Burgess Shale Faunas and the Cambrian Explosion

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Soft-bodied marine faunas from the Lower and Middle Cambrian, exemplified by the Burgess Shale of British Columbia, are a key component in understanding the major adaptive radiations at the beginning of the Phanerozoic ("Cambrian explosion"). These faunas have a widespread distribution, and many taxa have pronounced longevity. Among the components appear to be survivors of the preceding Ediacaran assemblages and a suite of bizarre forms that give unexpected insights into morphological diversification. Microevolutionary processes, however, seem adequate to account for this radiation, and the macroevolutionary patterns that set the seal on Phanerozoic life are contingent on random extinctions. They weeded out the morphological spectrum and permitted rediversification among surviving clades. Although the predictability of which clades will play in successive acts of the Phanerozoic theater is low, at least the outlines of the underlying ecological plot are already clear from the opening of the drama.

T HE FOSSIL RECORD MAY BE THE BOOK OF ORGANIC HIS-
tory, but like the worst of chroniclers, the scribe responsible
suffers from shocking lapses of memory and much prefers the
broad brush of interpretation to finicky minutia. His myrmidons,
the paleontologists, are largely resigned to documenting fossils in
the gloomy knowledge that it is at best an adumbration of original
organic diversity. The biases that militate against a complete record
are many: some are obvious, like the almost total absence of soft
parts because of the rapidity of decay in most sedimentary environ-
ments. Others are marginally more subtle, such as differential
behavior of hard parts in the face of transport, physical abrasion, and
chemical attack. The resulting jumbled heaps of shells and bones
may be the somber norm for paleoecological reckoning, but on rare
occasions a page of the great book flutters into our hands almost
intact, and by the preservation of soft parts we are afforded a
tantalizing glimpse into the riches of past life. Of such deposits,
arguably none holds greater significance than the Burgess Shale and
its congeners in the Cambrian.

Metazoan Origins

In order to explain the significance of Burgess Shale–type faunas,
they must be set in the context of early metazoan evolution (1–3). In
terms of the fossil record, our understanding centers upon the
abrupt appearance of metazoans during the latest Proterozoic
(Vendian) in the guise of the Ediacaran faunas, followed shortly

afterwards by an astonishing diversification that is colloquially
labeled the Cambrian explosion. In essence, the problems set by
these events are three-fold: Is the fossil record a reliable indicator of
first appearances? What phylogenetic links lie between Ediacaran
and Cambrian faunas, including those of Burgess Shale type? What
triggers and constraints underlay and channeled these adaptive
radiations? With regard to the possible timing of metazoan origina-
tion, there may be a major discrepancy between the fossil record and
molecular inferences based on proteins and RNA in extant species
(4). The molecular data suggest that metazoans emerged anytime
between 700 and in excess of 1000 Ma (million years ago).
Ediacaran faunas, in contrast, are substantially younger. A recent U-
Pb determination on zircons from a tuff that smothered an Edia-
caran community in southeast Newfoundland provides an apparent-
ly acceptable date of 565 Ma (5), and most of the other faunas are
probably younger than 600 Ma.

There is no shortage of candidates for pre-Ediacaran metazoans,
mostly in the form of putative trace fossils (6). Many have been
debunked, and their scarcity and lack of diagnostic features has
excited skepticism. The failure to find unequivocal evidence should
not necessarily be construed as a definitive rejection of the notion
that there were pre-Ediacaran metazoans. Rather, our expectations
have probably been misplaced by excessive reliance on Phanerozoic
examples. Any pre-Ediacaran metazoans probably were minute,
ecologically analogous to the modern meiofauna (7) (if benthic) or
zooplankton. Recognition might well depend on subtle interpreta-
tion of bioturbation fabrics (8) or minute fecal pellets (9).

Even with the appearance of Ediacaran faunas (2, 3), our knowl-
edge of the earliest definitive metazoans remains imperfect. The
majority of forms appear to be either cnidarians or of a comparable
organizational grade; others seem to represent arthropods, annelids
(10), and possibly even echinoderms (11). Almost all were soft-
bodied and some reached a substantial size. There is, however, a
striking lack of continuity with the succeeding Cambrian faunas (2).
In part this caesura must be taphonomic, reflecting the contrasts
between the prevalence of soft-part and skeletal preservation in
Ediacaran and Cambrian times, respectively. However, there are
also indications that this discontinuity may reflect major extinctions
(2, 3, 12) in the Ediacaran assemblages. Evidence for extinctions
includes the disappearance of Ediacaran faunas in several strati-
graphic sections (13, 14), even where overlying facies appear
favorable for soft-part preservation. The few fossils in this interval,
before the widespread onset of skeletal fossils, are only simple traces
(14). Indeed, could the subsequent Cambrian explosion be in part a
response to the ecological vacancies occasioned by the demise of
much of the Ediacaran faunas (2)?

The Cambrian radiations by necessity are largely documented by

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the burgeoning skeletal faunas (1). They occur first as distinctive assemblages of small skeletal fossils (15, 16) and archaeocyathids, but in due course are largely substituted by typical Cambrian faunas consisting of trilobites, brachiopods (especially inarticulates), hyoliths, tubicolous taxa, echinoderms, and sponges (the last two largely represented by dispersed ossicles and spicules, respectively). However, even had this planet not seen even a single species evolve with fossilizable hard parts, a not so implausible supposition given that the vast majority of metazoans have a minimum fossilization potential, the scope of the Cambrian explosion would remain obvious from the parallel diversification of soft-bodied animals (17). This diversification is apparent from the increase in variety of trace fossils close to the Vendian-Cambrian boundary and reflects a remarkable flowering of behavioral repertoires such as hunting strategies, ability to penetrate substrates, or methods of locomotion.

Whereas this diversity must reflect a corresponding range of morphologies, trace fossils suffer the disadvantage that with the habitual absence of a juxtaposed animal, the precise identity of the maker is seldom clear. This problem is compounded because effectively identical traces can be formed by very different animals. In addition, many soft-bodied animals fail to leave traces and so elude ichnological tally. Only by turning to the Burgess Shale–type faunas (18), in which the soft-bodied component accounts for the great bulk of species, individuals, and biomass, does the magnitude and extent of the Cambrian explosion become apparent.
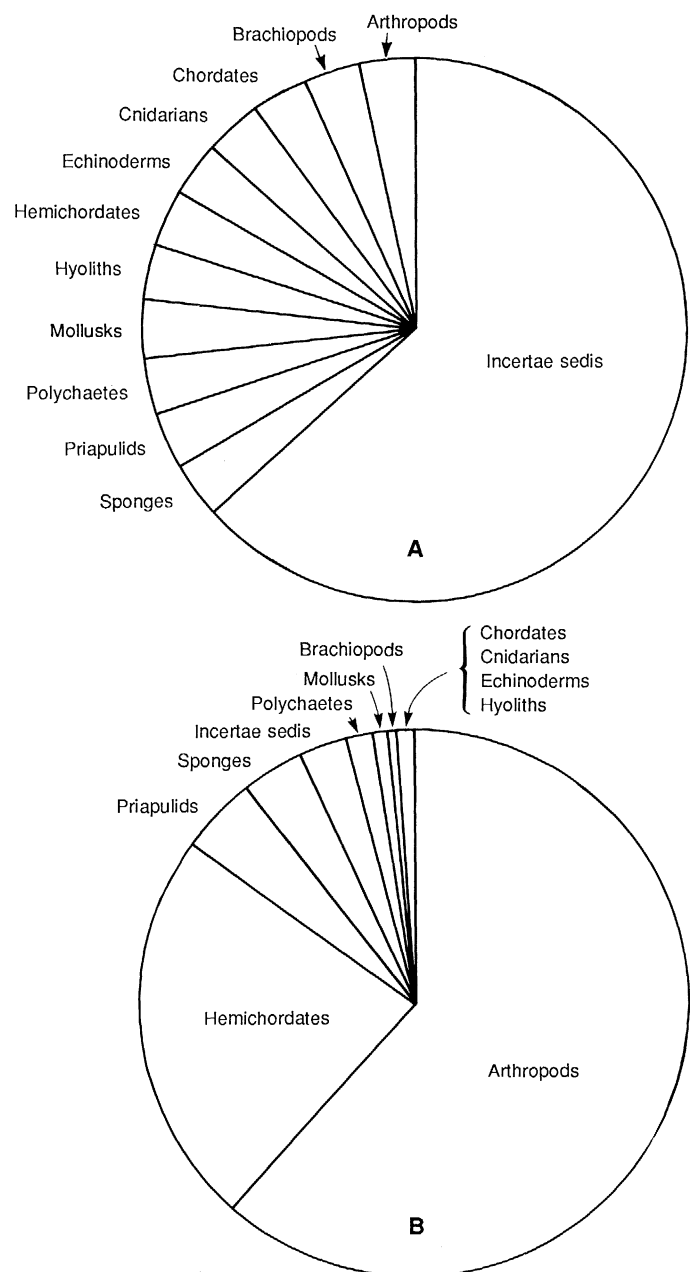
Burgess Shale–Type Faunas

The type example is the collection of approximately 73,300 specimens from the Phyllopod bed (19), exposed in the Walcott Quarry above the town of Field, British Columbia. This bed is an informal stratigraphic unit in the Stephen Formation (~310 m thick), a basinal sequence of mudstone and siltstone that was deposited beside, and finally overwhelmed, a carbonate reef. In the vicinity of Field, this carbonate reef formed a vertical escarpment that in places reached 200 m in height (20). The fauna (Fig. 1) is represented by about 120 genera, mostly monospecific. These fall into 12 major groups: arthropods, polychaete annelids, priapulids, sponges, brachiopods, mollusks, hyoliths, echinoderms, cnidarians, chordates, hemichordates, and incertae sedis; the informal category of incertae sedis comprises at least 19 distinct body plans that for the most part are as different from each other as any of the remaining phyla in the fauna. There is also a flora consisting of a variety of algae. This includes macroscopic filaments of cyanobacteria and probable red and green algae (21, 22), as well as acritarchs (23).

The reasons for the extraordinary quality of preservation are not clear. Rapid burial from turbid clouds of sediment, deposited as microturbidites, in an anoxic environment, as deduced from sedimentary laminations unbroken by bioturbation, were contributory (19). The soft tissues and calcareous hard parts are now composed of silicates (for example, chlorite, potassium micas), although some of the hard parts may contain relict patches of original mineralogy. Organisms that had phosphatic skeletons appear to have retained their original composition, albeit with diagenetic alteration (24). Bacterial replacement has been invoked as a mechanism for soft-part preservation in other deposits (25), and the ability of some bacteria to precipitate silicates (26) suggests that this mechanism was a possible diagenetic path for Burgess Shale–type fossilization.

Most Burgess Shale–type faunas lived in deep-water environments on the open shelves and facing the open ocean (19, 27). That they are typical Cambrian assemblages can be demonstrated, however, by imagining that the extraordinary preservational environment had been held in abeyance so that only normal shelly species passed

Fig. 1. Pi diagrams of the relative importance of different groups in the Phyllopod bed of the Burgess Shale, according to principal body plans (total number, n = 30) and number of individuals (n = 39,809). Upper circle (**A**) depicts 11 body plans that persist until the Recent as phyla, and 19 enigmatic taxa (incertae sedis) each with an anatomy that precludes assignment to any extant phylum [*Amiskwia* (Fig. 3C), *Anomalocaris* (Fig. 3D), *Banffia* (Fig. 4B), *Cambrorhytium*, *Dinomischus* (Figs. 3A and 4C), *Eldonia* (Fig. 4E), *Fasciculus*, *Hallucigenia* (Fig. 7), *Mackenzia* (Fig. 5, B and C), *Nectocaris* (Fig. 4A), *Odontogriphus*, *Oesia*, *Opabinia* (Fig. 3E), *Portalia*, *Priscansermarinus*, *Redoubtia* (forms distinct from that in Fig. 5D), *Tubulella*, *Wiwaxia* (Figs. 3B and 4D), and *Worthenella*]. Lower circle (**B**) refers to individuals inferred to have been alive at the time of burial. Such a supposition is based principally on preservation of soft parts, as well as estimates of living fraction of the skeletal groups of brachiopods, hyoliths, molluscs, trilobites. Among arthropods, trilobites probably account for only about 4.5% of individuals alive at time of burial. Data for lower circle derived from (19), but modified in that estimate of number of living trilobites has been revised upward on the assumption that a greater proportion of articulated material was alive at time of burial. In addition, *Eldonia* (Fig. 4E) has been transferred from echinoderms to incertae sedis.

through the taphonomic filters. The resultant assemblage is a pale shadow of actual diversity, representing perhaps 15% of the genera, and probably less than 5% of individuals alive at the time of burial (19). However, the taxonomic profile is indistinguishable from most other Cambrian faunas in being composed of trilobites, brachiopods, hyoliths, and monoplacophorans (28). Burgess Shale–type faunas, therefore, are not arcane and endemic oddities on the sidelines of Cambrian life; their relative completeness permits a detailed inspection of ecology and evolutionary processes in the throes of the Cambrian explosion.

Even if the Phyllopod-bed biota can be shown to be exceptional in terms of preservation rather than original composition, that it is representative of Cambrian life is much more certain now that comparable assemblages have been found. Walcott described another productive layer about 20 m above the Phyllopod bed (now termed the Raymond Quarry), and recently many other localities have been discovered nearby (29). Of greater significance is the recognition of more than 30 other localities (Fig. 2) beyond the vicinity of Field in which Burgess Shale–type faunas occur (27). The Laurentian (United States, Canada, Greenland) occurrences encircle the North American craton and typically face the open ocean; evidently the fauna could migrate around the craton margins. Localities on other cratons, including the South and North China blocks, Australia, and the East European platform, also demonstrate that transoceanic migration either via the deep-sea or pelagic drift occurred.

Not only do Burgess Shale–type faunas have a wide distribution, but they also encompass much of the Lower and Middle Cambrian. The earliest occurrence appears to be from deep boreholes in northeast Poland (Fig. 2) where cuttings of the Zawiszyn Formation have yielded lightly skeletalized arthropods and an anomalocarid (30), the latter best known from the Phyllopod bed where reconstructions (Fig. 3D) portray an extraordinary predator that may have reached 1 m in length (31). The mouth, which is encircled by a series of spinose plates that evidently acted as a contractible diaphragm to hold and contuse prey, was flanked by a pair of jointed appendages also inferred to have been used for prey capture and

manipulation (32). Typically these appendages have been found separated from the rest of the body, and as such the anomalocarids had been unequivocally classified as arthropods (33). However, the entire anatomy reveals a metazoan that, although segmented, has such an unusual body plan that attribution to the arthropods is difficult to accept (31). Co-occurring with these soft-bodied remains is Mobergella, a disk-like phosphatic fossil that although of uncertain affinities (34) dates the sedimentary rocks as upper Tommotian or possibly lower Atdabanian [Lower Cambrian (30, 34)].

Recent remarkable finds from Chengjiang, near Kunming in Yunnan Province, China, reinforce the view that Burgess Shale–type faunas were integral to the Cambrian radiations. Here, a prolific soft-bodied fauna includes arthropods (35), priapulids (36), sponges (37), cnidarians (38), and various problematical fossils (39, 40), some of which have been subject to reinterpretation (22, 27). Striking similarities with the Burgess Shale fauna include cogeneric occurrences such as Naraoia (arthropod), Leptomitus (sponge), Eldonia, Dinomischus (both incertae sedis; compare Figs. 3A and 4, C and E), and probably Ottoia (priapulid). Co-occurring trilobites have been claimed to be among the oldest known (41), but as beds beneath horizons with the soft-bodied fauna yield upper Atdabanian (middle Lower Cambrian) shelly fossils, this suggestion is unlikely (16, 42).

Most of the other Lower Cambrian occurrences are represented by only a few Burgess Shale–type taxa, with two conspicuous exceptions. One, the Kinzers Formation of Pennsylvania, is a widely exposed unit, but the key localities where soft parts are preserved (43) are no longer accessible. The other, from the Buen Formation of Peary Land in North Greenland, contains a rich fauna of arthropods, worms, and sponges (44). Both deposits are younger than the Chengjiang occurrences, but their position on the Laurentian craton (Fig. 2), which was far removed from South China in the Cambrian, argues for transoceanic communication. The distribution of deep-water, subthermocline trilobites in the Upper Cambrian around a proto-Pacific rim (27, 45) provides an apparently similar example. As with Recent deep-water assemblages, the Burgess Shale–type faunas may have been widespread in the oceans, and
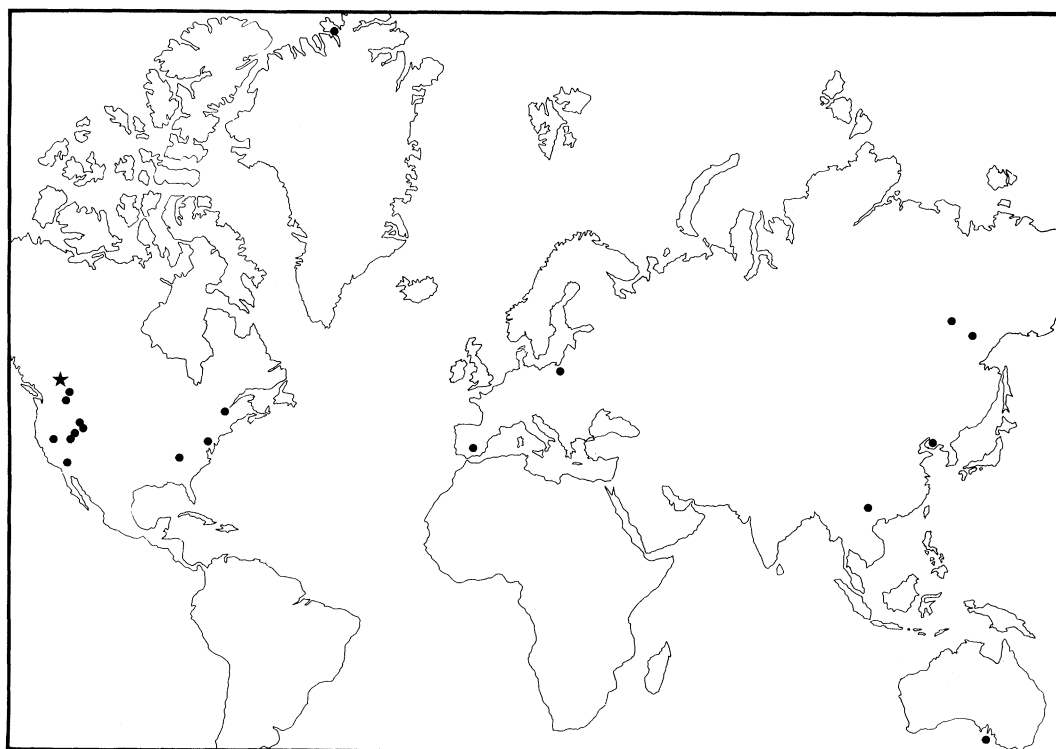

Fig. 2. Distribution of Burgess Shale–type faunas; type locality is starred. Localities include sites in North America (California, Nevada, Utah, Idaho, Tennessee, Pennsylvania, Vermont, British Columbia, and north Greenland), Spain, Poland, South Australia, South China, North China, and Siberia. Details of precise locations and stratigraphic horizons of the 34 localities currently known are given in (27).

their now scattered distribution on cratonic margins may represent preserved marginal onlaps from the ocean basins.

There are two important modifications to this general model of the distribution of the fauna that require further testing. Although the bulk of the Burgess Shale–type faunas are demonstrably benthic, at least as adults, rare components appear to have been pelagic (19). In the Burgess Shale, these include gelatinous worms with bizarre body plans such as *Amiskwia* (Fig. 3C) and *Odontogriphus*, perhaps the enigmatic medusiform *Eldonia* (Fig. 4E), and bivalved arthropods such as *Isoxys* and possibly *Tuzoia*. In some deposits (27) that appear to have been relatively nearshore, such as shales associated with archaeocyathid reefs in the Atdabanian Pedroche Formation of Spain, the Emu Bay Shale of South Australia, and the Eager Formation of British Columbia (both upper Lower Cambrian), the occurrence of *Isoxys* or *Tuzoia*, or both, indicates that these members of the fauna had a swimming mode of life. The more important qualification is that limited evidence suggests that the

Burgess Shale–type faunas had shallow-water origins. A trend of displacement into deeper water habitats with time might be contributory evidence to the general model of offshore migration of the three "evolutionary faunas" (Cambrian, Paleozoic, and Modern) during the Phanerozoic (46). The earliest Burgess Shale–type faunas, from the Polish boreholes and Chengjiang, both appear to represent nearer shore deposits than the great majority of ocean-facing sites known from the upper Lower Cambrian and younger rocks. In addition, the Polish localities contain *Mobergella* (30), which is typical of shallow-water environments (34).

Our understanding of the Lower Cambrian history of Burgess Shale–type faunas should substantially improve in the next few years, especially on account of the Chengjiang (35–40) and Buen (44) faunas. At present, however, much of our information comes from Middle Cambrian occurrences, most of which are from the western Cordillera (British Columbia, Idaho, and Utah; Fig. 1). These records attest to the striking generic longevity of many Burgess taxa, itself another characteristic of many other deep-water assemblages (27). Paradoxically, this longevity imparts an evolutionary conservatism to these faunas, and the Phyllopod bed's importance clearly lies as a sampling horizon. Thus, although it houses the greatest diversity of Burgess taxa (presumably a reflection of exceptional taphonomy and history of collecting), of the 41 genera known from other horizons, more than 90% occur in rocks that are older than the Phyllopod bed.

The ultimate fate of the Burgess Shale–type faunas is unclear. Their conspicuous absence in the Upper Cambrian could be attributed largely to deposition of inappropriate facies (27). Although a number of Burgess Shale–type sponges have been reported from the Lower Ordovician (Arenig) of Quebec, the next principal deposit containing soft-bodied fossils, the Upper Ordovician (Caradoc) "Beecher's Trilobite bed" of New York, appears to lack Burgess elements (47). This scanty evidence could be construed in terms of a gradual ebbing of Burgess Shale–type faunas, perhaps in the face of successive invasions into deeper water by displaced shelf-dwelling species, so that by the Middle Devonian only a few archaic survivors are recognizable (19, 27). An alternative possibility is that the demise of the Burgess Shale–type faunas was much more abrupt, such that most of the assemblage was extinct by the end of the Cambrian.

Cambrian Paleoecology

The limited contribution of shelly taxa to taxonomic diversity and their trivial importance in terms of numbers of individuals and inferred biomass in the Burgess Shale–type faunas means that the latter are becoming the cornerstone to understanding Cambrian ecosystems. The most detailed of paleoecological analyses are based on the biota from the Phyllopod bed (19), but the overall similarities among Burgess Shale–type faunas (27) support their general applicability. The ecological diversity is striking and includes abundant representatives of an infauna and epifauna, as well as a nektobenthos and even rarer elements from the pelagic realm. A conspicuous component of the infauna are priapulid worms. Some are inferred to have been active burrowers. Given their large size (up to 15 cm for the actively burrowing *Ottoia*) and abundance, it might be predicted that bioturbation was pronounced, with sediment mixing extending to at least 10 cm. Direct evidence, at least in the Phyllopod bed, of associated trace fossils is unavailable because redeposition from small turbidity currents destroyed sedimentary fabrics of the preslide environment (19, 20). Ichnological studies of Cambrian offshore carbonates, however, indicate little penetration deeper than a few centimeters (48), although much deeper burrows are known in shallow-water sediments (49). Other members of the infauna in-
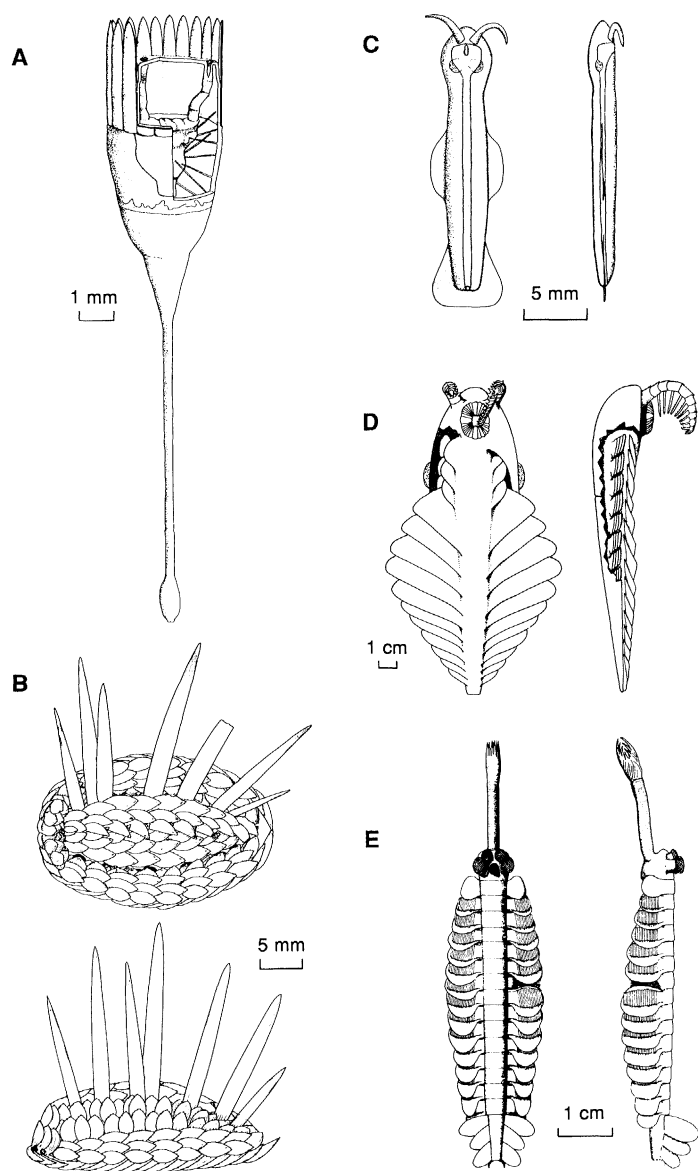

Fig. 3. Reconstructions of five problematical fossils from the Burgess Shale. (**A**) *Dinomischus isolatus*, part of calyx cut away to reveal internal anatomy of alimentary canal supported by mesenterial filaments; (**B**) *Wiwaxia corrugata*, in dorsal view with left-hand row of spines removed and lateral view; (**C**) *Amiskwia sagittiformis* in ventral and lateral view; (**D**) *Anomalocaris nathorsti* in ventral and lateral view; (**E**) *Opabinia regalis* in dorsal and lateral view.

clude polychaetes, palaeoscolecidans (*50*), and what appear to be hemichordate enteropneusts (*19*).

The sessile epifauna is dominated by sponges, brachiopods, *Chancelloria*, echinoderms, and the enigmatic *Dinomischus* (Figs. 3A and 4C). Study of the Phyllopod bed suspension feeders had indicated that the community was tiered (*51*) and that the maximum height of the community above the sediment-water interface was about twice that which has been inferred from general surveys (*52*). Arthropods account for most of the vagrant epifauna and are joined by monoplacophoran molluscs (*28*), wiwaxiids (Figs. 3B and 4D) (*53*), and hyoliths. Much of the vagrant epifauna is inferred to have been deposit feeders. A log-linear or geometric distribution of the dominance diversity curve (*19*) for this ecological category may indicate that resource portioning followed the model of niche preemption. In this model, the dominant species (in terms of number of individuals) apportions a given fraction (k) of a resource, the next dominant species the fraction (b) of the remainder, and so forth.

Another striking result of paleoecological analysis has been the recognition of the major role of predators. In the Phyllopod bed, benthic predators (and scavengers) account for about 13% of genera, 7% of individuals, and 30% of the biomass (*19*). Even in modern marine communities, this trophic group typically has a significantly lower preservation potential than other feeding types (*54*), and the absence of predators in other Cambrian assemblages is an artifact of incomplete preservation (*53*). In the Phyllopod bed evidence for predation comes from mouth parts, and more conclusively, gut contents [crushed shells have been found in the hind gut of *Sidneyia* (arthropod), and entire hyoliths and other shelly taxa occur in *Ottoia* (priapulid)]. Indirect evidence for the importance of predators also comes from *Wiwaxia* (incertae sedis): their sclerites evidently formed a protective coat (Fig. 3B), and the elongate spines, broken in many specimens, presumably helped also to deter attack (*53*).

Above the sediment-water interface, nektobenthic animals included various enigmatic forms [for example, *Anomalocaris*, *Opabinia* (Fig. 3, D and E)], some polychaetes and primitive chordates. Those that lived close to the sediment-water interface evidently faced greatest risk of burial by turbidity currents or storm events. A remarkable pelagic biota (Figs. 3C and 4, A and E), mostly of enigmatic taxonomic position, has adaptations that include prominent fins and gelatinous bodies. Some, such as *Eldonia* (Fig. 4E), may have formed shoals.

Ediacaran Survivors

At first sight, the contrasts between the Ediacaran faunas and those of the Cambrian seem almost absolute (*2, 3*). In the case of most Cambrian assemblages, which are composed only of robust skeletal remains, these differences could be attributed to taphonomic contrasts in that Ediacaran assemblages are soft-bodied. Inclusion of Burgess Shale–type faunas in these comparisons would also seem to support the proposal that there is indeed a profound biotic discontinuity across the Precambrian-Cambrian boundary. Such a discontinuity would be consistent with the hypothesis that there was a mass extinction of Ediacaran forms. However, just as any other mass extinction has its quota of survivors, so it seems reasonable to search for stragglers from the postulated catastrophe. One dubious candidate is a questionable specimen of *Dickinsonia* from the Lower Cambrian of Kazakhstan (*55*), a form that otherwise occurs in abundance in the richly fossiliferous Ediacaran beds (*3*) of the Flinders Ranges (South Australia) and White Sea exposures (Russia). Its record remains controversial (*3*), and *Dickinsonia* is not known from any Burgess Shale–type fauna. However, examples of a

chondrophore (*Rotadiscus grandis*) from Chengjiang (*38*) may be linked with the diverse assemblage of Ediacaran chondrophores (*Eoporpita*, *Ovatoscutum*) (*3*). In the Phyllopod bed, one specimen, erroneously attributed to the uniramian-like *Redoubtia polypodia* (Fig. 5D), may also be a chondrophore; its prominent reflective structure may represent a float surrounded by tentacles. Another intriguing organism is *Mackenzia costalis* (Fig. 5, B and C), which grew to about
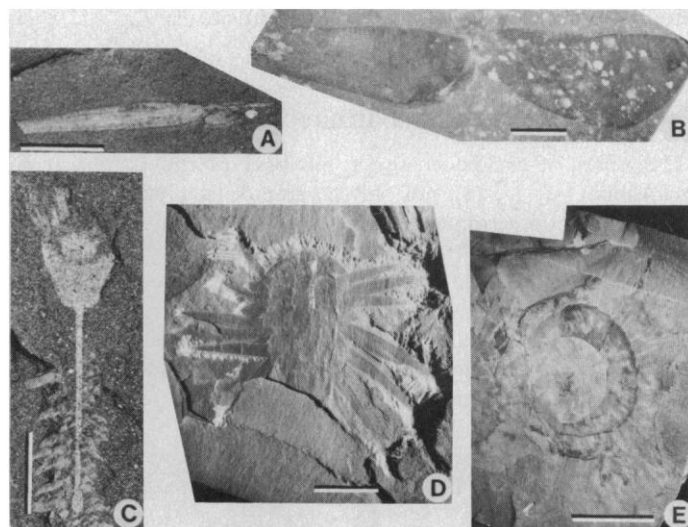
Fig. 4. Problematical fossils of the Burgess Shale, Field, British Columbia. (**A**) *Nectocaris pteryx*, a probable pelagic organism; (**B**) *Banffia constricta*, a benthic worm; (**C**) *Dinomischus isolatus*, a sessile animal with stalk supporting calyx-like body; compare with Fig. 3A; (**D**) *Wiwaxia corrugata*, a benthic animal with a covering of sclerites and spines; compare with Fig. 3B; (**E**) *Eldonia ludwigi*, a pelagic medusiform creature. Scale bars 5 mm in (A) and (C), 10 mm in (B) and (D), and 30 mm in (E).
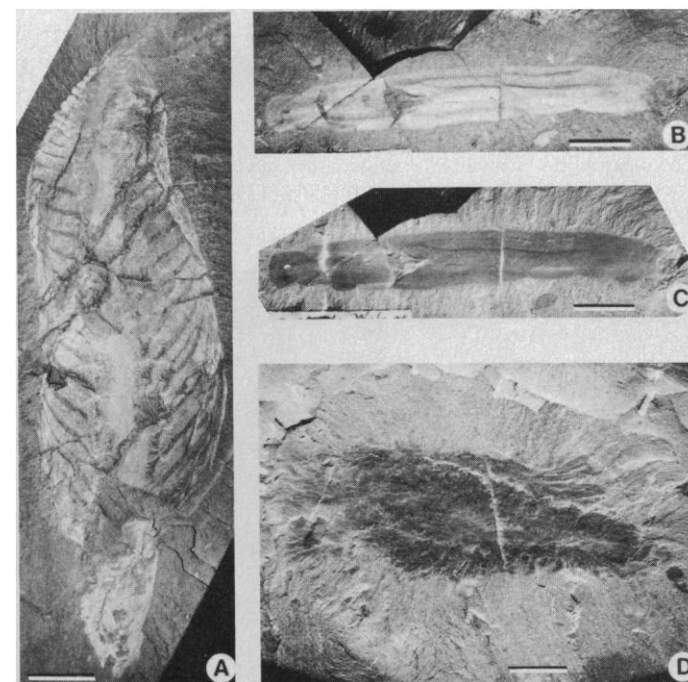
Fig. 5. Possible Ediacaran survivors from the Burgess Shale, Field, British Columbia. (**A**) An undescribed sea-pen–like organism; (**B** and **C**) *Mackenzia costalis*, an enigmatic bag-like organism; (**D**) "*Redoubtia polypodia*," an organism of uncertain affinities that might be compared to chondrophore-like animals. Scale bars, 10 mm in (B), (C), and (D) and 20 mm in (A).

16 cm in length. It has not been fully described and classified, but it appears to consist of a bag-like body, possibly with internal partitions. Evidence for a benthic mode of life includes attachment to isolated eocrinoid stems. Although allied to cnidarian anemones, *Mackenzia* might be better compared to similar Ediacaran animals (*2*), including *Platypholinia pholiata* (*56*). The Phyllopod bed also contains a number of pennatulacean-like animals (Fig. 5A) that are similar to some Ediacaran taxa. These Cambrian examples await detailed study, but available data suggest that these animals may differ in various respects from extant pennatulaceans.

The Rise of Skeletal Faunas

The onset of skeletogenesis at the base of the Cambrian is remarkable (*1–3, 15, 16*), not only because of its apparent abruptness, but also on account of the diversity of skeletal types. Some fossils can be attributed to major groups such as the mollusks and sponges, but many of the other small skeletal fossils are enigmatic. A number of categories have been identified, including tubes, conchs, or valves, sclerites, spicules, and teeth. Among spicule and sclerite-bearing animals, disarticulation of originally complex skeletons is nearly ubiquitous. Sclerite-bearing animals appear to have been
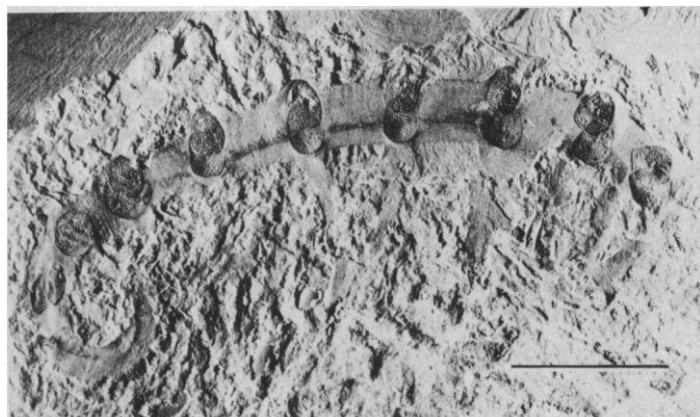
Fig. 6. *Microdictyon sinicum* from the Chiungchussu Formation, Chengjiang, Yunnan, South China. The paired phosphatic plates were previously the only known part of this animal (*58*), but here they can be seen to form a regular series along a lobopod-like structure that might represent an entire animal (*39*). Scale bar is 10 mm.
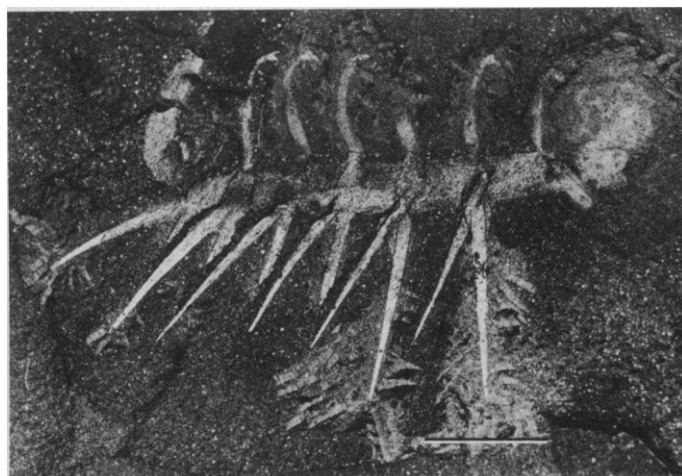
Fig. 7. *Hallucigenia sparsa* from the Phyllopod bed of the Burgess Shale, British Columbia. Composite photograph of part and counterpart of holotype. Scale bar is 5 mm.

abundant in the first skeletal faunas, but reconstruction of the scleritome, an important step toward understanding the phyletic relations of these problematic taxa, depends on rare articulated series, combined with analysis of articulation facets. The available scleritome reconstructions remain, therefore, provisional.

New evidence on the origin of skeletal faunas is emerging from the more favored taphonomic environments of Burgess Shale–type faunas. The best example to date lies with a distinctive group that includes the halkieriids and wiwaxiids (*57*). The halkieriids are confined to the Lower Cambrian, and are known almost entirely from disarticulated sclerites. They occur in a variety of distinctive shapes, but their original disposition is unresolved. However, in the Middle Cambrian the descendant form *Wiwaxia* (Fig. 3B) occurs as articulated specimens and therefore provides a template for halkieriid reconstruction. Halkieriids had a tightly integrated cataphract scleritome whose primary role appears to have been defensive. In *Wiwaxia* the sclerites are less tightly articulated and instead of being composed of calcium carbonate are unmineralized (*53*). *Wiwaxia* resembles the mollusks in a number of respects, including a broad ventral foot-like area, a radula-like feeding organ, and a dorsal secretory zone. However, the mode of secretion of the sclerites seems to have been different from that in mollusks, including the aplacophorans and polyplacophorans. In halkieriids and *Wiwaxia* each sclerite appears to have been secreted at a fixed size, and further growth was achieved not by interpolation but by molting of the entire scleritome (*53, 57*).

Another conundrum among small shelly fossils that now approaches a solution is for *Microdictyon*. These are best known as phosphatic disks, typically domed to subconical, composed of a hexagonal network with mushroom-like protuberances on the nodal areas. The affinities of *Microdictyon* were almost entirely enigmatic, and even their functional role has been difficult to establish (*58*). In the Chengjiang fauna, however, elongate soft-bodied structures bear paired plates of *Microdictyon* (Fig. 6) at regular intervals (*39*). These remains suggest that *Microdictyon* was a lobopod-like animal, bearing up to ten segments, although the possibility that the Chengjiang examples are part of some larger animal cannot be ruled out.

The Foundations of Metazoan Architecture

The Burgess Shale–type faunas make a significant contribution to one of the fundamental evolutionary questions, that of the origin of biological novelty. Nowhere is this problem more starkly posed than in the dynamics of the Cambrian explosion, where the rapid diversification produced an astonishing array of morphological designs. Among this riot of types, many of the extant phyla are recognizable, but there are also a diversity of geologically short-lived forms, morphologically so distinct that it is difficult to avoid the sobriquet of "extinct phylum," even though many may be represented by a few, in some cases only one, species.

In terms of skeletal faunas, the archaeocyathids have long been cited as an extinct phylum, but a growing body of opinion places them with the sponges (*59*). However, among the small skeletal fossils, increasing knowledge of scleritomes in groups such as the tommotiids, cambroclaves and halkieriids, or of tube morphology in the triradially symmetrical anabaritids, has reinforced the impression of taxonomic distinctiveness. In few cases, however, has the formal step been taken of erecting new phyla to house these morphological waifs, although the distinctive tubes of *Salterella* and *Volborthella* have been assigned to the Agmata (*60*).

Any doubts about the extraordinary morphological diversity of Cambrian organisms based on assemblages of only skeletal parts are dispelled by the bizarre soft-bodied assemblages in the Burgess

Shale–type faunas (Figs. 3 and 4). Some organisms are obviously segmented, and in the case of *Anomalocaris* (Fig. 3D) (*31, 61*), only the anterior pair of jointed appendages hint at an arthropodan affinity. *Opabinia* (*62*) may be related, but differs in several respects that include its five eyes perched on the top of the head and the elongate proboscis terminating in a grasping structure (Fig. 3E). In contrast, *Dinomischus* (*40, 63*) was a sessile animal, with its calyx supported on an elongate stalk (Figs. 3A and 4C). It might be compared distantly with the entoprocts, but its stiff feeding plates that encircle the calyx find no counterpart in other groups. *Banffia* (Fig. 4B) is one of several peculiar worms; this genus has an anterior section, bearing apparently spiral annulations and separated from a sac-like posterior by a prominent constriction. Even more enigmatic is *Hallucigenia* (*64*) with pairs of stilt-like appendages arising from an elongate trunk, from which on the opposite side a single file of tentacles arise (Fig. 7). In the case of *Hallucigenia* the known specimens may be detached from some larger organism, but it is not clear how its discovery might lead to a more secure taxonomic home.

The first question posed by these animals revolves around the problem of whether our conventional taxonomic procedures, that is assignment to an extinct phylum, is a useful operation. The second is whether we must appeal to special macroevolutionary mechanisms (*65*) to account for the range of metazoans produced in the Cambrian. I argue that the observed diversity is a consequence of occupation of an effectively vacant ecology and that the apparent absence of intermediate forms between major groups is an artifact. Moreover, the taxonomic hierarchy is an imperfect device designed to express an evolutionary genealogy (*66*) that arises because random extinctions allow the contingent occupation of vacated ecospace by cladogenesis of surviving taxa. None of these points is new, but they have a peculiar relevance to the Cambrian biotas on account of the growing realization of the extent and magnitude of these adaptive radiations.

The kernel of our difficulties lies with the taxonomic hierarchy, whose deceptive utility conceals a straitjacket into which phylogenetic thinking is constrained into an essentialist mode that lacks historical perspective and loses sight of the contingent processes that haunt every step of biological diversification. Nowhere is this more evident than in the definition of a phylum. Here is the quintessence of biological essentialism, a concept that is almost inextricably linked with that of the body plan. For most of the Phanerozoic, the status of phyla (and classes) seems to be effectively immutable, the one fixed point in the endless process of taxonomic reassignments and reclassification. However, for the Cambrian radiations, such precepts begin to fail and our schemes of classification lose relevance.

No assemblage shows this more clearly than the Burgess Shale–type arthropods (*67*). Not only does the Phyllopod bed show an astonishing diversity of types, but as new faunas are described, the cavalcade of morphologies seems to be almost inexhaustible. The overall impression is of an enormous mosaic, individual species being assembled according to differences in number and types of jointed appendages, number of segments and extent of tergite fusion, and overall proportions of the body. Notwithstanding the enormous range of Burgess Shale–type arthropods (*18, 22, 35, 44, 67*), we most likely have available only a small fraction of the original diversity. Apart from the trilobites, the classification of this riot of arthropod morphology has proved almost intractable in terms of assignment to the other three major groups: crustaceans, chelicerates, and uniramians. Some taxa share enough characters to deserve the epithet of crustacean-like or chelicerate-like, but others are an amalgam of arthropodan units that defy simple classification (*67*). Nestled among this welter of forms, however, are taxa whose respective places in the crustaceans (*68*), chelicerates (*69*), and

uniramians (*70*) seem assured. These species are the earliest representatives of the three arthropod clades that now dominate the biosphere.

Orthodox classification schemes are a hindrance and obscure the importance of this adaptive radiation. The fundamental problem is that taxonomic hierarchies are a product of hindsight and are not equipped to account for relations during the initial stages of an adaptive radiation. This problem can be demonstrated by imagining that a Cambrian systematist is invited to classify the arthropods extant at that time. Not only would he be unable to distinguish what we regard as major groups, but there seems no possibility that he could predict what few species would be destined for cladogenetic success, compared with the myriads doomed for speedy extinction.

Although Burgess Shale–type arthropods exemplify the problem of how to classify the products of an adaptive radiation, the same problem is seen by some to exist in the Cambrian with soft-bodied groups, for example, polychaetes (*71*) and priapulids (*72*), and skeletalized forms, for example, echinoderms (*73*) and brachiopods (*74*). Typically the morphological range appears enormous, characters occur as a mosaic that seemingly precludes coherent taxonomic decisions, and the literature is replete with descriptions of bizarre or puzzling animals. Orthodox taxonomy grapples with this problem by recording a plethora of monospecific or monogeneric higher taxa. As long as attempts persist to shoehorn these seeming intermediates into taxonomies largely established retrospectively, the result will be a series of procrustean exercises that conceal more than they reveal. In this respect, cladistic analyses (*75*) of these early diversifications are more useful in allowing a coherent classification based on serial acquisition of derived characters. Although not explicit to cladistic procedures, the above observations suggest that there is little need to invoke macroevolutionary processes (*76*) to account for the pattern of the Cambrian diversifications. Continuing investigations in a wide variety of Cambrian groups reinforce the impression of a morphological continuum, whose apparent punctuation is largely an artifact of incomplete sampling. The adaptive landscape occupied by the early products of these evolutionary radiations is likely to have been more subdued than at later stages, where extinctions weeded out intermediates and the adaptive peaks are more strongly defined (*77*).

Conclusion

What if the Cambrian explosion was to be rerun (*53*)? At a distance the metazoan world would probably seem little different; even the most bizarre of Burgess Shale animals pursue recognizable modes of life, and therefore the occupants of the ecological theater should play the same roles. But on close inspection the players themselves might be unfamiliar. Today, barring a mass extinction, the predictability of replacement is high. But at the outset of diversification the range of morphologies, combined with the majority of species failing to leave descendants, means that the processes of contingent diversification might produce a biota worthy of the finest science fiction.

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