PHYLOGENETIC HISTORY OF MAJOR TRILOBITE CLADES IN RELATION TO PALEOENVIRONMENT

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Because trilobites occupied a wide a range of Paleozoic marine habitats they are a good group to examine hypotheses concerning the sites in which new major clades first appear, and their subsequent history of diversification and decline. There are several problems in this endeavour. The first concerns classification. Until a complete phylogenetic classification is available, there is no objective way to assess the equivalence or otherwise of groups which have been claimed as orders. For example, Odontopleurida and Lichida are treated as separate orders in some classifications, but are considered as a single major clade - presumably of ordinal status - in others. Some of the most commonly accepted groups (Olenellida, Ptychopariida) are paraphyletic. The second problem is taphonomic. The first appearance of a major group often coincides with a major extrinsic change, such as a regressive-transgressive couplet. Does the event initiate the novelty, or simply permit it to be preserved? Does such an event "punctuate" the fossil record, such that earlier, ancestral taxa belonging to the same clade go unrecognised?

Trilobites are already paleogeographically diversified when they make their first appearance in the Lower Cambrian. Since trilobites constitute a true clade, this implies an earlier phase of vicariance of dispersal which is not recorded in the rocks. In China, Siberia, North America, and North Africa these first occurrences are in rocks of inshore origin: still earlier trilobites may have had thin cuticles which militated against their being preserved in the highest energy environments where "small shelly" fossils occurred. The groups Olenellida, Redlichiida, Corynexochida, Ptychopariina (?Lichida) appear in the early Cambrian. The earliest polymerids with morphology corresponding to deep water, atheloptic, is latest Lower Cambrian (*Atops*, Australia): there are many such in the mid-Cambrian.

Opinions differ on the classification of Agnostida. Our own view relates Agnostina to Eodiscina, and on this view the early representatives of the clade (Lower Cambrian, China) are inshore compared with later agnostid occurrences, which typify outer shelf to slope. Ordovician agnostids are comparatively rare; the youngest agnostids were not confined to deep water sites.

There is good evidence of early occurrences of Odontopleurida, Lichida s.s., Illaenina, Proetida and Phacopida in shallow water deposits. Evidence from Asaphida is more equivocal. Colonisation of deeper water habitats from shallow is rapid, although not achieved at the same time in each group. The scenario is of repeated production of deeper water forms from shelf taxa rather than wholesale movement of clades into that environment. After the demise of other groups in the late Devonian, for example, in the youngest Devonian and Carboniferous proetides radiated into deep water habitats. But the last trilobites of all in the Permian were shallow shelf inhabitants.