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Trilobites: an ongoing story

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Trilobites are among the most diverse of fossil invertebrates, and although they have been collected and studied for more than two centuries there is no sign that the discovery of new taxa is slowing down. The range and versatility of their morphologies continue to pose challenges to interpretation of their modes of life, while the appeal of well-preserved articulated specimens ensures that they are sought after by collectors as interested in their beauty as in their scientific importance. This issue of the *Journal of Paleontology* gathers together a selection of trilobite-focused papers exploring new discoveries and interpretations, and this introduction offers a few reflections on some of the issues they raise.

For some years, Jonathan Adrain and his colleagues have been describing the Early Ordovician trilobites collected in the Great Basin from magnificent, silicified material, the latest tranche of which appears in this issue, following a tradition established by the great Harry Whittington's pioneering studies in the Appalachians. The extraordinary perfection of preservation and detail offered by these trilobites – particularly Bathyuridae – probably offers the nearest thing we have to recognition of 'true' biological species among the trilobites. At the same time, this material points up the limitations of the usual preservation of 'crack out' material, let alone those historical collections including taxa based on flattened and even distorted specimens.

Since students of trilobites are obliged to follow the code of the *Rules of Zoological Nomenclature* (ICZN, 1999), imperfectly preserved types frequently carry the naming priority, which we have to respect. We often have to spend as much time discussing the limitations of crushed or incomplete cranidia and pygidia as we do when we describe new and better-preserved discoveries. It can become an unwieldy and lengthy process. Nonetheless, unscrambling these complexities eventually pays dividends, as this meticulous work in Nevada shows. The radiation of the Bathyuridae in Ordovician Laurentia is set to become as remarkable as that of the Calmoniidae during the Devonian of Gondwana.

As far as field preservation of trilobites is concerned, the distorting effects of flattening sclerites in sedimentary rocks alter many details of facial sutures and the apparent width of preglabellar areas or pygidial borders. Jikhan Jung and his colleagues have utilized manipulations of 3-D simulations to understand the changes in proportions that accompany preservation of exoskeletons in sediments. Perhaps this will provide an objective way to deal with the kind of preservation differences that have proved so difficult to evaluate in taxonomy. In the past, species have been distinguished on the basis of subtle features of the divergence of facial sutures that may be no more than preservational artifacts.

A preoccupation with *Konservat-Lagerstätten* faunas over the last two decades has perhaps tended to eclipse the importance of trilobites in biostratigraphy, yet their rapid evolution and frequently wide distribution has ensured their position in the Cambrian as prime paleontological 'chronometers' for that period in particular. Fine-tuning of this timekeeping continues, and trilobites maintain their crucial importance as their fossils can be recovered from formations otherwise lacking rocks suitable for other methods of dating. Discovery of such faunas depends on old-fashioned fieldwork and demonstrates that new discoveries are regularly made in what might be considered familiar territory. This volume includes a paper by Foster and colleagues on some hitherto inadequately known mid-Cambrian strata in the Uinta Mountains of Utah, while Webster and Caron document an older (Stage 4), olenellid-dominated fauna of the Cranbrook Lagerstätte, British Columbia. Such papers follow in a classical tradition and are permanent contributions that provide the necessary ground-truth for constraining future hypotheses – the latter change as scientific priorities develop but the specimens remain to anchor future speculations. It is just as important to link the trilobite narrative into newer methods of temporal calibration, as Sundberg et al. demonstrate with regard to the now well-known Steptoean Positive Isotope Carbon Excursion (SPICE). A section in Smithfield Canyon spanning the Nounan Dolomite and the lower St Charles Formation documents the trilobites that indicate the local expression of a marker interval that has now been recognized in all paleocontinents in later Cambrian strata.

It is crucially important that such trilobite collections are curated in permanent institutions to provide for their future interrogation. Workers yet to come should be free to re-determine previous identifications. For example, in my own institution in London, the huge (non-type) Cambrian collection of the late Franco Rasetti includes many specimens that are formally topotypes, identified by Rasetti himself, and many of these await revision by subsequent researchers. They certainly include free cheeks that Rasetti never figured. In the meantime, they are in safe keeping.

The abundance of trilobite fossils compared with those of other arthropods has meant that they have played a prominent part in the analysis of ancient marine habitats. Recognition of distinct assemblages of trilobite taxa in relation to paleoenvironments has contributed fundamentally to reconstructions of ancient terranes and paleocontinents, and in plotting the controls on temporal shifts of biofacies, frequently bearing a relationship to patterns of extinction. Once again, this relies on long-term fieldwork in logged sections, and it is acknowledged that studies of this kind owe much to the example of "Pete" Palmer and his

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successors in unscrambling the history of Cambrian "biomeres" in studies published during the latter part of the last century. In this volume, the extinction event at the boundary between the Steptoean and Sunwaptan stages is explored in detail. This study by S.R. Westrop and his colleagues spans a wide geographic area of North America, testifying to years of careful collecting in the field to build up a temporal understanding. The general model of extinction at this boundary still applies, coinciding with deepening and on-shelf movement of oxygen-poor waters—the accompanying, often homogenized and impoverished trilobite faunas lying at the base of subsequent on-shelf speciation. However, Westrop et al. demonstrate that a more nuanced understanding is possible, since Oklahoma sections display an exceptional abundance of brachiopod-rich deposits at the same time as the low-diversity *Taenicephalus* fauna in Nevada. Clearly, environmental interactions were more complex than we thought. It is also worth noting the great similarity of the generalized, Olenid-like trilobites such as *Taenicephalus* that are associated with dysaerobic habitats at Laurentian later Cambrian stage boundaries, although they are assigned to different genera: could this taxonomic subdivision just be a stratigraphic artifact?

The pattern of environmental controls on the Laurentian paleocontinent continued into the earlier half of the Ordovician, as recent work in the Great Basin has demonstrated, but deeper-water trilobite biofacies are distinctly rare despite the huge area over which Ordovician strata crop out. Fortey et al. demonstrate herein that such an Early Ordovician fauna does indeed exist in graptolitic strata well to the west, in the Inyo Mountains of California. Apart from on the Arctic island of Svalbard, which is very rich in the trilobites that dominated my early work, marginal biofacies are rarely encountered around the early Ordovician Laurentian paleocontinent. Yet spotty evidence from British Columbia and Alaska suggests that tectonics have not entirely erased the fossil record of such trilobites on what is now the western side of North America, and an expedition to the Seward Peninsula, Alaska, might well yield interesting results.

The Family Olenidae is probably the most widespread of those trilobites found in deep-water biofacies, comparable only to some agnostids. The present volume includes two examples consistent with this biogeographic independence. Ghobadi Pour et al. describe a late Cambrian (Furongian) fauna from Iran including the olenid *Parabolina* (*Neoparabolina*) *frequens*, a widespread species that extends almost globally in the right facies, and in Iran unsurprisingly coinciding with a deepening event. Other benthic trilobites, also mostly widespread, accompany it, including that attached to my least favorite replacement name for a favorite one preoccupied – *Indiligens* Ozdikmen replacing *Hospes* Stubblefield, a miniature trilobite originally described from Shropshire, UK. The Olenidae were the subject of one of the great trilobite monographs by Gunnar Henningsmoen published in 1957 and continue to supply important stratigraphic information alongside a particular paleoenvironmental signature.

Trilobites have a remarkable propensity to evolve similar morphologies repeatedly from origins rooted in separate clades. One of the challenges of trilobite systematics and taxonomy is to distinguish these homeomorphic traits to determine true phylogenetic relationships. Paedomorphic processes have commonly operated to produce taxa that achieve maturity at a small size. In some cases, suppression of release of thoracic segments is obvious—the example comes to mind of the Ordovician Gondwanan raphiophorid *Taklamakania* with three thoracic segments compared with the five or six of its many relatives. Handkamer and Pratt examine an intriguing case of two 'miniaturized' corynexochids from the middle Cambrian Mount Cap Formation, which they claim underwent rapid parallel paedomorphic evolution within separate clades in response to particular paleoenvironmental conditions in one site. Whether such rapid 'offshoots' merit separate generic recognition as claimed is an interesting question. At a higher taxonomic level, James Beech and colleagues re-examine the origins of the 'trinucleomorphs' using parsimony methods to confirm that 'perforated fringe' harpetids and trinucleids are indeed separate clades despite their outstanding convergent characters. Interestingly, these authors find evidence that trinucleids were part of the Order Asaphida as claimed in the first-ever cladistic analysis of trilobite phylogeny by myself and Brian Chatterton in 1988; a recent claim that 'Trinucleida' is a separate order is not supported.

Finally, as always, there is taxonomic revision. New collections often prompt reconsideration of taxonomy, and Pereira et al. have re-evaluated a Moroccan late Ordovician fauna with the beautiful large trinucleid *Declivolithus*. While confirming the close similarity of this fauna to a contemporary one from Bohemia, there are taxonomic differences from a previous treatment, mostly concerned with comparisons with the older European type material—a familiar problem. Shrivasta and Hughes offer a detailed quantitative study of the late Cambrian *Walcottaspis* including its field occurrence, variation, and its relationships to the well-known *Dikelocephalus minnesotensis*. It is a fitting bow to C.D. Walcott, the pioneering giant of Cambrian studies in North America.

Recent studies of lower Paleozoic arthropods have tended to focus on the early evolution of the phylum, especially with regard to the plethora of 'soft bodied' taxa that have proved that trilobites were but one of the clades that emerged from the Cambrian evolutionary 'explosion'. After marveling at the diversity of the Chengjiang fauna, we are now accustomed to visualizing those early seas as thronging with arthropods, with trilobites only more visible as fossils because of their calcified exoskeleton. However, that very visibility and abundance as fossils means that trilobites continue to offer possibilities for quantitative studies through time series that cannot be reached through *Konservat-Lagerstätten* alone. Studies such as that of Patterson et al. (2019) require input from systematic studies carried out over many years. Extinction patterns need input from data across critical boundaries, which can only be derived from prolific collections of fossils with preservable hard parts. It is to be hoped that this volume will encourage future students to value the morphological complexity and abundance of trilobites for tackling scientific issues, as well as appreciating their beauty, extraordinary variety of form, and speculating on their life habits.

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