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The Burgess Shale, retrospect and prospect

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Abstract. A brief account is given of events and influences that preceded my being invited to lead the palaeobiological reinvestigation of the Burgess Shale. Joining these studies were D.L. Bruton and C.P. Hughes, subsequently D.E.G. Briggs and S. Conway Morris at Cambridge, in Oslo, and in the National Museum of Natural History, Washington, D.C. The geological setting of the Shale was first revealed by W.H. Fritz. Concomitant studies of Precambrian fossils, trace fossils, small shelly fossils of the early Cambrian, and new discoveries of soft-bodied biotas in China, Sweden and Greenland, have stimulated thought on evolutionary processes, and given rise to the concept of the Cambrian explosion.

In looking forward I comment on the importance of new investigations on taphonomy, and the promise they have for deeper understanding of what is preserved in the fossils, and of how they may be better prepared for study. The description of *Anomalocaris* revealed that predation by larger animals was a factor in palaeoecology from the early Cambrian onwards. Geochronology has shown the relative brevity of the Middle and Upper Cambrian, and I suggest that the transition from these times into the Ordovician may present as great a challenge in the understanding of evolutionary events as does the earlier Cambrian explosion. Despite the sporadic nature of the fossil record, new collections and new approaches give palaeontology a great opportunity to continue giving its unique contribution to the understanding of how evolution proceeded.

Key words: Cambrian to Ordovician evolution, predation, taphonomy

Introduction

I am greatly honoured to have been awarded the International Prize for Biology in 2001, and hope that all palaeontologists will be pleased that the contribution of their studies to biology has been so recognized. It is palaeontology that provides the most accurate means for the relative dating of sedimentary rocks and of correlating them within and between continents, and so provides the evidence of evolution in animal and plant communities in successive environments.

When I retired from the Woodwardian Chair in 1983 much systematic work on the Burgess Shale fossils had been published, and I was able to complete my general account (Whittington, 1985). I had then to turn to my long-held commitment to organize work on the revision of the Trilobita for the *Treatise on Invertebrate Paleontology*, and to research in this connection, which has resulted in publication of the first volume (Kaesler, 1997). Hence I can only reflect here on past years, and comment on points that appear significant to me in the many studies which took place then and in more recent years.

Retrospect

The remarkably preserved animals and sea weeds of the Burgess Shale, made known by Charles D. Walcott between 1911 and 1931, were hardly mentioned when I was a student in the mid 1930s. That was long before the late Precambrian Ediacara fossils were described, and interest in Precambrian microscopic fossils was reawakened by finds in cherts of the Gunflint formation (Barghoorn and Tyler, 1965). In 1949 I came to teach at Harvard University, and joined the staff of the Museum of Comparative Zoology. I continued to visit the U.S. National Museum (now the National Museum of Natural History) in Washington, D.C., where I was able to photograph some of Walcott's type specimens. At that time, in the old building, the vast bulk of Walcott's collection was virtually inaccessible, stacked high up in large and heavy drawers, and had never been examined in any detail. At Harvard is the collection made from the Burgess Shale by Percy E. Raymond in 1931, and in 1962–70 the studies of Alberto M. Simonetta were published. These had intriguing new restorations of the animals, but the evidence for them was not brought out clearly, particularly by the accompanying illustrations. The specimens in the Walcott collection had been left just as they had been split from the

layers, usually without the counterparts, and not prepared from the matrix. Thus the Burgess Shale specimens were known largely from Walcott's photographs, but no species was understood from a series of prepared specimens described and interpreted in detail. Further, the geological setting and stratigraphy of the famous Phyllopod Bed of Walcott's quarry, and of the layers above it which had been collected by Raymond, were not well understood, though Rasetti's (1951) work had elucidated the zonal succession. Discussion of these matters with the palaeontologists of the Geological Survey of Canada, led then by Digby J. McLaren, resulted in my being invited to lead the palaeobiological investigation which was to follow a reinvestigation of Walcott's quarry and the surrounding area. So came my participation in 1966, in the party under the dynamic leadership of James D. Aitken, which David L. Bruton joined in 1967. Mrs Dorothy Whittington, companion and ardent fellow collector in all my fieldwork, was with the party both years as we split the productive layers in Walcott's quarry, and those from the higher beds which we called the Raymond quarry.

In the autumn of 1966 I came to the University of Cambridge, where I began studies of arthropods. Inspiring and encouraging me was the imaginative work on Triassic fossil scorpions (Wills, 1947) and on palaeogeography by my first teacher, L.J. Wills, at Birmingham University, and the sterling example of the long hours spent in preparing and photographing fossils by G. Arthur Cooper in the U.S. National Museum. At a conference held at the Museum of Comparative Zoology (Whittington and Rolfe, 1963), I had listened to arthropod workers' debates, and met for the first time Sidney M. Manton. She later spent many hours explaining to me her work, particularly on such vital matters of arthropod biology as how limbs were used in walking, catching food, macerating it and bringing it to the mouth.

The most abundant arthropod (some 15,000 specimens) in Walcott's collection is *Marrella*, on which I began my work by looking at, even cursorily, all the specimens, and then choosing a particular sample to illustrate my account. In order to compare the specimens, I drew them using the attachment to the microscope known as the camera lucida. This is a salutary procedure that forces one to look at a specimen carefully, and reveals the different levels at which parts of the body lie in the shale. It also revealed distorted, asymmetrical specimens, and the varied attitudes in which they lay in the shale - in dorsal, lateral, ventral and oblique aspect. Having observed slump structures in the quarry sediments, I explained these orientations as resulting from the live animals having been engulfed in a cloud of suspended sediment, and buried in varied attitudes by the sediment as it settled out of suspension. Obliquely orientated specimens were distorted by subsequent compaction

of the shale, but in spite of this apparent disadvantage, the specimens preserved in different attitudes enabled a more accurate reconstruction of the animal. The stratigraphical studies by William H. Fritz (1971), a member of Aitken's party in both years, first elucidated the geological setting of the Shale, showing how it had accumulated against the scarp wall of the Cathedral Limestone, eventually extending over this wall, and being succeeded by younger strata. This discovery, and subsequent work which revealed the extension of the scarp to the north and south of the quarry area, made clearer the deeper water, off-bank environment in which the shale was laid down, and supported interpretations made from the way the fossils are preserved.

The detailed study of *Marrella* (Whittington, 1971) was illustrated by photographs faced by explanatory camera-lucida drawings, a method used in all our monographs. Publication of the work, first by the Geological Survey of Canada, was later greatly aided by generous support from the Royal Society of London. The initial study on *Marrella*, in revealing the manner in which the fossils were buried and preserved, helped us all in the preparation and interpretation of the specimens. It also made me aware of the immensity of the task of investigating in detail the fauna and flora of the Burgess Shale. I have said "our" work, for I was joined in my studies by David L. Bruton in Oslo and Christopher P. Hughes at Cambridge, and I was very fortunate at Cambridge to have two such gifted research students as Derek E. G. Briggs and Simon Conway Morris. We all worked in the newly built wing of the National Museum of Natural History, to which the Paleobiology Department had moved. Every facility was given to us by the Collection Manager, Frederick J. Collier, the entire Walcott collection being readily accessible for the first time. Most of the arthropods, worms, and some of the problematic animals have been redescribed in detail, and a monograph on the sponges contributed by J.K. Rigby (1986). New work on the algae has not been published, so that after some forty years some investigations remain unfinished.

I have looked back at how the work of the Cambridge team came about, and some of the influences behind it, and touched on some of its results. Before and during those years many other investigations were in progress - on microscopic and macroscopic Precambrian fossils, on trace fossils, and on the variety and nature of small shelly fossils in the early Cambrian. The great new finds in Cambrian strata of soft-bodied fossils in China, in Sweden and in Greenland were being added to our knowledge. Organic geochemistry and molecular biology were making spectacular progress. To assess, against this extensive new knowledge, the significance of the Burgess Shale work on the manner and rate of evolution is a formidable task. Stephen J. Gould (1989) drew the attention of a wide public

to it, in a challenging way. A later account of the work (Briggs *et al.*, 1994) gives excellent new photographs and restorations of the fossils, and Conway Morris (1998) considers many aspects of the newer work in providing a different message from Gould on the significance of the Burgess Shale. A clear case is made for what is referred to as the Cambrian explosion, resting on the evidence of trace fossils, as well as that of the Burgess Shale and Chengjiang (Hou *et al.*, 1999) biotas. The complex nature of this explosion, the rate at which it happened, the triggers that caused it, are all questions which have yet to be unravelled.

Prospect

In reflecting on the endeavours of the past half-century in finding and studying exceptional Cambrian faunas, I comment on the following points:

Preservation and methods of study

The great majority of specimens described from the Burgess Shale come from the Phyllopod Bed of the Walcott Quarry, where preservation is exquisite. These individuals were buried in the manner described above, in the post-slide environment of Conway Morris' (1986) detailed analysis. Bruton (2001) refers to this preservation, but also describes an example of in situ burial of a death assemblage, which may have come from the Raymond Quarry higher up in the Shale. In these layers preservation is less perfect than in the Phyllopod Bed. Our preparation of all the specimens has been mechanical, dissection of the shale using a vibrating needle. How powerful methods of acid extraction may be on the Burgess Shale and other rocks has been shown by Butterfield (1990) and Butterfield and Nicholas (1996), and it is probable that wider use of these techniques will give much new information. Welcome also are the studies of taphonomy by Briggs and his colleagues, which have revealed how rapidly soft parts may decay (Briggs and Kear, 1993a,b) and have explored conditions under which mineralization of such parts may take place. In special conditions muscles may be replicated in calcium phosphate (Briggs and Kear, 1994; Briggs, 1995) or limbs preserved by lining with pyrite crystals. The timing of preservation of particular parts of the animal may also be important. Apatite fillings of the anterior portion of the gut in *Leaenochilia* (Bruton and Whittington, 1983, p. 571) and similar fillings in *Anomalocaris* (Whittington and Briggs, 1985, p. 584, figs. 31, 59), related to the somites and extending across the body, may have resulted from diagenesis of the gut and its diverticulae (Butterfield, 2002). These fillings are uncompressed, hence must be products of early diagenesis, and formed before compaction had progressed to its final stage. This research, although

in a preliminary stage, strongly indicates that more detailed study of exactly what is preserved, and in what manner, is needed in these exceptional occurrences. The results of further work will help in both deciding appropriate methods of preparation and in the interpretation of the specimens.

Predation

The description of *Anomalocaris* (Whittington and Briggs, 1985) and our interpretation of how the animal behaved brought a new dimension into Cambrian palaeoecology, that of predation by a large animal. The ingenious model maker used by NHK (the Television Company of Japan) demonstrated, with a life-sized model, how the animal may have swum in search of its prey, by wave-like movements of the lateral flaps, as we had suggested. A second model with movable anterior appendages and jaw plates demonstrated how plastic replicas of trilobites could be seized and bitten, in a manner similar to the healed injuries that have been described (Rudkin, 1985; Briggs and Whittington, 1985; Babcock, 1993). It was a rare privilege for Derek Briggs and me to see working models confirming the hypotheses that had been derived from study of fossil material.

Finds of anterior appendages have shown that *Anomalocaris* was widespread in Early and Middle Cambrian time, and Desmond H. Collins, in publication (1996) and informal talks, has made clear that other types of anomalocaridids are present in the Burgess Shale. In the Chengjiang fauna (Hou *et al.*, 1999) the grasping appendage and a partial specimen of a different species of *Anomalocaris* occurs, and other grasping appendages are also known. *Parapeytoia* appears to be a different predatory animal with a grasping appendage and biramous limbs on the body; no trace of such limbs has been observed in any specimen of *Anomalocaris* in the Burgess Shale. Large predatory animals were evidently more varied than we yet understand.

Geochronology and Cambrian-Ordovician transition

Before I began to work on the Burgess Shale fossils, my research had concentrated on Ordovician trilobite faunas, and I used to think in terms of a very long preceding Cambrian period - remote events long before the earliest Ordovician. Now (e.g. Gradstein and Ogg, 1996; Bowring and Erwin, 1998) we know this was not so, that the Middle and Upper Cambrian were each of a duration similar to that of the Tremadoc Series, and that each was of shorter duration than the Arenig Series. In addition are the uncertainties in correlation of strata at the Lower to Middle Cambrian boundary (e.g. Shergold, *in* Kaesler, 1997, p. 306), so that the Chengjiang and Burgess biotas may not be widely separated in time, and may have flourished only some 20 or 25 million years before the earliest Ordovician.

In trilobites, for example, Fortey (*in* Kaesler, 1997, p. 289, fig. 216) has emphasised the enduring character of family level taxa in Ordovician and younger rocks. Many of these families are present in the earliest Ordovician, the Tremadoc Series, but their ancestors in Cambrian strata are unknown with any certainty, and family-level taxa of the Upper Cambrian are much in debate. This situation, of clearly defined, burgeoning groups in the Ordovician and younger rocks, and uncertainty in knowledge of their Cambrian forerunners, may also be characteristic of other invertebrate groups, such as molluscs and echinoderms. Evolution during the transition from Cambrian to Ordovician time may present as great a challenge to our understanding as does that of the earlier Cambrian explosion. Again we have to ponder the mechanisms that were at work. The role of heterochrony in the evolution of trilobites has been described by McNamara (1986). His contention that peramorphosis was the dominant factor in the heterochrony of post-Cambrian trilobites, in contrast to the dominance of pedomorphism in Cambrian trilobites, needs further examination. The study of ontogeny in trilobites (Chatterton and Speyer, *in* Kaesler, 1997) has shown that each major group has a distinctive early growth stage; more finds of early growth stages of Cambrian trilobites may clarify relationships, and hence the composition of the major groups. A clearer understanding of pattern and process in the evolution of trilobites may have wider implications, at least in helping to resolve the problems of arthropod evolution.

Conclusion

In 1966 Walcott's quarry was clearly recognisable, particularly the back wall, from his photographs, made 50 years earlier. Now, as a result of the quarrying by the Royal Ontario Museum parties led by Collins, the appearance has greatly changed. Major new collections comprise a great treasure house that awaits detailed studies, using different and new techniques, with a better understanding of the geological setting of the Shale, and of taphonomy. The work on the Burgess Shale fossils, on the Orsten, Chengjiang and other new discoveries, has led to recognition of a Cambrian explosion, but what evolutionary processes were involved in this event are as yet unclear and much debated. The Cambrian to Ordovician transition may, as I suggest, conceal at present an equally challenging problem in evolutionary events. The work of Robison (1991) helped to demonstrate that the Burgess Shale biota was widespread in the outer shelf environments of the Laurentian continent, and the Sirius Passet fauna gives an earlier glimpse of such biotas. Living in an apparently shallower-water, shelf environment of Gondwana (Babcock and Zhang, 2001; Babcock *et al.*, 2001) was the Chengjiang

fauna, also arthropod dominated, with some taxa in common with the Burgess Shale. In between these regions was the shelf environment of Baltica, with its very different, younger, but again arthropod-dominated Orsten assemblage. Our larger samples of the Cambrian soft-bodied biota are thus widely separated geographically, from different environments, and preserved in disparate ways, the typical sporadic, incomplete samples afforded by the fossil record. Despite this characteristic nature of the record, palaeontology has much further to contribute to understanding Cambrian marine life and its evolution, particularly in detailed studies and the search for new evidence.

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