Report on the Edinburgh Geological Society's James Wright Memorial Lecture 13 March 1996

BURGESS SHALE FAUNAS AND THE EXPLOSION OF CAMBRIAN LIFE

presented by Professor Simon Conway Morris, FRS University of Cambridge

Professor Conway Morris was welcomed and introduced by the President of the Edinburgh Geological Society, Dr David Land. Members from both the Edinburgh and Glasgow geological societies made up the audience.

One of the most remarkable events in the history of life is the enormous evolutionary radiation of animals, colloquially known as the Cambrian "explosion". Although most obvious from the sudden appearance of fossil skeletons, it is now clear that this event involved much more than simply the acquisition of hard parts. Prior to this event the first reliable evidence of metazoans in the fossil record are the Ediacaran faunas, which appeared abruptly around 640 Ma (Vendian). These biotas are almost entirely soft-bodied and are known from South Australia, southwest Africa, England, Newfoundland, Scandinavia and Russia. The widespread occurrence and locally abundant preservation of soft-bodied fossils is unusual in comparison to the Phanerozoic where soft-part preservation is sporadic and usually reflects unusual combinations of preservational circumstances such as catastrophic burial or anoxic conditions, or both. An absence of predators and scavengers and the restricted degree of bioturbation during Ediacaran times is the most likely reason for the widespread soft-part preservation. The increasing levels of bioturbation and sediment disturbance during the Phanerozoic may explain why most of the major marine Lagerstätten are confined to the Palaeozoic. The majority of the Ediacaran forms appear to be enidarians. Stalked forms with an expanded leaf-like body such as Charnodiscus invite comparison with the pennatulaceans (sea-pens). Other organisms include a possible annelid worm, arthropod-like forms, and others of unknown affinity. In a reappraisal of the Ediacaran fauna, Seilacher proposed that they represent an entirely separate group, possibly a distinct kingdom.

Whatever the disagreement surrounding the biological affinities of the Ediacaran fauna, it is clear that they lacked skeletal material, the widespread appearance of which heralded the Cambrian Period at around 560 Ma. The advent of abundant skeletal parts composed of calcium carbonate, calcium phosphate or silica, which together provided for the first time in the history of the earth an adequate fossil record. Two major schools of thought exist on the rise of skeletal faunas:

- 1 Changes in the physiochemical environment Close to the Precambrian—Cambrian boundary there is evidence for substantial changes in ocean chemistry, such as stable isotope variations (particularly Sulphur and Carbon) and the widespread episode of phosphogenesis. Major rifting events and the break-up of the late Precambrian supercontinent with the consequent transgression may have also played a part. The extent to which these physical and chemical changes affected evolutionary events is, however, far from clear.
- 2 Ecological reasons Many groups possessed tightly interlocking sclerites or valves that enclosed or allowed retraction of soft parts; these features would seem to be a response to predation. This is also suggested by the marked rise in the variety of trace fossils close to the Vendian-Cambrian boundary which reflects expansion in behavioural patterns such as hunting strategies, methods of locomotion and ability to penetrate substrates. However, trace fossils have the disadvantage that the identity of the maker is seldom revealed, and that similar traces can be made by very different animals.

The magnitude and abundance of the Cambrian explosion is made apparent by the examination of the exceptionally preserved Burgess Shale-type faunas where soft bodied animals account for the great bulk of species and a vast range of animal types are present. Some of them relatively familiar, such as arthropods. Others, however, to our eyes look decidedly strange and seem to pose major problems in evolutionary interpretation.

The richness and diversity of Cambrian life is most vividly expressed in the Burgess Shale and similar deposits from areas such as North Greenland and South China. The spectacular Burgess Shale fauna was discovered by Charles D Walcott in 1909 and in the following ten years or so he collected over 65 000 specimens from the Phyllopod bed, the most prolific source of fossils in the Walcott Quarry, British Columbia. In 1966-7, an expedition led by H B Whittington reopened the quarry. The Burgess Shale (an informal unit in the Stephen Formation) is a Middle Cambrian basinal sequence of mudstone and siltstone that was deposited beside a carbonate reef forming a vertical escarpment. Most of the fauna lived on the mud surface, and in the water column above, at the front of the escarpment. They were overwhelmed by a weak turbidity current of fine sediment and transported a short distance down-slope to probable anaerobic, H₂S-rich environment.

At Walcott quarry the fauna is exceedingly rich and diverse being represented by about 120 genera, mostly monospecific. Twelve major groups are present: arthropods, polychaete annelids, priapulids, sponges, brachiopods, molluscs, hyoliths, echinoderms, chiodarians, chordates, hemichordates and incertae sedis. There is also a flora which includes cyanobacteria, red and green algae and acritarchs. The fauna is dominated by relatively few taxa, some nine species

account for 90 per cent of the total. Arthropods dominate the benthic fauna, but only a small fraction are trilobites. Many of these arthropods have walking appendages preserved. Early examples of the four main arthropod groups (Uniramia, Crustacea, Chelicerata, and Trilobita) are represented. These include Aysheaia, a caterpillar-like creature with some resemblance to modern onychophoran Peripatus which lives in the jungles of Brazil, and the common Canadaspis which is regarded as the earliest positively identified crustacean. But many of the arthropods have no modern relatives e.g. Opabinia with its elongated segmented body and five eyes. Other animals include Pikaia, a segmented wormlike creature which is probably the earliest chordate, and Hallucigenia which is probably an armoured lobopod. The Phyllopod bed also yields a number of pennatulacean-like animals that are similar to some Ediacaran taxa. Evidence for predation in the Burgess Shale fauna comes from mouth parts and gut contents. Entire hyoliths have been found in the gut of Ottoia (priapulid worm). Indirect evidence for predation comes from the enigmatic Wiwaxia which has a protective coat of sclerites and elongate spines which were presumably used to deter attack.

A locality in North Greenland has recently yielded an exceptional soft-bodied fauna from the Lower Cambrian Buen Formation. The lithologies present, black shale and dolomite are similar to those of the Burgess Shale. Lightly skeletalised arthropods dominate the assemblage, but it also includes polychaete and priapulid worms, sponges, palaeoscolecidans, simple trace fossils, and most significantly, articulated halkieriids. rior to this find halkieriids were known almost entirely from isolated sclerites and from reconstructions taking clues from *Wiwaxia corrugata*, a Middle Cambrian descendant form. The articulated specimens seem to belong to a single species assignable to *Halkeria*. In addition to around 2000 sclerites per specimen, there is a prominent shell at either end of the body. The presence of these shells and the accretionary mode of growth suggest the halkeriids are related to the molluscs and are a possible precursor to the brachiopods. In addition, molecular biology has shown that Brachiopods are surprisingly related to the annelids.

An understanding of the Burgess Shale-type faunas remains of the highest importance. This is for two reasons. First, there seems to be the possibility of tracing at least some of the steps that are involved in the appearance of new "designs" of animals. Second, study of these fossils helps to explain both the origins of the Cambrian "explosion", perhaps genetic, and its subsequent history. This latter aspect seems to have been largely a product of the unfolding ecologies of the Cambrian world, most notably predation. In conclusion, the Burgess Shale-type faunas give a series of insights into the early evolution of animals, the consequences of which are apparent until the present day.

A vote of thanks was given by Dr Euan Clarkson who paid tribute to Professor Conway Morrises skills as a speaker and presenter, particularly his verbal fluency and excellent slides. He commented on how at least some of the bizarre oddities of the Burgess Shale are now being understood as belonging to more ordinary 'respectable' groups; how in the words of one Swedish geologist 'oddballs from the Cambrian are beginning to get even'. As parting shot, Dr Clarkson left us with the striking visual imagery of bright orange slug-like *Halkeria* creeping across the sea floor and turning into brachiopods by morning!

Hugh Barron