DO TRILOBITES HAVE A TYPICAL ARTHROPOD CUTICLE?

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ABSTRACT. Problems with specimen preparation and diagenesis make it uncertain whether all trilobites had a laminated cuticle. However, in those trilobites that do show laminations, the cuticles are not only heavily calcified but also lack any evidence of microfibrils or parabolic structures. A heavily calcified cuticle lacking parabolic structures is contrary to that of the typical, generalized arthropod cuticle.

ON the basis of a broad study of both exoskeletal microstructure and composition, Teigler and Towe (1975) concluded that the trilobite cuticle does not compare as favourably with the generalized arthropod cuticle as had been thought. They suggested the calcified ostracod carapace as a better over-all comparison. In a recent paper on the cuticle of *Asaphus raniceps* Dalingwater and Miller (1977) have criticized this conclusion extensively. With a view towards clarification, some discussion in rebuttal is necessary.

The main point of contention concerns comparison of the cuticular laminations (laminae, lamellae) in trilobites and in the cuticle of the majority of arthropods living today. Two major questions may be addressed: (1) does the trilobite cuticle always contain laminations, and (2) if so, are these laminations typical of those found in most other arthropods?

At present the answer to the first question is unclear. Dalingwater (1973) observed fine, parallel laminae in nine of the fifteen species he studied but none showing these laminae was figured. Teigler and Towe (1975) reported that only six of the twenty species they studied contained laminations. Examples of both types were figured. Dalingwater and Miller (1977) now report that in all nine of their trilobite species some laminae were seen, but only those in *Asaphus raniceps* were figured. Normalizing these data for those species reported more than once there are twenty of forty-four species which show evidence of laminations. It appears that some trilobite cuticles contain laminations and others do not. Recognizing that other interpretations are possible Teigler and Towe (1975, pp. 140, 144) noted that 'the presence or absence of lamellae in trilobites may be due to genetic factors or to fossil preservation . . .' and tentatively inferred on the basis of their statistically inadequate data that 'Until further work can be done, a genetic control appears to be the major factor in their distribution'. Dalingwater and Miller (1977) have now suggested that diagenesis and/or specimen preparation are the controlling factors involved. Indeed, in his 1973 report Dalingwater was unable to find distinct laminae in about 100 sections of *Asaphus raniceps* from the lower 'Raniceps' Limestone (Haget, Öland, Sweden), whereas Dalingwater and Miller (1977) have now found distinct laminae in all of their specimens from this same locality and horizon. One must agree with them that the absence of laminae from *Asaphus* cuticle in the first report was most likely due to methods of specimen

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preparation. Whether this holds true for other species presently said to lack laminae remains to be demonstrated. It seems fair to conclude from all of this that while distinct laminations in trilobite cuticle may not always be seen, the controlling factors involved have yet to be firmly established. It is likely that each case will have to be decided on its own merits. At present, then, a tentative answer to the first question is: it is not known for certain whether the trilobite cuticle always contains laminations.

But it is the second question that is the more important: are the laminations, when observed, typical of those found in most other arthropods? Dalingwater and Miller (1977, p. 21) argue that they are, stating: 'The laminae and organization of the cuticle... are considered comparable to those of many extant arthropod cuticles.' Teigler and Towe (1975, p. 144) suggested that they are not, stating: '... the absence of parabolic structures (and helical pore canals) indicates that those lamellae that are found are not the same as those normally observed in the typical extant arthropod endocuticle.'

Laminations are obviously not unique to arthropods so their presence alone is insufficient to make valid a close comparison between the trilobite cuticle and that of the typical arthropod. The typical arthropod cuticle has other characteristics which include 'pore canals', parabolic structures, and a general absence of dense calcification with preferred crystallographic orientation. Teigler and Towe (1975) noted that while some trilobites had laminations and some had 'pore canals' *none* had parabolic structure and all with well-preserved cuticle (i.e. not impressions or replacements, etc.) were heavily mineralized with calcite having c-axis preferred orientation. Agreeing that this is unusual, Dalingwater and Miller (1977) have attempted to play down the significance of heavy, preferred calcification noting that, in addition to many ostracods, some cirripedes are also heavily calcified. Yet barnacles are certainly not typical arthropods and the functional significance of a heavily calcified cuticle attributed to the trilobites by those authors is irrelevant to the present problem.

But conceding these points for the moment, we are still left with the parabolic structure so characteristic of the arthropod cuticle. Teigler and Towe were unable to find parabolic structure in any of their trilobite preparations. They described and figured it in *both* fossil crab cuticle and fossil crab tubercles but they were unable to find it in either the cuticle or tubercles of *Phacops rana* similarly prepared. *P. rana* was chosen because it had clear laminations and therefore should have had parabolic structures were they present; i.e. diagenetic obliteration cannot be invoked. Earlier (1973, p. 837), Dalingwater himself observed that '... microfibrils were not seen even in the best-preserved material . . .'. Nor did Dalingwater and Miller (1977) report parabolic structure or microfibrils in any of their newly prepared trilobites. Yet Neville and Berg (1971) found parabolic structure in a Jurassic crustacean and Dalingwater (1975*a*) has figured it in some eurypterids. Dalingwater (1975*b*) has, for another purpose, figured it beautifully from *Austropotamobius pallipes*—the very same extant crustacean whose cuticle he and Miller feel most typically resembles that of trilobites!

If the trilobite cuticle is to be accepted as a typically laminate arthropod cuticle then it should show parabolic structure. A reasonable answer to the second question then is: until parabolic structures can be shown in trilobite cuticle the laminations observed are not those of the typical arthropod cuticle. When *this* feature is clearly demonstrated in several taxa then the general conclusion that trilobites have a typical arthropod cuticle will make better sense. Until then, and with all other things presently known

considered, 'the trilobite exoskeletal microstructure compares more favorably with that of calcified ostracodes than with the typical, generalized arthropod cuticle' (Teigler and Towe 1975, p. 137).

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