TRILOBITE PALEOBIOLOGY: PAST, PRESENT, AND FUTURE

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The first major international trilobite conference (which also dealt with related arthropod groups) was convened by David Brund in Oslo in 1973. That meeting resulted in a 467 page proceedings volume (Martinsson, 1975) that has become an indispensable reference on arthropod paleobiology. With its abundance of high-quality empirical work and influential ideas, the ongoing utility of “Fossils and Strata 4” is assured, yet it is also a fascinating microcosm of the themes and concerns of paleontology as a whole a quarter of a century ago. Paleobiology blossomed in the late 1960s and early 1970s. Aucology, and particularly functional morphology, dominates the volume, accounting for about one-third of the contributions. Plate tectonics was a relatively recent development in 1973 and, following the lead of Whittington and Hughes (1972), several papers tackled trilobite paleobiography. They vary from a bold attempt to determine oceanic circulation through the Ordovician by Ross to more conventional studies of biogeographic distribution that were aimed at providing further support for concepts of continental drift. There was a burgeoning interest in community paleoecology, and Richard Fortey's (1975) now-classic paper on the Early Ordovician faunas of Spitsbergen was the first to define trilobite “communities.” The volume was rounded out by diverse papers on trilobite anatomy based on material from the Burgess Shale and Beecher's Trilobite Bed, the microstructure of the trilobite cuticle, trilobite eyes, high level classification of trilobites, and various evolutionary themes (character displacement inagnostoids; adaptive radiation in Cambrian trilobites).

The Oslo meeting and its proceedings were by every indication a tremendous success. It is somewhat puzzling, then, that it spawned no sequel. A glance at any volume of the Journal of Paleontology published in the 1990s will confirm that trilobite study still ranks among the most active fields of invertebrate paleontology. Yet while workers on other groups (e.g., brachiopods, conodonts, graptolites) schedule regular conferences to bring their communities together for an exchange of new results and ideas, there have been no specialist meetings devoted to trilobites and related arthropods since Oslo. The time for such an event seemed ripe, and in August of 1997 we co-organized the Second International Trilobite Conference, which took place on the campus of Brock University, St. Catharines, Ontario, Canada. Eighty-five trilobite specialists from around the world gathered for a four day program of talks. In this issue it has been our welcome task to assemble 14 full-length papers derived from those presentations. The content of this issue and a survey of recent papers published elsewhere provide an opportunity to compare current research themes with those of 25 years ago, to consider how they reflect the emergence of new areas of interest in the intervening period, and to look toward the next such meeting, to be held in Oxford in 2001.

Easily the most profound change in trilobite paleobiology, and indeed in systematic biology in general, during the past 25 years has been the emergence and general acceptance of cladistic methodology. At the time of the Oslo meeting, Niles Eldredge (1972, 1973) was the sole trilobite worker to embrace the nascent field of phylogenetic systematics. Nowadays, while still far from routine, cladistic parsimony analyses are commonplace (Adrain, 1998; Adrain and Chatterton, 1994; Edgecombe and Ramsköld, 1996; Hughes and Rushon, 1990; Lespérance and Desbiens, 1995; Lieberman, 1998; Ramsköld and Chatterton, 1991; Sunberg and McCollum, 1997). Cladistic approaches have been successfully applied to longstanding problems ranging from the species-level phylogenies of notoriously intractable families (Adrain and Edgecombe, 1997; Ramsköld and Werdelin, 1991; Westrop et al., 1996) to the high-level classification of major trilobite groups (Fortey and Chatterton, 1988). Herein, Edgecombe and Ramsköld use the spectacular Early Cambrian fossils from China's Chengjiang lagerstätte in a cladistic analysis of perhaps the most basic phylogenetic issue in trilobite study—the systematic position of the trilobite clade and basal arachniform relationships.

As interest in the hierarchical relationships of taxa and the distribution of characters grew, so too did one of the richest sources of phylogenetic data: silicified larval and post-larval ontogenies. Because trilobite hardparts are calcified from an early stage in larval development, it is often possible to assemble nearly complete growth series for the entire exoskeleton. Harry Whittington's classic work (e.g., 1956, 1959) revealed the potential of silicified faunas. Fortey and Owen's (1975) proposal of the order Proetida was among the first studies to incorporate comparative ontogenetic data into phylogenetic analyses, an approach that has continued to lead to fresh insights into the relationships of taxa (Chatterton et al., 1990, 1994). In the past quarter century, Brian Chatterton has taken study of trilobite ontogenies to a new level of understanding (e.g., Chatterton, 1971, 1980; Chatterton and Spey er, 1997). With increases in SEM technology and a growing appreciation that silification is a fairly common phenomenon, ontogenetic work has the potential to unlock many of the remaining long-standing problems of trilobite classification and evolution. In this issue, Chatterton and colleagues illustrate the first fully documented ontogenies of the family Telephiniidae and in the process raise important issues about the composition and ancestry of the order Proetida. Crönier et al. contribute a beautifully described growth series of a Late Devonian phacopid, a group for which early ontogenetic data has been scarce, despite its cosmopolitan distribution.

Paleobiogeography, a major concern of the previous generation of trilobite workers, has apparently lost its luster. This decline in interest perhaps reflects the fact that plate tectonics and continental drift are now core organizing principles of the earth sciences rather than novel hypotheses to be evaluated with faunal data. Cladistic biogeography certainly offers new approaches to problems such as speciation but with few exceptions (e.g., Lieberman, 1997), this avenue of research has yet to be exploited.

Paleoecology is as important as ever but the thrust of research has changed. Functional morphology, one of the core areas of trilobite paleoecology 25 years ago, has ceased to be pursued in any meaningful way. Studies of trilobite "communities" have flourished, but the emphasis has shifted from simple description
to consideration of their macroevolutionary or biostratigraphic significance. This change in focus can be traced to the rise of evolutionary paleobiology, a movement that has led to a wholesale transformation of how paleontologists view their discipline (the inaugural issue of the journal Paleobiology appeared a few months before the publication of the Martinsson volume). As early as 1980 Gould had noted that classical functional morphology and descriptive community paleoecology were waning because they failed to address questions of evolutionary significance. Five years later, “evolutionary paleoecology” had become firmly entrenched in the lexicon of paleontology (Keithell, 1985; see also Valentine, 1973) and is now a flourishing discipline in its own right. Paleoecological studies of trilobites have, and will continue, to contribute to such areas as mass extinctions (Ludvigsen and Westrop, 1983; Westrop, 1989; Chatterton and Speyer, 1983; Owen et al., 1991), evolutionary radiations (Fortey and Owens, 1990; Adrain et al., 1998), turnover rates and coordinated stasis in paleocommunities (Fortey, 1980; Westrop, 1996), and patterns and processes of major biotic transition in the history of life (Westrop et al., 1995; Westrop and Adrain, 1998). Herein, evolutionary paleobiology forms the single largest category of papers in the issue, including studies of trilobite diversity and distribution (Brezinski), turnover and extinctions (Mikulic and Klussendorf; Westrop and Cuggy), biostratigraphy and biofacies (Taylor et al.), and Cambrian macroevolution (Lieberman).

The transformation of paleoecology has been paralleled by a resurgent interest in the ways in which fossil accumulations are formed. At the time of the last international trilobite conference, many participants would have been hard-pressed to define taphonomy, which, if discussed at all, was viewed as an area concerned with the limitations of paleontology (e.g., Lawrence, 1968). Taphonomy has emerged as a vibrant discipline that has stepped beyond this narrow vision (Behrensmeyer and Kidwell, 1985). Trilobite workers have been at the forefront of this new taphonomic research and have demonstrated novel applications of preservational data in paleoecology (Speyer and Brett, 1985) and in sedimentary facies analysis (Speyer and Brett, 1986). More conventional work on the interpretation of trilobite accumulations has also flourished, with contributions ranging from experimental (Hesselbo, 1987; Lask, 1993) and field-based (Speyer, 1987) studies of sclerite orientation and its hydrodynamic significance, to the implications of taphonomic sorting for paleoecologic interpretation (Westrop, 1986; Mikulic, 1990). This issue features detailed taphonomic studies of two Late Ordovician trilobite assemblages: Hughes and Cooper look at a calymenid-dominated deposit from the Kope Formation of Ohio, while Brett and colleagues examine the famous Walcott-Rust Quarry of New York State along with providing a much-needed modern overview of the fauna.

Morphometric analysis of trilobites was completely absent from the Martinsson volume (with the exception of Temple’s plea for a standardization of trilobite measurements), but has become a growth industry in recent years, with contributions ranging from comprehensive surveys of the group as a whole (Foote, 1991, 1993), to detailed investigations of a single species (Hughes, 1994; Hughes and Chapman, 1995). The expansion in morphometric approaches must stem in part from the advent of fast computers and software packages that make even the most arcane multivariate technique readily accessible. However, it also reflects the increased interest in evolutionary problems such as patterns of morphospace occupancy over time and the evolutionary significance of morphologic variability. Detailed morphometric analyses are carried out by Webster and Hughes on the marked distortions introduced by compaction preservation, even when the preservation of detail is very fine, and by McCormick and Fortey in an attempt to prove the species identity of widespread geographic occurrences of a pelagic Ordovician trilobite.

Two papers reflect a continuity of scholarship rather than the departures of the past two decades. Dalingwater et al. continue their work on the exquisitely preserved ultrastructure of Silurian trilobites, a series that extends naturally from the senior author’s papers in the Martinsson volume. Fortey and Droser, using field-based descriptive paleontology, show that trilobite biostratigraphy and systematics have much to contribute to debates about major international stratigraphic boundaries, with their unexpected finds immediately above the Ibexian-Whiterockian boundary in the Great Basin.

Given the changes in emphasis in trilobite studies over the past quarter-century, looking ahead even a few years is a risky business. In 1975 nobody would have predicted the decline of functional morphology and paleobiogeography. Based on current trends, cladistics is likely to remain the method of choice in systematics and phylogeny reconstruction. We expect increasing numbers of trilobite workers to incorporate morphometric techniques into their studies, and we would be surprised indeed if the current emphasis on evolutionary paleoecology and taphonomy became reversed in the foreseeable future. However, we would also be surprised if the future did not bring some new developments, and the Oxford Conference of 2001 will provide another opportunity to gauge current trends in trilobite paleobiology.

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REFERENCES


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