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# Concluding Remarks

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# Concluding remarks

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Charles Walcott's discovery of the Burgess Shale was by no means the first exceptional fossil locality with soft-part preservation to be unearthed, but in many ways his publications (spanning 1910–1931) provide a landmark in the history of the documentation of soft-bodied fossil biotas. Over the last 50 years the record and interpretation of exceptional preservation has grown dramatically. Milestones include the recognition of the exquisitely preserved microbiotas of the Precambrian Gunflint Chert (Barghoorn & Tyler 1965) and Bitter Springs Chert (Schopf 1968) (see also Knoll, this symposium), the superb palaeoecological and taphonomic documentation of the Carboniferous Mecca and Logan quarries (Zangerl & Richardson 1963), the continuing research programmes on deposits such as the Carboniferous Mazon Creek (Nitecki 1979; see also Baird *et al.* (this symposium) and Broadhurst (this symposium)), the Jurassic Solnhofen Limestone (Barthel 1978) and comparable lithographic limestones such as those of Cerin (Jurassic), Lebanon (Cretaceous) and Montana (Carboniferous), the Jurassic Posidonia Shales (Seilacher 1982; Seilacher *et al.*, this symposium) and other bituminous deposits (Martill, this symposium) and the various Ediacaran sequences (Glaessner 1984; Fedonkin, this symposium). There have been impressive advances in our understanding of these and many other biotas, not least the meticulous morphological descriptions of exquisitely preserved material. The broad aim of this meeting was to try and set such exceptional deposits in a broader ecological and evolutionary context, and while we may hope to claim partial success there remain a series of interrelated points, five of which receive brief attention here.

## 1. How best are such deposits classified?

The scheme erected by Seilacher (1970) with a basic division into 'concentration-Lagerstätten', almost entirely omitted from consideration in this volume, and 'conservation-Lagerstätten' has been widely adopted. Seilacher *et al.* (this symposium) suggest some further refinements within the latter category. Their distinction and definition of the twin factors obrution (cf. smothering) and stagnation have generated discussion here, while recognition of the likely role of microbial activity such as cyanobacterial mats as a third significant factor is noteworthy. The plotting by Seilacher *et al.* (this symposium) of various exceptional biotas on such a ternary diagram is a welcome innovation.

It might also be asked whether alternative schemes of classification are worth considering, such as one perhaps based on the mineralogy of preservation. Soft-part preservation occurs in a wide variety of replacement minerals and although there are substantial areas of ignorance concerning the diagenetic pathways, detailed documentation may reveal a commonality of patterns and perhaps related processes, especially microbiological.

## 2. TO WHAT EXTENT ARE THESE EXCEPTIONAL BIOTAS REPRESENTATIVE?

My interest in this question arises from convincing indications that the Phyllopod bed (Burgess Shale) fauna is representative of a broad range of faunas occupying outer-shelf Cambrian environments (Conway Morris, this symposium). One objective of this volume is to see whether other soft-bodied Lagerstätten can be regarded literally as the fleshed-out equivalents of the shelly assemblages that are the normal domain of the palaeontologist, or are themselves biased or composite accumulations. It is becoming increasingly obvious that the great majority of exceptional fossil localities may not be regarded as entirely representative: that is, the very conditions that promote soft-part preservation may also act to limit the nature or availability of the original assemblages. Thus, unusual environmental (*pre-mortem*) or diagenetic (*post mortem*) conditions act separately or together as biasing filters that do not allow either the expression or the preservation of more typical biotas. Various examples are discussed in this volume. Among the Precambrian cherts (Knoll, this symposium) only the more decay-resistant cells or enclosing sheaths survive. Moreover, there is good reason to believe that chertification was typically restricted to such areas as hypersaline lagoons where the microbial assemblages were taxonomically distinct and probably more evolutionarily conservative (see below) than those occupying open-shelf environments in which the early eukaryotes were flourishing. Fine-grained muds, now shales, deposited in these latter areas may indeed offer opportunities for exceptional preservation as carbonaceous compression fossils (for example, Walter *et al.* 1976; Duan 1982), but as pointed out elsewhere (Knoll 1984) there are profoundly different techniques in the study and analysis of Precambrian chert and compression assemblages. Among Phanerozoic biotas the problems of representativeness persist. In the Lower Cambrian Emu Bay Shale Lagerstätte (Conway Morris, this symposium) the low diversity combined with an absence of brachiopods, hyolithids and echinoderms, elements otherwise typical of many Cambrian assemblages, is indicative of an atypical fauna. Comparable arguments apply to a variety of exceptional biotas such as the Silurian Waukesha (Mikulic *et al.*, this symposium) and Jurassic Osteno deposits (Pinna, this symposium) where a variety of marine organisms otherwise typical of these respective geological periods are either very rare or absent. In a related vein Seilacher *et al.* (this symposium) suggest the Jurassic Gmünd Lagerstätte is biased towards echinoderms that were unable to escape sudden burial; as Clarkson (this symposium) notes such an explanation must also be considered when assessing the many other 'star-fish' beds and similar deposits. Another sort of bias in the record is discussed by Scott & Rex (this symposium) where it appears that Carboniferous coal-balls typically encapsulate the remains of relatively primitive and evolutionarily conservative plant communities. More dynamic aspects of plant evolution may indeed be recorded as fossils in other environmental settings, but seldom in the exquisite detail available in permineralized peats (see also Knoll, this symposium). Distortion of the record may also arise during the earliest stages of diagenesis. Thus, Müller (this symposium) notes that within the Upper Cambrian anthraconitic Orsten the exquisite preservation by phosphate coating and replacement is restricted to organisms under 2 mm in size, and most typically arthropods where the exoskeleton appears to have provided an especially suitable template.

To conclude, it seems that few, if any, exceptional fossil localities provide a complete and undistorted picture of former life. Notwithstanding comments made above, even the Phyllopod bed fauna (Burgess Shale) is not completely intact: many of the trilobite species appear to lack soft-parts, other forms are known largely from dismembered fragments, and it appears that the smallest size range of animals that includes larval stages (and perhaps a meiofauna) are not readily preserved or recognizable.

## 3. The evolution of taphonomic factors

No soft-bodied biota can be assessed properly without a detailed knowledge of the surrounding taphonomic circumstances. It is becoming increasingly clear that such factors that conspire to hinder or promote exceptional preservation through geological time have changed, although as yet only the broadest outline of this history of changing preservation potentials is available. Biological and physical influences apparently are of equal importance. Regarding the former appeal may be made to the degree of bioturbation and other sediment disturbance (for example, Thayer 1983), the appearance and diversification of scavengers and predators, and even conceivably changes in microbial activity. Thus, the widespread occurrence of the soft-bodied Ediacaran biotas has been repeatedly linked to restricted bioturbation and an absence of scavengers, although Fedonkin (this symposium) considers a wide range of other potential factors and Seilacher (this symposium, see also Seilacher 1984) presents even more radical alternatives. Regarding changing physical parameters careful attention should be given to factors such as diminished levels of oceanic oxygen, as registered in black shale horizons, and long-term changes in ocean chemistry. Thus, Walker & Diehl (this symposium) demonstrate how the early diagenetic development of marine cements in some Lower Palaeozoic carbonates may well be instrumental in literally 'locking in' shelly assemblages, and so providing a far more faithful picture of biotic composition than might be predicted in such shelf settings.

It seems likely that a number of subtle taphonomic circumstances, some either very rare or absent on the surface of the Earth today, made given intervals of Earth history especially propitious for certain types of special preservation. Scott & Rex (this symposium) highlight the curious fact that coal-ball formation with its exquisitely preserved plant remains has a restricted and as yet problematic distribution, and I suspect that is only one of many cases where close cooperation with sedimentologists, geochemists and palaeo-oceanographers will place much of our understanding of special preservation in entirely new contexts.

## 4. The role of microbial activity and decay in exceptional preservation

A somewhat unexpected and paradoxical development in the study of soft-part preservation is the likely role of bacterial activity in at least some cases. Thus, Knoll (this symposium) indicates how a certain degree of decay within the organic matter of Precambrian microbiotas is actually a prerequisite for the growth of silica crystals that will hermetically seal the assemblage. Seilacher *et al.* (this symposium) in a somewhat different vein hypothesize the likely importance of prokaryotic films and scum as a factor in special preservation, particularly in the binding and matting of sediment and associated macrofossils. The role of micro-organisms in these processes must usually be inferred, and so it is all the more remarkable to learn that the replacement of the soft-parts in the Eocene Grube Messel is due to the growth of bacterial films with individual bacteria preserved as identifiable fossils in siderite (Franzen, this symposium; see also Wuttke 1983). Martill (this symposium) comments on the recognition of bacteria in Jurassic vertebrate remains. These instances of bacterial association with special preservation are unlikely to be isolated examples, but rather may be indicative of their vital role in the preservation of exceptional fossils including the soft-parts. Outstanding questions surround the types of bacteria involved in these processes, the reasons why decay does not reach completion, and the mechanisms by which the bacteria may be rapidly mineralized.

## 5. FUTURE PROSPECTS

Are there areas that in the next few years may prove especially fruitful? Given adequate funding and imagination the following seem promising lines of enquiry.

(i) The development of special techniques. A paramount example is the isolation by careful acid digestion of the minute phosphatized arthropods from the Upper Cambrian Orsten, a technique greatly refined by Müller (this symposium) which may be applicable to other calcareous nodules, (see also Shear *et al.* (1984) for spectacular discoveries of arthropod remains from the Devonian). Scott & Rex (this symposium) emphasize the role of cathodoluminescence in elucidating hitherto obscure diagenetic features of Carboniferous coal balls, while current research by myself and K. Pye is investigating soft-part preservation with scanning electron microscopy, especially in the backscattered electron mode. Such studies may enhance substantially our understanding of the diagenetic pathways involved in special preservation. In a related field, although attempts at experimental fossilization have had a chequered history there are a number of promising studies (for example, Leo & Barghoorn 1976; Zangerl 1971) that suggest that reappraisal of this neglected area is perhaps appropriate.

(ii) Can we predict new occurrences of exceptional biotas? Recent work is encouraging. A number of new soft-bodied localities adjacent to the Burgess Shale has been discovered recently (Collins *et al.* 1983), while Baird *et al.* (this symposium) have successfully extended the search for Mazon Creek-like preservation over a very substantial area, and comparable discoveries in France (Rolfe *et al.* 1982) are promising. Equally encouraging is the report by Hook & Ferm (this symposium) of new localities that at least hint of the palaeontological riches recovered from the classic Linton site. Müller (this symposium) reports scattered occurrences of exceptionally preserved arthropods in various concretions, and a more systematic search will almost certainly be rewarding. Future investigations will also need to place greater emphasis on systematic and coordinated excavations, as may be judged from the success of bulk quarrying at localities such as the Walcott and Raymond Quarries (Burgess Shale), Kaisergrube (Hunsrückschiefer), Fergus County, Montana (Bear Gulch Limestone), Bearsden (Top Hosie Limestone), Cerin (Cerin lithographic limestone), and Grube Messel (Eocene oil shales).

(iii) How radically will these exceptional deposits change our evolutionary and ecological perspectives?

To a certain extent this question depends on the degree of representativeness (see above), but it is worth recalling that some 20% of the metazoan clades used by Sepkoski (1981) in his factor analysis of Phanerozoic diversity patterns are known only from three of the major Palaeozoic Lagerstätten (Burgess Shale, Hunsrückschiefer, Mazon Creek). Not surprisingly nearly all of the clades are soft-bodied, and many are of problematical affinities. Their documentation will be important in understanding metazoan evolution. The possibility that some exceptional taphonomic circumstances may favour conservative biotas, perhaps even to be regarded as 'evolutionary museums' (Knoll, this symposium; see also Conway Morris, Scott

& Rex, and Chaloner, all this symposium) also requires special attention. Among marine communities it will be interesting to see whether biotas adapted to low levels of oxygen (such conditions tending to promote exceptional preservation) have a greater proportion of evolutionary relics in comparison with surrounding biotas occupying better oxygenated sites.

In terms of palaeoecology exceptional biotas also provide important insights. The identification of a variety of predators in the Burgess Shale fauna (Conway Morris 1985; Whittington & Briggs 1985) is important because this trophic group has often been considered of minor importance in Cambrian marine communities. As Hutchinson (1961) so perceptively suggested the apparent rarity of Cambrian predators is simply because most were soft-bodied.

In conclusion, the literature on exceptional preservation is already very substantial, but is both widely scattered and for the most part lacks general themes of enquiry. The data sheet presented by Seilacher *et al.* (this symposium) is an important attempt to bring some order into this area of palaeontology. Nomothetic questions in the life sciences are notoriously difficult to answer, but the need for coordinated research programmes to tackle some of the fundamental problems surrounding the evolutionary and ecological significance of exceptionally preserved biotas is overdue.

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