal, ecdysial sutures). Presence of protaspis and terrace ridges were additional, unnumbered characters of that study. Dorsal sutures was a key character of Lauterbach (1980, 1983). Only one or possibly two reversals are present in this cladogram, in character 10 (hypostomal articulation is absent in Eodiscoidea, see text) and 8 (rostral plate may be absent in Eodiscoidea). An alternative (conventional) topology would have Agnostoidea and Eodiscoidea as sister taxa. However, that topology would necessitate reversals in Agnostoidea in all five characters at node 4 and in all three characters at node 5. Although such reversals are in themselves perfectly conceivable, parsimony criteria demand that the topology presented here is preferred. It must be emphasized, that this cladogram is based exclusively on the characters of Fortey and Whittington (1989), with one character, dorsal sutures added. Trilobita, as defined by Fortey and Whittington (1989) includes taxa above node 3, and is defined by one character (calcification). Trilobita, as defined by us, includes taxa above node 4 (supported by five of Fortey's and Whittington's characters). The topology below node 4 would change radically with the inclusion of other characters and taxa, such as those discussed by Walossek and Müller (1990); in particular, Agnostoidea would move towards the base of the cladogram.

ocular suture in "olenellines" is mainly circumstantial, but we tentatively accept it (the view forwarded by Hahn, 1989 that most olenellids were blind is puzzling and contradicts all published evidence; several references herein). Most importantly, the generality of circumocular sutures must be determined with reference to Chelicerata (where this feature is, to our knowledge, absent). The common presence of this character in stratigraphically-early trilobites does not in itself indicate an apomorphic or plesiomorphic condition.

It should be noted that Lauterbach also regarded this character (as part of the dorsal ecdysial suture system) as a synapomorphy for trilobites. Lauterbach suggested that the presence of a suture along the corneal margin is intimately coupled with a calcified cuticle. We would agree that the presence of a circumocular suture is not an independent character, but regard it as more likely constrained by the presence of a calcified visual surface (cornea). In our view, the following hypothesis can be proposed: The occurrence of a calcified cornea necessitated a circumocular suture, to enable the shedding of the cornea during ecdysis. This early phylogenetic stage, represented by olenelloids, was followed by the appearance of a complete ecdysial suture system incorporating the circumocular suture. The cornea thus being shed with the separation of the free cheeks from the cranidium, a separate circumocular suture was redundant, and the calcified cornea was therefore subsequently fused to the free cheek in the vast majority of trilobite groups.

Character 10. The structure of hypostomal articulation is argued by Fortey and Whittington to be a trilobite apomorphy. Homology of the hypostome among Trilobita, as defined by calcification, was supported in the discussion by Müller and Walossek (1987), where they compared the hypostome morphology of agnostids with that of eodiscids and other trilobites. Softening of the hypostome in agnostids was regarded by them (1987) as a secondary loss, but Walossek and Müller (1990) argue in favour of an originally soft hypostomal forehead structure in this group.

It is obviously critical that possible homologues of the trilobite hypostome itself be evaluated in the other groups under consideration. Subsequent to this, the detailed morphology and topological relationships of the trilobite hypostome must be discussed with reference to homologous structures in other groups. Our knowledge of these structures is, as yet, inadequate. Uncalcified forehead structures were identified as true hypostomes (not labra of crustaceans) in Upper Cambrian "precrustaceans" (Walossek and Müller, 1990). A similar structure is present in Nectaspida (*Naraoia*; personal examination; Zhang and Hou, 1985). Again in the primitive merostome *Kodymirus* Chlupáč and Havlicek there is a structure similar to a hypostome possessing wing-like structures; its topological relation to the dorsal shield is unknown. In the recent branchiopod crustacean *Triops* (see, e.g., Eldredge, 1971, text-figs. 4–6, and Jell, 1975b, pl. 1), the distal surface of the labrum is strongly sclerotized and its structure superficially resembles a trilobite hypostome, even having anterior "wings". These "wings" do not, however, articulate against the dorsal shield, and the high sclerotization of the structure is a response to a bottom-dwelling habitat (D. Walossek, pers. comm., 1990). Hypostomes of eodiscids do not articulate against the dorsal shield (Jell, 1975a), nor do those of agnostids (Müller and Walossek, 1987; Whittington, 1988b). This circumstance must be regarded as a secondary loss if the assumption of a "polymerid" ancestry for these groups is upheld (Fortey, 1990). As suggested by Figure 1, this assumption is supported for Eodiscoidea, but not for Agnostoidea.

The presence of a calcified and plate-like hypostome structure thus may appear to be an apomorphy for a Trilobita exclusive of agnostids but inclusive of olenelloids. The above and other identifications are necessary prerequisites to the more detailed testing of the anterior wing in hypostomal articulation. Similarly, discussion concerning the value of spinosity of the larval hypostome, a character cited by both Lauterbach and Fortey and Whittington, is premature.

It may be noted that Bergström (1973a:11) suggested that the intimate relation between the hypostomal anterior wings and the fossulae was a condition serially homologous to the dorso-ventral connection between apodemes and appendages. The fossula was interpreted as S5 and the hypostomal part which includes the anterior wings as representing the "altered remnants" of a preantennal limb. We do know that the anterior wing was in immediate closeness to the ventral surface of the fossula structure. Such a relation is extremely difficult to interpret in terms of the outer surface of the hypostome being completely externally situated, and at the very least the distal parts of the wings must have been internal structures, embedded in soft tissues. Bearing this in mind, Bergström's idea, strange though it may seem at first, is perhaps worth some consideration. If not else, it may serve to stimulate investigation of the possible multisegmental origin of the hypostome (B. D. E. Chatterton, pers. comm., 1990).

It may be concluded that this character can be an apomorphy for Trilobita (*sensu* Fortey and Whittington) only if (1) the absence of articulation in agnostids and eodiscids can be made likely to be secondary losses, and (2) a similar relation between the homologous dorsal and ventral structures in non-trilobites can be demonstrated to be absent.

Other Characters

Fortey and Whittington forward four more characters which they argue may be additional apomorphies for Trilobita. For one of these, a protaspid period in ontogeny, the plesiomorphic absence in Chelicerata is implicit in their discussion. "Olenellines" and nectaspids are not known to have had protaspides. Thus this character might be informative to diagnosing Trilobita *sensu* Lauterbach, but its plesiomorphic absence provides no evidence towards resolving the relationships of "olenellines". The independence of this character is ambiguous, since cuticle calcification is a necessary prerequisite to the presence of a protaspid. The protaspid is itself defined as possessing a calcified dorsal cuticle, so "presence of protaspid" is difficult to separate from "presence of calcification". The former condition does not follow automatically from the latter, but is constrained by it.

A protaspid stage of an eodiscid has recently been discoverd (Zhang, 1989), but agnostids apparently lacked a protaspid stage (Müller and Walossek, 1987). This lack was regarded by Fortey (1990) as a secondary loss. Walossek and Müller (1990) express doubts that agnostids share more than a superficially similar morphology with eodiscids due to similar life strategies, and therefore may not be closely related to a thus restricted Trilobita (exclusive of agnostids but inclusive of eodiscids). In view of eodiscid ontogeny this view needs to be seriously considered, on the basis of this character and the remaining seven characters defining nodes 4 and 5 in Figure 1.

For other of Fortey's and Whittington's characters, the state for the Chelicerata is given as unknown (spinose larval hypostome; terrace ridges on the doublure). The discussion of their second character (cephalic appendages) leaves the reader uncertain as to what aspect is regarded by Fortey and Whittington as a putative trilobite synapomorphy. Three different characters are collectively discussed (presence or absence of first antennae; number of cephalic appendage pairs; limb structure). Fortey and Whittington admit that neither of the latter two characters provides unambiguous support for trilobite monophyly. The presence of first antennae in "Olenellinae", which they suggest weakens Lauterbach's claim for that taxon's relationship with Chelicerata, may not be of the importance they suggest. Lauterbach's hypothesis is compatible with the generally accepted inferrence of loss of antennae in Chelicerata (e.g., Weygoldt, 1986), supported by evidence forwarded by Müller and Walossek (1986), since presence of antennae is symplesiomorphic for the trilobite-chelicerate clade (see also Lauterbach 1989). As Fortey and Whittington indicate, the number of cephalic appendage pairs in trilobites, as well as in the other groups under consideration, is variable and of little use in defining a monophyletic trilobite clade (4 and 5 cephalic appendage pairs are known in trilobites; Bergström and Brassel, 1984). Likewise, Fortey and Whittington state that limb structure affords no obvious synapomorphy for this clade. This view is contrary to previous opinions (e.g., Whittington, 1977, 1985), where the lamellate spines in trilobite exopods were regarded as apomorphic for trilobites. Such spines were later shown to be absent in agnostids (Müller and Walossek, 1987), and if the latter groups is regarded as ingroup Trilobita (as by Fortey and Whittington), it follows that this character cannot be used to define Trilobita. If, however, agnostids are positioned outside Trilobita, the presence of lamellate exopod spines can be forwarded as an apomorphy for Trilobita.

The last of the possible trilobite apomorphies, presence of doublural terrace ridges, is known from, e.g., "olenellines" and eodiscids (Jell, 1975a, pl. 20, Figs. 5, 11, pl. 29, Fig. 2). They are also present in an aglaspidid with calcified cuticle (J. Dalingwater and D. J. Siveter, pers. comm., 1990). Similar structures have been described for some chelicerates (eurypterids; Miller, 1975) although in these there seems to be a morphologic continuum from "terrace ridges" to "lunules" (Selden, 1981). The homology of these eurypterid structures with terrace ridges in trilobites remains to be substantiated. Terrace ridges are, as far as is known, absent in Nectaspida and Agnostoidea. In agnostids the absence may be due to original absence (if agnostids are more primitive than eodiscids; Figure 1), or due to secondary loss (if agnostids are derived from eodiscids, see e.g., Jell, 1975a). The presence of this character in aglaspidids indicates that it is either plesiomorphic for trilobites, or is developed parallel in the two groups (trilobites and aglaspidids). In the latter case it may still be an apomorphy for Trilobita, but, as so many other characters, one that appears to be intimately coupled with calcification. The cuticle composition may well be a constraint to the development of terrace ridges, in that a calcified cuticula is a necessary prerequisite for the formation of these structures. If so, then the presence of terrace ridges can only doubtfully be treated as a character independent from calcification (at the same node).

In this context Briggs' and Fortey's (1989) attempt to cladistically analyse the phylogeny of the major arthropod groups should be mentioned. In Briggs' and Fortey's cladogram nectaspids (represented by *Naraoia*) form the sister group of (*Agnostus* (*Olenoides*+ *Triarthrus*)), i.e., Trilobita as conventionally defined. The latter group (node 25) is supported by (1) calcite [exo]skeleton, (2) eyes on carapace, (3) marginal suture, (4) genal spines, and (5) two trunk tagmata; while node 26, defining (*Olenoides*+ *Triarthrus*), is based on (1) dorsal ecdysial sutures, (2) eye ridges, and (3) [articulating] half-ring. Several of these characters are identical or close to some of those discussed above, and our objections to regarding them as apomorphic at the respective nodes are the same. In spite of this, it is interesting to see that the topology in this part of Briggs' and Fortey's cladogram is identical to that of Figure 1 herein. Both cladograms suffer, however, from being based on characters that need much more analysis before their status at the various nodes can be evaluated.

CONCLUSIONS

Lauterbach's (1983) hypothesis—the exclusion of "Olenellinae" from the conventional Trilobita and this group's placement as a paraphyletic group on the stem lineage of Chelicerata—has been refuted by evidence forwarded by Fortey and Whittington (1989) and in this paper. However, Fortey's and Whittington's (1989) hypothesis, that Trilobita comprises a monophyletic unit inclusive of "Olenellinae", is insufficiently supported by character evidence. Of Fortey's and Whittington's seven characters, only one—dorsal cuticle calcification—would support the Trilobita as conventionally defined (node 3 in Figure 1). Presence of this character in aglaspidids and other taxa universally accepted as non-trilobites weakens its diagnostic value.

Much of the ambiguity of Fortey's and Whittington's characters is caused by the character states in Agnostoidea. The position of this group presents problems, in that calcification is the only one of Fortey's and Whittington's characters that remains as a possible synapomorphy uniting agnostids and other trilobites. Agnostoidea can be placed as a sister group to Eodiscoidea only if a case can be made for reversals in Agnostoidea in all eight characters at nodes 4 and 5 in Figure 1 (one or possibly two such reversals—characters 10 and ?8—are present in Eodiscoidea). In such a topology, the five characters defining node 4 would be additional apomorphies for Trilobita. On the other hand, Trilobita may be equally well defined, by the same five characters, if all the putative "loss characters" of agnostids are interpreted as primary absence, and agnostids are thus regarded as only distantly related to trilobites. The majority of these characters are intimately coupled with calcification. However, we would uphold that this evidence appears to support monophyly of a Trilobita excluding Nectaspida and Agnostoidea, but including "olenellines". Considering the positive evidence (i.e., not loss structures but presence of anatomical features) forwarded by Walossek and Müller (1990), indicating the possibility of a position of agnostids far from trilobites and perhaps close to "stem-lineage" crustaceans, we conclude that substantial evidence can be forwarded in support of monophyly of Trilobita only when Agnostoidea is excluded from this group.

It is our hope that this critique will stimulate rigorous character analyses which might produce valid synapomorphies for grouping taxa within the trilobite-chelicerate clade.

POSTSCRIPT

After this paper was submitted, the article by Hahn (1989) and the reply by Lauterbach (1989), came to our knowledge. Some of the information presented in these papers has been incorporated above, but they raise questions that warrant a more detailed discussion.

Hahn (1989) recognizes a Trilobita of the same extent as that of Fortey and Whittington (1989). Following Lauterbach (1980, 1983), he states that "one can accept the accentuation of facial sutures and of the pygidium as the most important autapomorphies in trilobites". However, Olenellida and Agnostoidea lack dorsal, ecdysial sutures, and we regard this lack as primary. Further, a pygidium (of more than one segment) is absent in Olenellinae and apparently in Emuellida, the two groups generally accepted, also by Hahn (1989), as among the most plesiomorphic trilobites. These features cannot therefore be apomorphic for Trilobita so defined. Hahn recognizes the Eutrilobita of Lauterbach (1980) as a formal subclass of Trilobita, including "Polymera" and "Miomera", the latter synonymous with the conventional Agnostida and including agnostids as well as eodiscids. He further erects the subclass Protrilobita for Emuellida + Olenellida (inclusive of Olenellinae) on admittedly plesiomorphic characters, stating "The Protilobita may be a paraphyletic group, but this does not affect their usefulness in an evolutionary system". We are unable to accept this reasoning, and recognise neither of the groups Protrilobita and Eutrilobita, the former for being paraphyletic, the latter for being polyphyletic (of the included "Polymera" and "Miomera" we regard the latter as diphyletic, including the non-trilobite agnostids).

Some of the weaknesses in Hahn's paper were pointed out by Lauterbach (1989) in an immediate reply. Besides the patronizing and abusive language, Lauterbach's reply suffers from severe methodological deficiencies. It is also regrettable that no distinction is made between hypotheses based on empirical evidence and unverifiable speculation (e.g., "Grundpläne", "Urarthropode").

Lauterbach (1989:201) states that "phylogenetic systematics only can satisfy the requirements for a scientific method". In this he is correct, and it is regrettable that he has failed to realize that all scientific methods must be applied to verifiable data. Lauterbach applies a scientific method to a poor data base, without critical data analysis, and his results are haphazard. He, for example, without questioning accepts the conventional conception of an "Agnostida" including agnostids as well as eodiscids. Like Fortey and Whittington (1989) and Hahn (1989), he also fails to consider nectaspids and other ingroup taxa. For the most part, Lauterbach repeats his previous characters and arguments for positioning members of Olenellida as a sequence of chelicerate stem groups, admitting only that one feature previously used by him, the presence of a "telosoma", needs reconsideration following work by Whittington and Almond (1987).

Our most serious objection to Lauterbach's reasoning is that the status of each of his three "characters" can not be evaluated separately, and that Lauterbach has misunderstood the concept of synapomorphy.

Lauterbach (1989:208) states regarding his character 1 (the spine on the fifteenth thoracic segment in olenellines) that "Only in combination with all the other [i.e., two; our comment] features of this set of characters . . . does the olenelline spine give evidence of the phylogenetic relationships".

Regarding his character 2 (the macropleural third segment in "olenellines"), Lauterbach (1989:207) accuses Hahn of failure to recognize "the salient point", namely that "the occurrence of a macropleural third postcephalic segment in the olenellines in question is regularly coupled with the occurrence of additional specific characters which likewise imply closer phylogenetic relationships of olenellids with the extant chelicerates than with the Trilobita (*sensu* Lauterbach)". Lauterbach goes on to state that "It is this combination of characters . . . which clearly foreshadows features characteristic of the ground pattern of the Chelicerata!".

Lauterbach thus admits that each of his "characters" can not be independently regarded as a synapomorphy uniting "olenellines" with chelicerates. This is in conflict with the essence of phylogenetic systematics, since the status of a synapomorphy can not be conditional to the presence of other synapomorphies. As a consequence, Lauterbach's three "characters" are not independent characters, but are in fact only a single, complex character. Further, Lauterbach's reasoning is similar to that of evolutionary systematics, where combinations of characters, rather than unique apomorphies, are used to characterize taxa. We reject such reasoning.

Lauterbach (1989) repeatedly confuses verifiable evidence with unfalsifiable speculation. In refuting homology between various macropleural segments, he states "There is however no evidence at all for the assumption of such a blocking of the food groove in all the instances where macropleurae do occur on other segments than the third postcephalic ones in olenellids or on various segment in the Trilobita (*sensu* Lauterbach)." Nor has any evidence been forwarded by Lauterbach or other workers indicative of the presence of such a blockage in "olenellines" as was suggested by Lauterbach. On the contrary, the evidence presented under character 2 above refutes the morphological base for Lauterbach's "hypothesis". As a consequence, the latter can neither be used to support claims of homology of this segment with a particular segment in chelicerates, nor can it be used to refute homology between this and other macropleural segments.

In other instances, Lauterbach is led astray by simple lack of information. For example, he attempts to explain the common lack of corneae in Olenellidae by stating "Obviously the cornea of [Olenellidae] differed in composition from the remaining cuticula", apparently unaware of the existence of circumocular sutures.

Finally, it should be noted that, contrary to Hahn's (1989) usage, none of Lauterbach's new taxonomic names are valid in the sense of the ICZN. Lauterbach (1989) patronizes Hahn for his attempts to bring order out of Lauterbach's (1980, 1983) unranked taxonomic names. Hahn need not have made that attempt, since Lauterbach states (1989:202–203): "The IRZN... are still obliged to the systematic ranks of the taxa in the sense of Linnean categories on historical grounds. What is required today is a radical reworking of the IRZN from the point of view of phylogenetic systematics which discards with the now obsolete systematic ranks of taxa and the implications for the naming of taxa".

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