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Cambrian Lagerstätten: their distribution and significance

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The geological setting, biotic diversity and taphonomy of Cambrian soft-bodied Lagerstätten are reviewed with special reference to the Lower Cambrian Emu Bay Shale (South Australia) and Kinzers Formation (Pennsylvania), and the Middle Cambrian Stephen Formation (Burgess Shale and adjacent localities, British Columbia). Brief mention is made also of a number of more minor occurrences in the U.S.A., China and Spain. Exceptional preservation in the Upper Cambrian is discussed by K. J. Müller (this symposium). These soft-bodied Lagerstätten afford a series of special insights into the nature of Cambrian life. Emphasis is laid on the information they provide with regards (i) levels of diversity and the proportion of skeletized taxa; (ii) the origin and relative success of bodyplans; (iii) community ecology and evolution.

1. Introduction

The dramatic diversification of metazoans during the early Phanerozoic (latest Precambrian (Vendian) and Cambrian) has attracted wide attention (see, for example, Stanley 1976; Bengtson 1977; Sepkoski 1978) on account of the relatively abrupt appearance of many bodyplans and a corresponding series of ecological strategies that appears to have set the pattern of community evolution in some marine environments for hundreds of millions of years. There are, however, a number of problems in unravelling the original course of events that dictated the style of these evolutionary radiations. The fossil record of metazoans effectively begins with the latest Precambrian Ediacaran faunas (Fedonkin 1983; Glaessner 1984), although various lines of evidence perhaps point to an origin much further back in the Precambrian (for example, Kauffman & Steidtmann 1981; Runnegar 1982; Kauffman & Fürsich 1983; Glaessner 1984). The Ediacaran faunas are almost entirely soft-bodied, dominated by cnidarians or cnidarian-like creatures and a motley selection of worms and other apparently triploblastic metazoans that have been compared with annelids and arthropods. Cambrian faunas are generally better documented, principally on account of the widespread appearance of skeletal hard-parts. The differences between the Ediacaran and Cambrian faunas are profound and must in part reflect the rapid rates of evolution that included the appearance of various groups, for example, echinoderms, brachiopods, that cannot be readily envisaged as functioning without skeletal support (see, for example, Cloud 1948). There is, however, some limited evidence for the survival of Ediacaran taxa into the Lower Cambrian (Glaessner 1984; see also Muir 1980), and several authors have emphasized that taphonomic factors may have accentuated the differences between Ediacaran and Cambrian faunas. Sokolov (1976) commented on the geographically widespread and locally abundant preservation of soft-bodied fossils in sediments of Ediacaran age, and contrasted this with the rest of the Phanerozoic where soft-part preservation is sporadic and usually reflects an unusual combination of preservational circumstances often involving catastrophic burial or anoxic conditions, or both. Sokolov's explanation of Ediacaran preservation reflecting an absence of predators and scavengers has won wide acceptance by various workers (for example, Sepkoski 1979; Cloud & Glaessner 1982; Glaessner 1984), who have emphasized the restricted degree of bioturbation as an additional factor favouring soft-part preservation (see also Fedonkin, this symposium). Careful attention should also be given to changing taphonomic circumstances during the remainder of the Phanerozoic. Thayer (1983) and Larson & Rhoads (1983) document increasing levels of bioturbation and sediment disturbance during the Phanerozoic, and such observations might conceivably be used to explain why most of the major marine Lagerstätten (for example, Burgess Shale, Hunsrückschiefer, Mazon Creek) are confined to the Palaeozoic.

If contrasts between Ediacaran and Cambrian faunas are distorted by the closure of a 'taphonomic window' (Sepkoski 1979) with the latter known very largely from shelly remains, clearly it is important to document fully occurrences of soft-part preservation if our knowledge of early metazoan diversification is to be put into better perspective. It would be a curious irony if the greater proportion of groups that evolved in the early Phanerozoic actually lacked preservable skeletal parts. At present information on Cambrian faunas is based largely on the well skeletized groups of trilobites, brachiopods (especially inarticulates), hyolithids, echinoderms, sponges and a variety of tubicolous organisms. As is explained in more detail below taken in isolation these groups would appear to give a distorted view of the palaeoecology of the original biotas, and that normally non-preservable elements were indeed a highly significant component. The problem is compounded by examples where Lower Cambrian groups with mineralized exoskeletons with at least a moderate preservation potential have become effectively soft-bodied by the Middle Cambrian and so disappear from the 'normal' fossil record (§4*a*).

Study of Cambrian soft-bodied Lagerstätten (figure 1, table 1) may be expected, therefore, to yield fresh insights into (i) the factors controlling and delineating the scope of early metazoan radiations, including the appearance and relative success of a multiplicity of bodyplans; (ii) the relative importance of soft-bodied and lightly skeletized taxa and their ecology in comparison with well mineralized groups; (iii) the possibility that some Ediacaran forms survived into the Cambrian; and (iv) a comparison of Ediacaran, Cambrian and post-Cambrian community structure with particular emphasis on relative ecological complexities and the possibility of ecological replacement.

TABLE 1. THE STRATIGRAPHIC POSITION WITHIN THE CAMBRIAN OF THE PRINCIPAL AND MORE MINOR SOFT-BODIED LAGERSTÄTTEN

(Radiometric dates are based on Harland *et al.* (1982) and may be subject to revision. Within each Series of the Cambrian listing of deposits is alphabetic and not in terms of relative stratigraphy.)

series	major occurrences	minor occurrences
Upper Cambrian (525–505 Ma)	anthraconitic 'Orsten'; Sweden and neighbouring areas	—
Middle Cambrian (540–525 Ma)	Stephen Formation, esp. Burgess Shale (Phyllopod bed); British Columbia, Canada	Mansilla Slates; Spain Marjum Formation; Utah, U.S.A. Spence Shale; Utah and Idaho, U.S.A. Tangshih Formation; Liaoning, China Wheeler Formation; Utah, U.S.A.
Lower Cambrian (590–540 Ma)	Emu Bay Shale; South Australia Kinzers Formation; Pennsylvania, U.S.A.	Las Ermitas 'Archaeocyathid' beds; Spain Latham Shale; California, U.S.A. Qiongzhusi Formation (Yuanshan Member); Yunnan, China

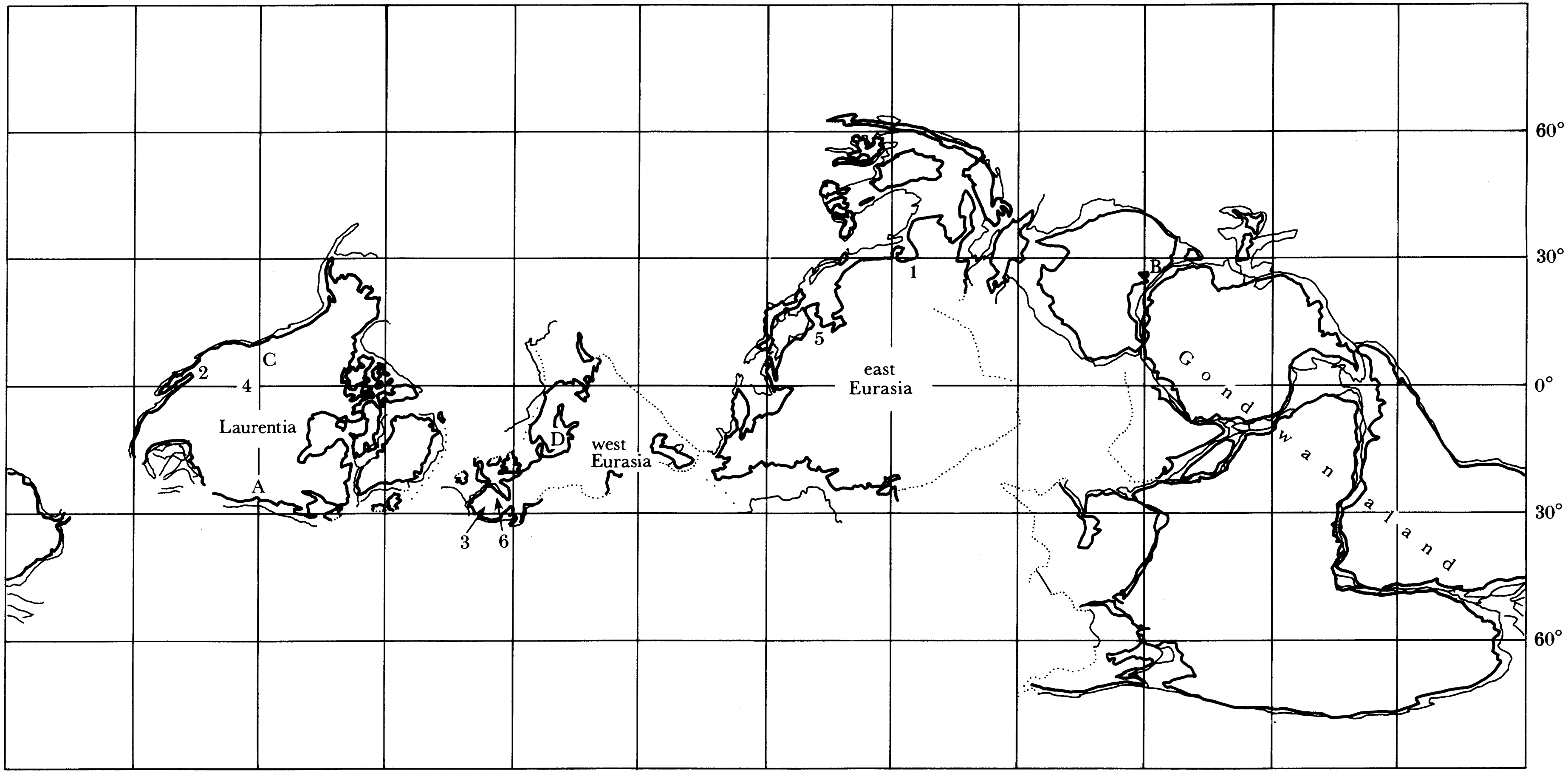

Figure 1. Palaeogeographic reconstruction of the Middle Cambrian world, with relative positions of the principal soft-bodied localities indicated (see table 1 and text for further details). A–D, major occurrences: A, Kinzers Formation; B, Emu Bay Shale; C, Stephen Formation, especially the Burgess Shale; D, Anthraconitic 'Orsten' (see Müller, this symposium). 1–6, minor occurrences: 1, Qiongzhusi Formation; 2, Latham Shale; 3, 'Archaeocyathid' beds; 4, Marjum Formation, Spence Shale, Wheeler Formation; 5, Tangshih Formation; 6, Mansilla Slates. Projection is cylindrical equidistant and is based with permission on Smith *et al.* (1981). The distribution of the continents is tentative. Bold outlines delineate present coastlines as a guide to recognition, fine continuous lines the 1000 m isobath, dotted lines putative plate junctions or margins of the continental blocks. Approximate distribution of land and continental seas in this reconstruction is given by Whittington (1981, figure 2).

2. LOWER CAMBRIAN LAGERSTÄTTEN

(a) *Emu Bay Shale, South Australia*

The Emu Bay Shale is exposed at two localities on the northern coast of Kangaroo Island, South Australia, approximately 100 km southwest of Adelaide. The type section is in Emu Bay itself, while further east another outcrop lies adjacent to a prominent ravine known as Big Gully, about 3 km west of White Point. On the basis of its trilobites the Emu Bay Shale is reliably dated as Lower Cambrian, and in reviewing the evidence Glaessner (1979) considered this deposit to lie 'in about the upper third of the Lower Cambrian'. Correlations, however, with other Cambrian sections beyond Australia are far from secure.

The Emu Bay Shale rests on the White Point Conglomerate that includes spectacular fanglomerates that at some localities include abundant clasts of archaeocyathid limestone. In an early report Sprigg (1955) proposed that these conglomerates were shed from submarine reef slopes, and such a reconstruction would be reminiscent of the physiographic setting of the Middle Cambrian Burgess Shale and some other Lagerstätten. More recent work by Daily *et al.* (1980), however, indicates that the conglomerates and associated clastic sediments were deposited in a largely subaerial setting of alluvial fans and associated fluvial systems, with the succeeding sediments of the Emu Bay Shale and overlying Boxing Bay Formation accumulating in the intertidal zone. The thin horizon that contains prolific soft-part preservation may represent, however, somewhat deeper-water conditions (Conway Morris & Jenkins 1985).

Soft-part preservation in the Emu Bay Shale is restricted to the locality at Big Gully, where it occurs in a 3–4 m thick succession of dark micaceous shales near the base of the formation. No detailed study of the taphonomy of the fauna is available. The dark colour and finely laminated nature of the enclosing sediment without obvious bioturbation point to anoxic conditions (Pocock 1964), but the processes by which the organisms were buried is not clear. In contrast to the Emu Bay locality articulated trilobites at the Big Gully horizon are abundant (*ca.* 80 %) and at least some of the fauna may have been pelagic (Pocock 1964). The soft-bodied and lightly skeletized component was described by Glaessner (1979) and this horizon also contains abundant trilobites of the genera *Estaingia* and *Redlichia* (Pocock 1964). Specimens of the latter genus up to 35 cm in sagittal length have been recorded (Daily *et al.* 1979), and there are also instances of injury in *Redlichia* from this locality that apparently reflect predatory attack (Conway Morris & Jenkins 1985). In contrast with many Cambrian faunas inhabiting argillaceous substrates the locality at Big Gully appears to lack hyolithids or inarticulate brachiopods, although they do occur at the type locality in Emu Bay (Sprigg 1955; Pocock 1964).

The soft-bodied component includes both arthropods and worms (Glaessner 1979). Apart from a single 'crustacean' with poorly preserved appendages, the arthropods are represented by the genera *Isoxys* (*I. communis*) and *Tuzoia* (*T. australis*). Both these occurrences are noteworthy because of their wide distribution elsewhere in the Lower and Middle Cambrian (Glaessner 1979). In the Lower Cambrian *Isoxys* occurs in the 'Archaeocyathid' beds near Las Ermitas, Cordoba, Spain (Richter & Richter 1927), within the Chilhowee Group of Tennessee (Walcott 1980), and possibly in the Kinzers Formation of Pennsylvania (Campbell & Kauffman 1969), while the carapace described as *Cymbia auritus* (Jiang Zhiwen 1982, see also Luo Huilin *et al.* 1984) from Yunnan Province, China, has a striking similarity to *Isoxys*. *Tuzoia* is also recorded from the Lower Cambrian of Yunnan, southern China (P'an 1957), the Eager Formation of British Columbia (Resser 1929), and the Kinzers Formation (Resser 1929; Resser & Howell 1938; Campbell & Kauffman 1969). Both *Isoxys* and *Tuzoia* occur in the Middle Cambrian Stephen Formation (Walcott 1908; Simonetta & Cave 1975; Collins *et al.* 1983), while the latter genus has been recorded elsewhere in the Middle Cambrian of the western Cordillera, U.S.A. (Robison & Richards 1981) and Liaoning, northern China (Resser 1929; Endo & Resser 1937). Apart from poorly defined 'abdominal somites' in some specimens of *Isoxys* from the Emu Bay Shale (Glaessner 1979) only the carapaces of this genus and *Tuzoia* are known. The apparently cosmopolitan distribution of *Isoxys* and *Tuzoia* and their occurrence in both nearshore habitats as well as depositional environments facing the open oceans may be consistent with a pelagic existence. Pocock (1964) proposed such a mode of life with respect to *Isoxys*, and Conway Morris (1979*a*) and McKenzie (1983) independently drew parallels between the carapace shape of this genus and Recent pelagic ostracodes such as *Conchoecia daphnoides*.

The worms include the papillate genus *Palaeoscolex* (*P. antiquus*), and the more enigmatic *Myoscolex ateles* and *Vetustovermis planus*. The overall resemblance of *P. antiquus* to other species from the Middle Cambrian Spence Shale (Robison 1969) and the Lower Ordovician of Shropshire (Whittard 1953) is clear, but there is some question of whether it belongs to this genus (Conway Morris & Robison 1985). Glaessner (1979) compared the other two worm genera to annelids. *V. planus* is known from a single rather indifferently preserved specimen. In contrast, *M. ateles* is abundant, and in my opinion its known morphology is difficult to reconcile with the annelid bodyplan.

Preservation in the Emu Bay Shale has not been studied in particular detail. The trilobites, other arthropods and worms, for example, *P. antiquus* are preserved in a fibrous pink calcite (Glaessner 1979). In the case of the trilobites this may represent a replacement of the calcitic exoskeleton, but this is unlikely to be the case in the other arthropods which presumably lacked a calcareous exoskeleton or *P. antiquus* which presumably had no mineralized parts during life.

(*b*) *Kinzers Formation*, *Pennsylvania*

The Kinzers Formation consists of a complex series of lithologies, principally shales and carbonates, exposed in southeastern Pennsylvania. The area is structurally complex, the sediments and enclosed fossils are often tectonically deformed, and the Formation is relatively poorly exposed. All these factors make the tracing of facies relationships hazardous. Not surprisingly soft-part preservation is restricted to fine-grained shales, with two localities proving especially noteworthy (locality lists are provided by Campbell (1969) and Sprinkle (1973)). The Getz Quarry (USNM locality 12x) is located about 2.8 km north of Rohrerstown, Lancaster County, but according to Campbell (1969) 'the most prolific bed has been buried'. An even more important site was USNM locality 22L, situated 0.8 km south of East Petersburg, Lancaster County. This exposure has been consumed by a housing development and although an immediately adjacent field has abundant loose blocks of shale there is little indication of exceptional preservation.

The presence of the trilobites *Bonnia* and *Olenellus* is an unequivocal indicator of a late Lower Cambrian age (see, for example, Fritz 1972), as is the enigmatic conoidal shell *Salterella* (Yochelson 1981) that occurs in abundance in the carbonate facies (Campbell & Kauffman

1969; Yochelson 1970). On the basis of the discovery of a fauna with a striking similarity to that of the *Ogygopsis* Shale which is situated on the opposite side of the American craton adjacent to the Burgess Shale, Campbell (1971) believed that the Kinzers Formation extended into the Middle Cambrian. It seems more likely, however, that this unit is a lateral equivalent of the Conestoga Formation (M. E. Kauffman, personal communication), a deeper-water succession deposited to the southeast (Rodgers 1968). Even if the position of this fauna within the Kinzers Formation is questionable, the occurrence of *Ogygopsis* nevertheless may be of considerable palaeo-oceanographic significance and could reflect the incursion of oceanic water (reviewed in Conway Morris 1985*a*, p. 518).

Summaries of the biota exist (Resser & Howell 1938; Campbell 1969; Campbell & Kauffman 1969), but an up-to-date systematic review is not yet available and there remain a number of undescribed species, including worms. Within the Kinzers Formation Campbell & Kauffman (1969) identified six faunules, of which the *Wanneria walcottana* faunule is by far the most diverse and is exposed at a number of localities including USNM 12x and 22L. Various elements of the fauna, however, have received more detailed attention. Campbell (1969; Campbell & Kauffman 1969) synonymized 14 species of *Olenellus*, in particular emphasizing the misleading effects of tectonic deformation. One specimen of *O. thompsoni*, formerly identified as a separate species *O. peculiaris* by Resser & Howell (1938), lacks a genal spine apparently owing to predation (Campbell 1969). Another specimen of this species (formerly *O. getzi*) possesses antennae (Dunbar 1925), but no other soft-parts have been recognized. The presence of antennae and hypostome, however, may not necessarily mean that this individual was alive at the time of burial and it could represent a moult with the antennae attached to the dorsal exoskeleton via the thinner ventral cuticle. An undescribed specimen of *Olenoides serratus* from the Burgess Shale consists of a partly disarticulated individual consisting of the cephalon with attached antennae and hypostome, the anterior thorax with some segments only linked by what appears to be unmineralized cuticle, and some isolated thoracic segments. No other appendages are visible.

Other groups represented include a variety of early echinoderms, some of which use trilobite fragments as an attachment substrate (Sprinkle 1973; Derstler 1975, 1981; Paul & Smith 1984). There are also worm body fossils, for example, *Protoscolex*, and tubes (Conway Morris 1977), brachiopods, molluscs, hyolithids, non-trilobitic arthropods (Resser 1929; Briggs 1978*a*; see also Briggs (1976) and Bruton (1981) for misidentified material), the anterior appendages of the enigmatic metazoan *Anomalocaris* (Resser 1929; Briggs 1979; Whittington & Briggs 1985), sponges, and algae.

Little detailed information on the taphonomy of the biota appears to be available. Sprinkle (1973) commented on the likelihood that some of the echinoderms were gregarious, and that articulated specimens owe their origin to episodes of catastrophic burial, such as turbidity currents. Rare finds of articulated hyolithids with attached opercula and helens (Campbell 1969) also indicate rapid burial as *post mortem* disassociation would have occurred rapidly. The factors surrounding the fossilization of soft-parts have not been investigated in detail. Locality 22L is remarkable for the fine grained sediment (Campbell 1969), and this presumably contributed to the quality of preservation.

The setting of the Kinzers Formation bears some striking resemblances to the somewhat younger Burgess Shale. Both appear to have faced the open ocean, albeit on opposite sides of the craton. The overall physiographic setting is similar, with the Kinzers Formation representing an off-bank sequence that as well as presumably relatively deep-water shales includes spectacular slump breccias such as those at Thomasville (Reinhardt 1977), that were derived from the shallower carbonate banks. The Burgess Shale was deposited as part of a clastic sequence adjacent to a precipitous algal reef escarpment, from which carbonate debris flows were also derived (McIlreath 1977), and broadly comparable depositional settings have been identified at various other points around the Laurentian craton (see, for example, James 1981; Read & Pfeil 1983) suggesting that detailed examination of untectonized off-bank shales in circum-Laurentian sites could reveal new soft-bodied occurrences.

Given the depositional similarities faunal comparisons between the Kinzers Formation and Burgess Shale could be significant but are not straight-forward because of (i) incomplete revision of the biotas, especially in the former unit; (ii) differences in taphonomy and (iii) age differences of perhaps 15 Ma. Undoubted similarities exist with the faunas sharing approximately 12 genera, although the Burgess Shale has four times the generic diversity and the faunal lists of the Kinzers Formation (Campbell 1969; Campbell & Kauffman 1969) are probably in need of some revision.

Regarding other examples of Lower Cambrian soft-part preservation attention has been drawn above to occurrences in China and Spain. Other units that deserve mention are the Parker Shale, Vermont, and Latham Shale, California. The Parker Shale appears to be a direct correlative of the Kinzers Formation (Rodgers 1968), and has yielded a number of exceptionally preserved fossils (see, for example, Resser & Howell 1938; Briggs 1976). Potentially one of the most interesting species is *Emmonsaspis cambriensis* which conceivably represents an early chordate (see Durham 1971). If so, this would predate *Pikaia gracilens* which is the earliest well attested chordate (Conway Morris 1982). Unfortunately the specimens appear to have been mislaid (F. J. Collier, personal communication). The pattern of 'a "herring bone" ribbing' mentioned by Resser & Howell (1938) may represent myotomes, but to judge from their illustrations the 'central rod' might be interpreted better as a sediment-filled gut rather than a notochord. The Latham Shale also falls within the *Bonnia–Olenellus* Zone and thus is much the same age as the Kinzers Formation and Parker Shale. Exceptional preservation includes the isolated appendages of *Anomalocaris* (Briggs & Mount 1982), while evidence of predation in trilobites (Alpert & Moore 1975) could represent either the activities of this enigmatic metazoan or some other predators. Other examples of soft-part preservation apparently include worms (Mount 1980) that so far as can be judged from a line illustration appear to be related to *Palaeoscolex* or *Protoscolex*, a group of papillate ?annelids that ranges from Cambrian to Silurian (Conway Morris 1977). Reference to other occurrences of this group in the Cambrian are given above. The Latham Shale also contains articulated echinoderms (Durham 1978), whose occurrence points towards episodes of catastrophic burial.

3. MIDDLE AND UPPER CAMBRIAN LAGERSTÄTTEN

The outstanding example of a soft-part biota in the Middle Cambrian is the Burgess Shale, which forms part of the Stephen Formation. This is a basinal succession deposited adjacent to a carbonate bank that in the vicinity of Burgess Shale assumes precipitous proportions as the Cathedral Escarpment (McIlreath 1977). An extensive revision of the biota is largely complete and recent reviews (for example, Conway Morris 1979*a*, *b*; Conway Morris & Whittington 1979; Whittington 1980, 1981) require no repetition here. As is discussed below, restudy of this extraordinary biota has done much to focus attention on questions such as the nature of early metazoan diversification and the palaeoecology of Cambrian communities, especially the role of predators.

Notwithstanding apparent proximity to anoxic conditions the diversity of well skeletized taxa indicates that the pre-slide environment of the Phyllopod bed (Burgess Shale) was tolerably well oxygenated (see Rhoads & Morse 1971) and was not ecologically impoverished owing to hostile conditions. All that needs to be stressed here is that the uniqueness of the Burgess Shale thus appears to lie in its preservational history rather than its original composition (Conway Morris 1981). Had the exceptional conditions of taphonomy failed to materialize so that only taxa with robust mineralized hard-parts fossilized, then the resulting assemblage of predominantly trilobites, inarticulate brachiopods and hyolithids would be indistinguishable from what is usually regarded as a 'normal' Cambrian fauna found in a wide range of open-marine environments.

One of the most significant of recent developments has been the discovery of comparable biotas both elsewhere in the Stephen Formation (Collins *et al.* 1983) and further south in Utah and Idaho. In the latter case earlier work (e.g. Resser 1931, 1939; Brooks & Caster 1956; Robison 1969, see also Conway Morris 1977) gave indication of potential diversity, and recent research has provided ample confirmation (Conway Morris & Robison 1982, 1985; Rigby 1978, 1980, 1983; Willoughby & Robison 1979; Robison & Richards 1981; Briggs & Robison 1984; Robison 1984, 1985). Soft-part preservation at these new localities, especially in the Wheeler Formation, Spence Shale and Marjum Formation, does not match the quality or range of preservation in the Phyllopod bed of the Burgess Shale. Less favourable taphonomic conditions in the former deposits have probably biased the record in comparison with the Burgess Shale, the number of taxa in common is still noteworthy even if their original proportions in the communities varied widely.

Beyond the Laurentian craton there are few examples of Middle Cambrian soft-part preservation. Examples include a possible non-trilobitic arthropod (Linan 1978) and new worm material (Conway Morris & Robison 1985) from Spain, and the arthropod *Tuzoia* from northern China (Resser 1929; Endo & Resser 1937).

Upper Cambrian occurrences are best known from the arthraconitic 'Orsten' of Sweden and neighbouring regions (Müller, this symposium). As Müller notes, comparisons with other Cambrian Lagerstätten are not straight-forward because exceptional preservation in the 'Orsten' is size-limited (under 2 mm) and mostly confined to arthropods. Müller stresses the importance of special techniques and the need for extensive sampling throughout the geological column to uncover similar examples. The discovery of comparable material in the Middle Cambrian of Queensland, Australia (McKenzie & Jones 1979) may herald further discoveries elsewhere in the Cambrian.

4. The setting of Cambrian Lagerstätten

Cambrian Lagerstätten with soft-part preservation occur in a variety of depositional settings, although not surprisingly all entail fine grained sediments deposited under anoxic or dysaerobic conditions. Those from the Kinzers Formation and Burgess Shale (and related occurrences elsewhere in the Middle Cambrian of the Cordillera) show strikingly similar palaeogeographical and physiographic settings (figure 1). Both face an open ocean, albeit on opposite sides of the craton. They were deposited on passive margins in the outer detrital belt, but adjacent to the median carbonate belt and a pronounced change in slope that in the case of the Burgess Shale formed a precipitous escarpment and elsewhere around the craton may be inferred from carbonate slump deposits. The Emu Bay Shale, however, appears to have accumulated in a markedly different tectonic and depositional setting, that of a near-shore environment under the possible influence of faulting that may have controlled submarine topography and the formation of anoxic 'ponds'. In all these cases, however, soft-part preservation is apparently rather localized and may have been centred on anoxic 'ponds', sometimes combined with catastrophic burial. In contrast, the depositional environment of the arthraconitic 'Orsten' appears to have been much more widespread, with a relatively extensive basin containing sediments accumulating under broadly dysaerobic rather than anoxic conditions. Martinsson (1974) noted that the arthraconitic concretions increase in an off-shore direction, and while phosphatization of the arthropods was presumably very early, as Müller (this symposium) notes, little is known of either the source of phosphate or the palaeoceanography and other factors that controlled its precipitation.

(*a*) *Bias in soft-bodied Lagerstätten*

In principle soft-part preservation should lead to a far more detailed reconstruction of a palaeocommunity. In a general vein Seilacher (1970) has noted that Lagerstätten tend not to be representative. More specifically, Brett & Eckert (1982) have pointed out in discussing exceptionally preserved crinoid assemblages that it is important to establish whether the very conditions that promote exceptional preservation such as propensity to catastrophic burial and proximity to anoxic conditions favour assemblages of taxa that are otherwise not representative of shelf benthos as a whole.

However, in the case of the Burgess Shale and most probably related Middle Cambrian units, for example, Wheeler Formation, and the Lower Cambrian Kinzers Formation, arguments exist (Conway Morris 1981; Conway Morris & Robison 1982) that they are indeed more broadly representative of that very wide spectrum of Cambrian faunas that are otherwise characterized by trilobites, inarticulate brachiopods, monoplacophorans, eocrinoids and hyolithids (see Sepkoski 1978, 1981). However, no claim is made for exact representativeness either in terms of taxa or their relative proportions. In contrast there is some reason to believe that environmental adversity has resulted in an atypical Cambrian assemblage in the Emu Bay Shale. At the Big Gully locality where soft-part preservation occurs the generic diversity is remarkably low (six soft-bodied species, two skeletized species), a value that is compounded by the absence of hyolithids and inarticulate brachiopods. As noted above these latter groups are widespread in Cambrian faunas, and they do occur elsewhere in the Emu Bay Shale (Pocock 1964; Daily *et al.* 1979). Some of the organisms that occur at the Big Gully locality may have been pelagic; the large trilobite *Redlichia* (Pocock 1964) and possibly the arthropods *Isoxys* and *Tuzoia* (see above) conceivably belong to this category. It seems likely, however, that some of the fauna, such as the worms, was benthic. The fauna, therefore, may be an ecological mixture and it is not yet clear which elements were co-associated in life. The reasons for its depauperate nature are speculative, but appeal could be made to low oxygen conditions which conceivably excluded benthos with mineralized hard-parts (see Rhoads & Morse 1971) or abnormal salinities. Palaeogeographic maps (for example, Scotese *et al.* 1979; Smith *et al.* 1981) indicate that this area of South Australia was within a restricted sea-way, albeit at relatively low latitudes (figure 1).

In the anthraconitic 'Orsten' various workers have postulated that the low diversity faunas reflect dysaerobic conditions (see Martinsson 1974). More significantly Müller (1983, this symposium) has demonstrated that soft-part preservation is size-selected to fossils under 2 mm. Fragments from larger organisms may thus be phosphatized, but this preservational threshold makes comparison with other Cambrian Lagerstätten difficult. Differences between the arthropods of the Burgess Shale and 'Orsten' may be evolutionary, but Müller's (1983) argument of taphonomic bias is more compelling. Ostracods occur in the Burgess Shale, but apparently without their appendages or other soft-parts. It is arguable whether arthropods of equivalent size to those from the 'Orsten' could be readily recognized as flattened compressions in argillites.

5. SOME IMPLICATIONS OF CAMBRIAN LAGERSTÄTTEN

While caution is needed if information from Cambrian Lagerstätten is to be extrapolated to a more general setting, nevertheless they provide a series of privileged insights into the ecology and diversity of Cambrian life that often are not readily apparent amongst shelly assemblages. In particular study of the Burgess Shale biota has highlighted a number of points, three of which are discussed briefly here (see also Conway Morris 1985*a*).

(*a*) *Diversity levels and the proportions of skeletized taxa*

In the Burgess Shale only about 14% of genera (mostly monospecific) and a mere 2% of individuals (alive at the time of burial; samples exclude sponges and the ?crinoid *Echmatocrinus*) have hard-parts capable of fossilization in unexceptional taphonomic circumstances. Whether other Cambrian marine biotas had as large or even greater non-preservable components is difficult to assess (see above), but there is some reason to think that comparable figures prevailed in some broadly similar Lower and Middle Cambrian settings. Whether Cambrian faunas tended to have a higher proportion of soft-bodied taxa as against younger Phanerozoic communities is highly problematic. Comparisons with post-Cambrian Lagerstätten are equivocal, in part because the extent of soft-part preservation in such deposits may be less extensive than the Burgess Shale, while some may sample unusual communities living in environmentally marginal environments.

One of the most obvious aspects of the Cambrian radiations is the relatively abrupt appearance of hard parts in at least ten phyla (Bengtson 1977). What has only recently become apparent is that at least some groups lost preservable hard-parts during the Cambrian and so effectively 'disappeared' from the fossil record. A good example exists amongst the halkieriids where the Lower Cambrian *Halkieria* and related genera had calcareous exoskeletons (often diagenetically phosphatized), whereas its Middle Cambrian descendant *Wiwaxia* had a lightly sclerotized skeleton with a minimal preservation potential (Bengtson & Conway Morris 1984; Conway Morris 1985*a*). Given the frequency of shell reduction and loss in groups such as the molluscs (see, for example, Gosliner & Ghiselin 1984), other examples may well be forthcoming.

(*b*) *The origins and relative success of metazoan bodyplans*

It has long been appreciated (for example, Brough 1958; Nicol *et al.* 1959; Valentine 1969, 1981; Raup 1983) that most of the major bodyplans, typically designated within the taxonomic hierarchy as phyla and classes, appeared early in the Phanerozoic. All extant phyla with fossilizable hard-parts had evolved by the Lower Ordovician and most appeared considerably earlier. The later appearance in the geological record of many soft-bodied phyla (Conway Morris 1985*b*) that are still extant is presumably a sampling artefact of an incomplete fossil record and they too may have originated in the early Phanerozoic. Recent work has also identified a variety of skeletalized and soft-bodied metazoans, many apparently confined to the Cambrian, that on account of their distinct morphology could be regarded as extinct classes of otherwise extant phyla or even extinct phyla. Among the former the echinoderms have been taken as the cardinal example, with a perceived evolutionary pattern of a multiplicity of relatively short-lived classes (Sprinkle 1976, 1983; but see Paul & Smith 1984). Among shelly taxa other classic examples are various microproblematica (small shelly fossils) that are especially characteristic of the earliest Cambrian (Bengtson 1977), the enigmatic conoidal shells *Salterella* and *Volborthella* that Yochelson (1977) has placed in the extinct phylum Agmata, and possibly the archaeocyathids. In the absence of associated soft-parts and sometimes disarticulation of skeletal elements (Bengtson & Conway Morris 1984) a detailed discussion of the likely affinities of these enigmatic groups is often frustrated; for example, there has even been disagreement whether archaeocyathids are better considered as animals or plants (Sepkoski 1979; see also Debrenne & Vacelet 1984). Recent research in Cambrian soft-bodied Lagerstätten, however, has provided important insights on problematical groups in Cambrian biotas. In the Burgess Shale, for example, there are at least ten soft-bodied species that, if found in a modern marine biota, would probably be hailed as new phyla. This figure compares with the ten extant phyla known from this deposit, taking arthropods as a single phylum.

There is an understandable reluctance to designate these problematica, some of which are monospecific and may be known from only a few specimens, as individual phyla. While most workers would accept the morphological distinctiveness of *Salterella* and *Volborthella*, the phylum Agmata has yet to win wide recognition. While the taxonomic inflation that would follow the establishment of large numbers of extinct phyla could formalize observations on the morphological diversity in early metazoan biotas, it provides no explanation of the evolutionary mechanisms involved and may even be potentially misleading. Because the inter-relationships of the problematic groups with each other and extant phyla are so speculative this latter point is better explained by reference to major diversification within a clade, especially as the evolutionary mechanisms that produced a taxon now regarded as a class or phylum are arguably no different from those operating in the evolution of lower taxonomic ranks, that is, speciation (see below).

To illustrate this point perhaps no better example can be found than the problems surrounding the relationships and classification of the Burgess Shale non-trilobitic arthropods (Briggs & Whittington 1981), although comparable features characterize the less diverse priapulids (Conway Morris 1977) and polychaete worms (Conway Morris 1979*c*). One of the most notable achievements of the redescription of the Burgess Shale arthropods has been the detailed documentation of the 30-odd species and the inability to accommodate securely practically any of them in one of the four extant classes (phyla of some authorities): Chelicerata, Crustacea, Trilobita, Uniramia. The only exceptions are *Canadaspis*, an unequivocal crustacean (Briggs 1978*b*), and possibly *Perspicaris* and *Aysheaia* (Briggs 1983). A few other genera appear to have crustacean (for example, *Plenocaris*, *Waptia*) or chelicerate (for example, *Sidneyia*) characters, but otherwise these and the remaining genera are a morphological amalgam that prohibits their inclusion in a major arthropod clade. Classification of these arthropods presents seemingly insurmountable problems. On the one hand *Canadaspis* can be securely and precisely classified within the taxonomic hierarchy, and the emphasis of its being 'the earliest positively identified crustacean' (see Briggs 1983) is understandable given that crustaceans were to prove a supremely successful clade. It is, however, the only taxonomic straw to clutch and the higher order classification of the remaining arthropods remains in a state of flux. The resolution of this problem seems to depend largely on the temporal perspective adopted by an observer; a higher level classification is largely a matter of hindsight (see, for example, Runnegar 1978; Glaessner 1984). A hypothetical Cambrian arthropod systematist, having no means of predicting the future success of clades (Conway Morris & Whittington 1979), would have been unlikely to single out *Canadaspis* for special attention. Such a worker presumably would have been faced with the same taxonomic problems that confront systematists that classify a Recent group in the throes of an adaptive radiation. They may erect a myriad of species separated by trivial differences, but tend to find a higher order classification difficult to apply. This was succinctly summarized by Stasek (1972) who in considering the origin of molluscs made a crucial statement that 'some of the very traits now held to be basic in defining the individual phyla were, in their incipient stages, nothing more than variable minor traits of specialization integrated in a single broad framework'.

If bodyplans are recognized only in hindsight then this has interesting implications on both our interpretation of early metazoan evolution and the fate of what appear to us as early evolutionary 'experiments' or 'failures'. The former problem is exemplified by Valentine's (1973) hypothesis of metazoan coelomate superphyla evolving in the late Precambrian and ancestral to the coelomate phyla. Conjuring up again my hypothetical systematist, this time in the late Precambrian, it seems impossible that he would have been in a position to recognize a superphylum. Rather, the observer would have seen generalized species of metazoans with the incipient traits of specialization, for example, metameric segmentation, radula, undivided coelom, that are now regarded as the cornerstones of the major phyla.

Many authors have drawn attention to the apparent abundance in the Lower Palaeozoic of morphologically distinct forms that were geologically short-lived, and have inferred a 'weeding out' that eliminated both adaptive strategies and morphotypes (for example, Strathmann 1978; Strathmann & Slatkin 1983; Sprinkle 1983). While there is no reason to doubt this happened, its importance may be exaggerated according to our now distant perspective. Among the Cambrian arthropods, for example, only four (chelicerates (or their immediate ancestors), crustaceans, trilobites, uniramians) were in the long term sucessful in terms of cladogenesis and geological longevity. Assuming each class is monophyletic they must have evolved from four separate species (possibly sharing a common ancestor) each undergoing a series of subsequent adaptive radiations that have populated the planet with tens or hundreds of millions of species over the last 500 Ma. The numerous Cambrian arthropods of uncertain systematic position, so well exemplified in the Burgess Shale, that became extinct may owe their demise to 'several reasons: they turn out to be inferior competitors or unsuccessful avoiders of newly arising predators; their body plans offer limited potential for diversification; they fail to adapt to changes in the physical environment; or they simply happen to decline by chance before attaining high enough diversity for stochastic fluctuations to pose no threat' (Stanley 1976). Given the very high proportion of Burgess Shale arthropods that appear not to be ancestral to a major group it seems that chance factors played an important role in moulding the direction and style of metazoan evolution. As already pointed out in discussing the comparative merits of wiwaxiids and molluscs (Conway Morris 1985*a*), a rerunning of the early Phanerozoic adaptive radiations might well result in a very different suite of successful bodyplans emerging to dominate subsequent evolutionary history.

Problematic groups are not confined to the Cambrian, but their relative abundance in contrast to later in the Phanerozoic calls for an explanation, in the context of early metazoan evolution. Many authors have considered that the initial opportunities presented by the invasion of an effectively empty ecospace permitted a wide range of morphological designs to be unleashed on the early Phanerozoic world. Various proposals have been made to explain this morphological diversity by radically restructuring the genome (see, for example, Valentine & Campbell 1975; Valentine & Erwin 1983; Erwin & Valentine 1984). However, it is not clear whether the underlying genetic mechanisms differed materially from those operating during any other period of metazoan history. For example, Runnegar (1982) drew attention to the continuing evolution of 'major evolutionary experiments' such as those among Cainozoic molluscs, and suggested that 'the peculiarity of the Cambrian fauna does not reflect any fundamental difference in the mode or tempo of the evolutionary process; rather it is a reflection of our distance from it'. Until objective criteria permit the morphological distance between and within groups to be judged, and linked to underlying changes in the genome it may be premature to consider the Cambrian metazoan diversification as qualitatively distinct from any other set of adaptive radiations.

(*c*) *Community ecology and evolution*

Attendant on the adaptive radiations of the early metazoans was a series of ecological innovations, best studied palaeoecologically by the relationship of the organism to the substrate and its trophic niche. Among shelly groups such as echinoderms (Sprinkle 1976, 1980) valuable information regarding their evolving ecological ranges is already available, but among many other groups, for example, trilobites, their palaeoecology, especially trophic analysis, remains insecure. Information from shelly remains may be supplemented by trace fossils that provide useful insights, particularly among deposit feeders, grazers and on occasion carnivores (Alpert & Moore 1975). Nevertheless, study of the synecology of the Burgess Shale biota (Conway Morris 1981) indicates that by themselves shelly assemblages provide a woefully inadequate picture. Deposits such as the Burgess Shale that appear to be representative of Cambrian communities should provide fresh insights into marine ecology. On the basis of shelly species Cambrian communities are characterized as ecologically generalized and dominated by deposit feeders and some suspension feeders (for example, Valentine 1973*b*; McBride 1976). Study of the Phyllopod bed community of the Burgess Shale confirms the importance of these trophic groups, but indicates hitherto unexpected complexities that include possible tiering in suspension feeders (Conway Morris 1979*a*) and the important role of predation (Conway Morris 1977, 1979*a*, 1981, 1985*a*). Proper documentation of Cambrian communities must include data from soft-bodied Lagerstätten, and in doing so we may be in a position to understand to what extent the underlying ecological structure of some Palaeozoic marine communities was laid down the early stages of metazoan diversification.

Some aspects of long term evolution of the community structure and ecology of Palaeozoic marine life will be discussed elsewhere, and space permits only some brief comments. There appears to be evidence to suggest that certain (by no means all) soft-bodied Lagerstätten tend to sample evolutionarily conservative marine faunas that may have inhabited cooler, deeper waters with possibly lower levels of oxygen. Such environmental conditions probably would have helped to promote exceptional preservation, especially in combination with catastrophic burial that might be favoured on deeper water slope sites. One facet of any debate concerning the extent to which soft-bodied Lagerstätten are representative of marine communities will be the need to examine their preservation potential across the shelf slope transect, the palaeo-oceanographic conditions, and the ecological and phylogenetic longevity of the associated marine biotas.

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