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THE BURGESS SHALE (MIDDLE CAMBRIAN) FAUNA

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INTRODUCTION

The preservation of soft parts in fossils is rare because fossilization usually occurs long after decay has destroyed soft tissues. A notable exception is the soft-bodied fauna from the Middle Cambrian Burgess Shale (about 530 million years old) located near Field in southern British Columbia, where both completely soft-bodied groups (e.g. polychaetes) and the soft parts of creatures with resistant skeletons (e.g. trilobites) are beautifully preserved. In addition, this fauna includes animals with fragile skeletons of thin cuticle that normally do not fossilize. The Burgess Shale fauna is of special importance because it permits a unique glimpse of the period shortly after the upper Precambrian–lowermost Cambrian radiation of the Metazoa (26).

In 1909 Charles Doolittle Walcott (Secretary of the Smithsonian Institution), returning from a field season, stopped to split open a rock that blocked a trail on the western slopes between Wapta Mountain and Mount Field. The rock contained soft-bodied fossils. The following year Walcott and his two sons located the original stratum: the Burgess Shale. Quarrying continued for several seasons (1910–13, 1917), and more than 40,000 specimens were shipped to the Smithsonian Institution (USNM). Subsequent expeditions by Harvard University (MCZ) in 1930 (92, 94), the Geological Survey of Canada (GSC) in 1966 and 1967 (153), and the Royal Ontario Museum (Toronto) in 1975 collected more material. After Walcott's preliminary publications (135–137, 139–146, 148), a much needed reinvestigation was undertaken by the GSC, with H. B. Whittington directing the paleontological work.

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PALEOENVIRONMENTAL SETTING

The Burgess Shale is a predominantly shale unit within the thick succession of shales and impure limestones that forms the Stephen Formation. Although an integral part of the Stephen Formation, the Burgess Shale is singled out for recognition because of its tectonic isolation and unique fauna (46). The Stephen Formation was deposited in a deep-water basin southwest of an algal reef with a precipitous escarpment that can be traced for at least 16 km along a northwest trend (Figure 3B) (77–79). In addition to the Burgess Shale a number of other prolific faunas have been discovered within the Stephen Formation. All are located at the foot of the reef; basinwards all become impoverished. Only the Burgess Shale contains abundant soft-bodied fossils; the other faunas are dominated by trilobites (78). One of the latter, the famous *Ogygopsis* Shale exposed on Mount Stephen (Figure 3B), has yielded a rich fauna with some exceptionally well-preserved species (14, 30, 54, 75, 76, 89, 93, 97, 107, 108, 112, 131, 133, 134, 136, 137, 139, 141, 144, 146, 147, 152, 154).

Two levels within the Burgess Shale yield abundant soft-bodied fossils (138). The lower Phyllopod bed (2.31 m thick) is exposed in the Walcott quarry. About 20 m higher another excavation (the Raymond quarry) has yielded a sparser and less well-preserved fauna (36).

The Phyllopod bed, at least, was deposited from turbidite flows (86, 87, 153, 154). It is therefore possible to distinguish between a pre-slide environment where the benthonic fauna lived and a deeper post-slide environment to which the fauna was transported, there to be buried and preserved. The distance of transport was probably not more than a few km; the direction was probably parallel to the reef (36, 37). The vertical displacement of trilobite zones from basin to reef indicates that the Phyllopod bed was deposited at a depth of about 160 m (46). The superb preservation and almost complete absence of scavenging or bioturbation suggest that the post-slide environment was inimical to metazoan life; poisonous hydrogen sulphide may have extended above the sediment-water interface.

PRESERVATION

The soft-parts of the Burgess Shale fossils are now composed of very thin films which in part are highly reflective (Figure 1) (153). The fossil film is composed of calcium aluminosilicates with the reflective areas containing additional magnesium (30). Owing to the seeping of sediment during transport, specimens with appendages (e.g. arthropods, polychaetes) have usually been preserved on several levels of microbedding. The split tends to jump from one level to another across a specimen (156). Various factors control the level of splitting and thus the exposure of different parts of the body (37, 156). Transport also resulted in the specimens' adopting different orientations upon burial (153, 154); this facilitates an understanding of their morphology. The reasons for the remarkable preservation are obscure. The fauna was rapidly buried in fine sediment (86, 87) under anaerobic conditions (36, 37, 153), so decay was greatly retarded. However, some additional influence must be invoked to explain the cessation of decay and consequent astonishing preservation. Other examples of arrested decay in fossil (5, 20, 21, 39, 47, 81, 82, 85, 100, 121–124, 127, 128, 150) and modern situations (10, 40, 49, 118) are known, but they throw little light on the Burgess Shale preservation. No other Cambrian locality matches the diversity of the Burgess Shale. However, a few exceptionally well-preserved fossils, some of which are comparable to Burgess Shale genera, have been found in other Cambrian rocks (12, 15, 16, 30, 37, 42, 48, 96–99, 103, 104, 129, 130, 132, 137).

THE FAUNA

The fauna apparently lived on the edge of the open ocean close to the paleo-equator; it seems neither atypical nor aberrant. It consists of about 119 genera (140 species). The approximate composition of the fauna by genera is shown in Figure 3C, a scheme that differs slightly from two earlier compilations (33, 34, 36) in its organization and the values given. Research on the fauna is still unfinished, but the final values should not differ greatly from those given here. A rich flora of uncalcified algae (108, 143, 149) has also been partially restudied (111).

Arthropods

Arthropods account for the largest fraction of the fauna (37%). In addition to typical Cambrian trilobites there is a remarkable assemblage of lightly sclerotized nontrilobitic arthropods. The trilobites are mostly benthonic (about 75% of genera), but pelagic agnostids and eodiscids are numerically abundant (89, 137). With the possible exception of *Elrathina cordillerae* and *Elrathia permulta,* soft parts are known only from *Olenoides serratus* and a single specimen of *Kootenia burgessensis* (91, 137, 141, 157). The other benthonic trilobites lack their appendages, probably because they were originally scarce (89, 141) as living members of the fauna. Although the exoskeletons survived, by chance no living specimens were caught in the turbidite flows. *Olenoides* bore uniramous anterior antennae and posterior cerci. The intervening biramous appendages consisted of an inner jointed and spinose walking leg and an outer filamentous gill. The leg and gill arose from a large gnathobasic coxa (157). In contrast to the dorsal exoskeleton, the biramous appendages of this and other trilobites are notable for showing no distinct tagmosis (9, 21, 73, 122). *Nathorstia transitans* (137) is an exuvium of *O. serratus,* as Raymond (91) originally suggested (H. B. Whittington, in preparation). *Naraoia compacta* (91, 117, 137, 148) had an anterior pair of antennae and trilobitan biramous appendages. The carapace, however, consisted of two subcircular shields. *Naraoia* is thus comparable to an enormous larval trilobite and may be neotenic (158).

The nontrilobitic arthropods comprise a diverse assemblage. Many were accommodated in the Trilobitoidea (120), but this is an artificial group (158). The limbs of *Marrella splendens, Burgessia bella,* and *Waptia fieldensis* may show some trilobite-like features (57, 159), but the majority of genera cannot be placed in any higher taxon. They demonstrate an early facet of arthropod radiation, but they throw little light on the question of arthropod polyphyly (73).

The most abundant arthropod is *Marrella* (91, 108, 113, 117, 137, 148). A wedge-shaped cephalic shield bore two pairs of elongate spines. Uniramous first and second antennae preceded biramous appendages composed of a jointed walking leg and filamentous gill branch (Figures 1H, 2E) (153, 154). *Burgessia* (91, 116, 117, 137, 148) had a circular carapace. The cephalon carried anterior antennae and three pairs of biramous appendages consisting of a jointed walking leg and a slender flagellum. With the exception of the last pair, all of the trunk appendages were biramous with a walking leg and gill branch (56). The cephalic region of *Waptia* (91, 117, 137, 148) was equipped with two pairs of antennae, four pairs of walking legs, and pedunculate eyes. The trunk had six pairs of gills. The legs and gills, therefore, show alternate reduction from a more primitive biramous condition (57). The notion that *Waptia* is closely comparable to the decapodan protozoea larva (52) appears to be unfounded (C. P. Hughes, personal communication).

The cephalon of *Yohoia tenuis* (91, 116, 117, 137) bore a shield and appendages; the latter included three pairs of walking legs and a remarkable pair of large appendages with distal articulating spines that could have been used to grasp food (155). *Leanchoilia superlata* (94, 116, 117, 137, 148) had a cephalic shield with upturned rostrum and a pair of enormous anterior appendages. The trunk appendages were biramous and each included a filamentous branch (17). The anterior part of *Branchiocaris pretiosa* (96, 117) was enclosed in a bivalved carapace. The cephalon possessed antennae and chela-like appendages. The trunk seems to have consisted of a large number of segments bearing lamelliform appendages (12).

Sidneyia inexpectans (91, 114, 117, 134, 137, 140) and *Emeraldella brocki* (91, 115, 117, 137) both had gnathobasic limbs. *Sidneyia* had certain similarities to the modern merostome *Limulus* (17). The triramous appendages of *Emeraldella* with an inner walking leg and two large foliaceous lobes

(Bruton in 53) are crustacean in aspect (17). Arthropod remains comparable to *Sidneyia* have also been noted from Indochina (72), but the supposed specimen from Greenland (25) is inorganic (44).

Tuzoia [supposedly represented by four or five species, type *T. retifera:* (13, 96, 117, 137)], *Carnarvonia venosa, Hurdia victoria* and *H. triangulata, Isoxys acutangulus* and *I. longissimus* (117, 137), and *Proboscicaris agnosta* and *P. ingens* (106, 117) are only known by their carapaces. In the absence of appendages, identification as phyllocarid crustaceans cannot be positive. *Tuzoia* and *Isoxys* have been recorded from other Cambrian strata (48, 84, 96, 99, 101, 132), but the supposed *Hurdia* from Australia (19) is inorganic (3). *Tuzoia* and *Isoxys* may owe their wide geological and geographical ranges to comparatively heavy sclerotization.

Phyllocarids with soft parts preserved include *Canadaspis perfecta* (14, 117, 137), *Perspicaris dictynna* and *P. recondita* (13, 117), and more tentatively *Plenocaris plena* (117, 137, 155). In *Canadaspis* a bivalved carapace covered the cephalon and thorax. Anteriorly there were two pairs of antennae and a pair of pedunculate eyes. Chewing mandibles were succeeded by first and second maxillae. The latter appendages were primitive and similar to the eight pairs of thoracic appendages, each having an inner jointed walking leg and a filamentous outer branch (14). *Anomalocaris gigantea,* generally regarded as the abdomen of a phyllocarid (96, 117, 137), has recently been reinterpreted as the appendage of a large arthropod (13, 15). *Anomalocaris* is found in much greater abundance in the nearby *Ogygopsis* Shale (133, 152) and has been recorded from other Cambrian strata (15, 96, 99).

Aysheaia pedunculata (18, 58, 59, 136, 148, 159) has excited the greatest interest on account of its remarkable resemblance to the modern onychophores (e.g. *Peripatus*), which resemble the hypothetical ancestral uniramian arthropod (73). Whittington (160) concluded that *Aysheaia* differs in certain respects from modern onychophores and tardigrades, but conceded that the uniramian ancestor probably closely resembled *Aysheaia.*

The placement of *Skania fragilis* with trilobite-like forms (120, 148) has been criticized (18), but whether comparison with the peculiar *Parvancorina minchami* from the latest Precambrian (47) can be upheld is uncertain (C. P. Hughes, in preparation). Additional arthropods awaiting detailed redescription are: *Mollisonia gracilis* and *M.* (?) *rara* (93, 115, 117, 137, 148), *Odaraia alata* (117, 137), *Alalcomenaeus cambricus* (116, 117), *Molaria spinifera, Habelia optata* (91, 115, 117, 137), *Helmetia expansa* (117, 142, 148), ostracode-like forms (137, 154), and several other genera (117).

Echinoderms

The Burgess Shale has yielded the earliest known crinoid, *Echmatocrinus brachiatus.* A large conical calyx and tapering holdfast was covered with irregularly arranged plates. Plated uniserial arms with probable tube feet arose from the calyx. An eocrinoid, *Gogia*(?) *radiata,* and the "arms" of an unknown ?eocrinoid have also been described (119). The edrioasteroid *Walcottidiscus* (6, 7) awaits restudy (J. Sprinkle, personal communication). The notion that the soft-bodied medusiform *Eldonia ludwigi* was a holothurian (22, 23, 135, 140; but see 24) was reaffirmed by Durham (43), who demonstrated that the interpretation of *Eldonia* as a siphonophore (69–71) is untenable. The supposed specimens of *Eldonia* from Eire (110) are inorganic (41). *Laggania cambria* has been interpreted both as a holothurian (23, 135) and a polychaete (70), but the only known specimen is a composite fossil formed by the superposition of the medusoid *Peytoia nathorsti* and a sponge (35).

Molluscs

A single specimen was identified as *Helcionella* (46), but it is undeterminable. A low orthoconic shell attributed [perhaps incorrectly (E. L. Yochelson, personal communication)] to the monoplacophoran *Scenella* (90, 137) is abundant. Hyolithids, which however may not be molluscs (109), are common. *Hyolithes carinatus* sometimes has the operculum and associated curved appendages in place (136, 162). *Wiwaxia corrugata* (75, 136, 148) was covered with ribbed scales and bore elongate dorso-lateral spines. It has been regarded as a polychaete (55, 136), but the radula-like feeding apparatus suggests an affinity with primitive molluscs (S. Conway Morris, in preparation).

Lophophorates

The brachiopods are typical Cambrian forms. Two species, however, are exceptional: In some specimens the mantle setae and pedicle have been preserved (8, 97, 139, 146). *Odontogriphus omalus* had a dorso-ventrally compressed body with a ventral feeding apparatus identified as a lophophore (27). Criticism of this interpretation (65) appears unfounded. Minute conical objects associated with the lophophore have been interpreted tentatively as conodonts, and *Odontogriphus* is regarded as a conodont animal (27; see also 80).

Chordates and Hemichordates

"Ottoia" tenuis (136), which is unrelated to the type species *Ottoia prolifica,* is similar to an enteropneust worm. Another undescribed animal resembles an enormous rhabdopleuroid pterobranch (S. Conway Morris, in preparation). Although Cambrian graptolites are known (102), those described as *Chaunograptus scandens* from the Burgess Shale (108) require restudy.

The presence of a longitudinal bar (notochord) and sigmoidally deflected segments (myotomes) in *Pikaia gracilens* (Figure 1D) indicates that it is a

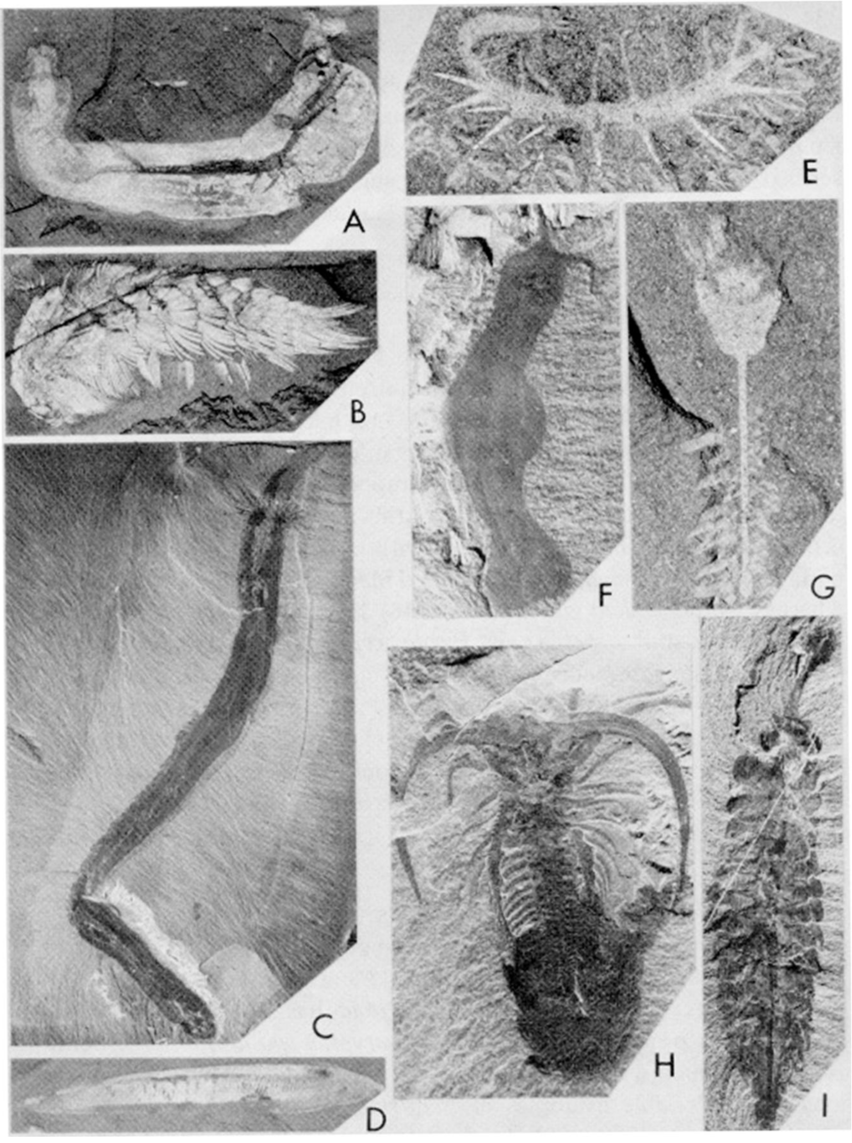


Figure 1 Representative Burgess Shale specimens photographed in ultraviolet light—A: *Ottoia prolifica* Walcott (G.S.C. 40972), priapulid, X 0.7 (30); B: *Canadia spinosa* Walcott (U.S.N.M. 198724), polychaete, X 1.4 (37); C: *Louisella pedunculata* Walcott (U.S.N.M. 198648), priapulid, X 0.5 (30); D: *Pikaia gracilens* Walcott (U.S.N.M. 198684), chordate, X 1.2.; E: *Hallucigenia sparsa* (Walcott) (U.S.N.M. 198658), phylum uncertain, X 3.7 (29); F: *Amiskwia sagittiformis* Walcott (U.S.N.M. 57644), phylum uncertain, X 2.3 (32); G: *Dinomischus isolatus* Conway Morris (M.C.Z. 1083), phylum uncertain X 2.1 (31); H: *Marrella splendens* Walcott (G.S.C. 26592), arthropod, X 2.5 (154); I: *Opabinia regalis* Walcott (U.S.N.M. 57684), phylum uncertain, X 0.9 (156).

primitive chordate (34) rather than a polychaete (55, 136, 148). The earliest fish scales are Upper Cambrian (95), and *Pikaia* may not be far removed from the ancestral fish. Whether study of this chordate and another undescribed form will lend credence to the suggestion that the vertebrates are derived from mitrate echinoderms (60) is uncertain (S. Conway Morris, in preparation).

Polychaetes

The only annelids represented are the Polychaeta. None of them has a mouth armature (37); polychaetes acquired jaws in the Ordovician (62). The parapodia of *Canadia spinosa* (136, 148) had broad notosetae extending across the dorsal surface, large fascicles of narrower neurosetae, and interramal lobate gills (Figure 1B). The parapodia bear a striking resemblance to those of the modern Palmyridae, but this may be due to convergence. The other genera show no close affinities with modern families (37). The parapodia of *Burgessochaeta setigera* carried identical notosetae and neurosetae, whereas *Peronochaeta dubia* (136, 148) had uniramous parapodia with acicular and capillary setae (37). *Insolicorypha psygma* had biramous parapodia with elongate neuropodia bearing cirri and long slender setae (37). The leaf-shaped *Pollingeria grandis* has been regarded as the detached scales, supposedly furrowed by a commensal worm, of a polychaete (55, 136). This interpretation appears very doubtful; *Pollingeria* may not even be an animal (S. Conway Morris, in preparation).

Priapulids

There is a rich assemblage of priapulids (30) which morphologically, at least, are more diverse than modern forms (64, 88). *Ottoia prolifica* (136) shows magnificent preservation (Figure 1A): The intestine, retractor muscles, and nerve cord are identifiable. *Ottoia* has the closest relationship with modern priapulids, especially *Halicryptus spinulosus* (30). *Selkirkia columbia,* which was mistaken for a polychaete (55, 136, 148), is a tubicolous form. Possible examples of *Selkirkia* have been noted from other Cambrian rocks (30, 98, 99). *Louisella pedunculata,* which has been misinterpreted both as a holothurian (23, 136) and a polychaete (55, 70), is the largest (up to 20 cm) of the priapulids. It was unusual in having papillate proboscis scalids and a trunk armed with concentric zones of spines and two longitudinal rows of papillae (Figures 1C, 2C) that probably functioned as gills (30). *Fieldia lanceolata,* previously mistaken for an arthropod (137), had a small proboscis and a very spiny trunk (30). *Ancalagon minor* (136, 148) is of special interest because although it is a priapulid it has a marked resemblance to a hypothetical free-living ancestor (50) of the endoparasitic Acanthocephala (30).

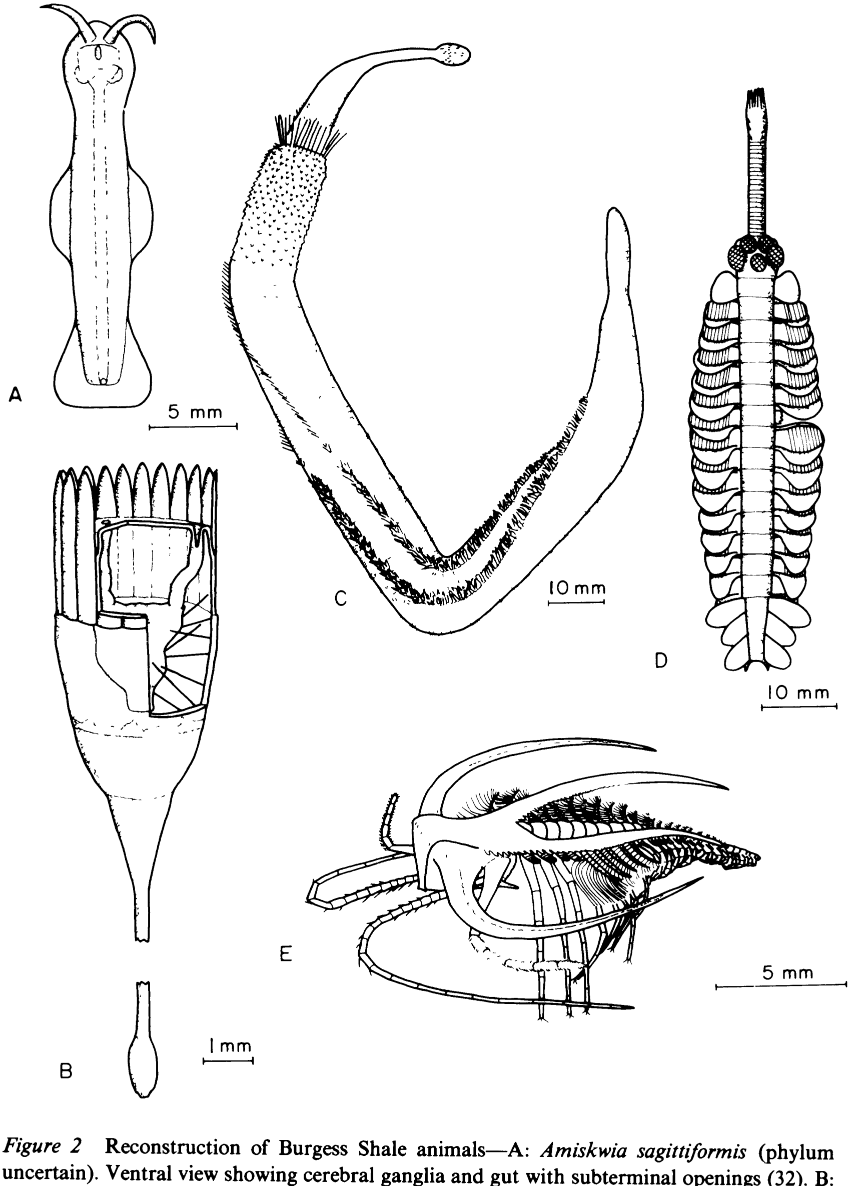


Figure 2 Reconstruction of Burgess Shale animals—A: *Amiskwia sagittiformis* (phylum uncertain). Ventral view showing cerebral ganglia and gut with subterminal openings (32). B: *Dinomischus isolatus* (phylum uncertain). Portion of the upper calyx and pointed bracts cut away to reveal gut supported by fibers. Most of the stem is omitted (31). C: *Louisella pedunculata* (priapulid). Proboscis fully everted and trunk twisted along its axis to show spinose zones and papillate gills (30). D: *Opabinia regalis* (phylum uncertain). Dorsal view with frontal process extending forward. Right lateral lobe and pleated gill of segment 7 cut away to reveal lobe and gill of segment 8 (156). E: *Marrella splendens* (arthropod). Oblique lateral view. Left gill branches 1–4 and 10–26 cut away to reveal walking legs (154).

Miscellaneous Worms

This heterogenous and artificial group is united solely by our inability to accommodate its members in any known phylum. Some of these specimens probably represent new phyla. *Opabinia regalis* has been placed in the arthropods (58, 91, 94, 116, 117, 120, 137), but it has only a most distant connection with that group. The cephalon bore five eyes and a frontal process that was flexible and armed with distal teeth. The trunk carried lateral lobes and, with the exception of the first segment, gills with dorsal lamellae (Figures 1I, 2D) (156). *Nectocaris pteryx* had an elongate and streamlined body. The head carried anterior appendages, large eyes, and more posteriorly a shield-like structure. Dorsal and ventral fins supported by fin rays arose from the segmented trunk (28).

Hallucigenia sparsa (136, 148) had a most unusual appearance. A globular head and elongate trunk that curved upwards posteriorly were supported by seven pairs of elongate spines. Seven tentacles terminating in cuticularized bifid tips arose from the dorsal trunk (Figure 2E). Its zoological affinities and mode of life remain problematical (29). In *Banffia constricta* (136) an anterior annulated section was separated from a sac-like posterior by a constriction. This curious anatomy may represent a primitive adaptation that isolated a more passive posterior from pressure fluctuations set up by the locomotory movements of the anterior (33).

Amiskwia sagittiformis had a prominent pair of tentacles arising from an oval head and a trunk supporting lateral and caudal fins (Figures 1F, 2A). This worm has been regarded both as a chaetognath (55, 136) and a bathypelagic nemertean (63, 83), but since neither assignment can be supported the animal's phyletic position remains obscure (32). The calyx of *Dinomischus isolatus* was supported by an elongate and slender stem with swollen terminal holdfast. Plate-like bracts arose from the calyx edge. A recurved gut with an enlarged stomach was supported in the body cavity by fibers (Figures 1G, 2B). *Dinomischus* has certain similarities, which may be only superficial, to the Entoprocta (31).

Oesia disjuncta had a swollen anterior section, which contrary to Walcott's (136) observation appears to be unarmed, and an elongate trunk. *Oesia* has been identified as both an annelid (55, 125, 136) and an appendicularian tunicate (68), but neither suggestion seems likely (S. Conway Morris, in preparation). *Redoubtia polypodia* and *Portalia mira* were interpreted as holothurians (142, 148), although Madsen (70) considered them to be a polychaete and sponge, respectively. None of these proposals is convincing; together with *Worthenella cambria* (136) and other miscellaneous worms, these animals await restudy.

Coelenterates

Mackenzia costalis (135) is generally regarded as an actinian (23, 24, 142, 151). *Peytoia nathorsti* had a peculiar medusiform body composed of thirty-two lobes around a central cavity. Each lobe was armed with a proximal pair of prongs (35, 135). Despite the claim that *Peytoia* is a scyphozoan (135), it remains of uncertain systematic position (51). An undescribed form has a strong resemblance to a pennatulacean or sea pen (S. Conway Morris, in preparation).

Sponges

The prolific fauna is represented by demosponges [e.g. *Hazelia* (type species *H. palmata*)], hexactinellids (e.g. *Protospongia hicksi*), and heteractinids [e.g. *Eiffelia globosa, Chancelloria eros* (45, 103, 144)]. Some of the genera are known from other lower Paleozoic strata, but the Burgess Shale specimens are exceptionally well-preserved (103). Phylogenetic discussions have often referred to Burgess Shale species, and *Hazelia* has been given a key position in demosponge phylogeny (45, 161). However, a comprehensive restudy of the sponge fauna is now underway (J. K. Rigby, personal communication).

Trace Fossils

Evidence for trace fossils, especially in the Phyllopod bed, is almost completely lacking (86, 153). Rare structures filled with pyrite from the Phyllopod bed may represent infilled burrows. Narrow burrows associated with arthropod carapaces (*Leanchoilia, Canadaspis*) have also been recorded, although these rare specimens apparently originate from above the Phyllopod bed (D. M. Rudkin, personal communication). Irregularly shaped clumps of hyolithids, sometimes with associated brachiopods, may represent coprolites of an unidentified (?arthropod) predator. They are especially common from the Raymond quarry.

PALEOECOLOGY OF THE BURGESS SHALE FAUNA

Most (87.5%) of the fauna was benthonic; the pelagic component was less well-represented (Figure 3D). The benthonic fauna evidently inhabited the muds of the pre-slide environment adjacent to the base of the algal reef (36). The presence of burrowing worms and an extensive epifauna suggests the sediment was fairly well consolidated. Nevertheless the muds were unstable, perhaps due to rapid rates of deposition on submarine slopes, and periodically they slumped into the poisonous post-slide environment.

The persistence of abundant genera [e.g. *Marrella* (153, 154), *Ottoia, Selkirkia* (30), and *Canadaspis* (14)] throughout the Phyllopod bed suggests that only one association or community was present (36). The fluctuations in abundance of these common forms, together with the more restricted vertical distribution of other species (29, 30, 37, 56, 137, 155, 157), probably reflect a patchy distribution of the fauna over the seafloor (37).

The presence of an infauna demonstrates that it, and probably the rest of the benthos, was present from the inception of the mud flows (37). As the flows moved downslope they may have eroded additional epifauna. The movement of the sediment destroyed most evidence of the life-positions of the fauna. Life-positions within the pre-slide environment can be established only by comparing the morphology of each species with that of living relatives and analogous forms.

Infaunal, Epifaunal, and Pelagic Components

The vagrant infauna was dominated by burrowing priapulids (Figure 3D). *Ottoia* (30) and *Louisella* (Figure 1A, C) may also have occupied temporary burrows, while the latter genus probably aerated its gills by dorsoventral undulations of the compressed body. Other members of the vagrant infauna probably include the polychaete *Peronochaeta* (37) and the probable enteropneust worm. The polychaete *Burgessochaeta* possibly lived in a semipermanent burrow (37), but in general the sessile infauna appears to have been restricted.

In contrast the sessile epifauna was extensive and included the sponges (Figure 3D) (144), brachiopods (139, 146), echinoderms [(119); except *Eldonia* (43, 135)], the enigmatic *Dinomischus* (Figure 1G) (31), and, among the coelenterates, *Mackenzia* (135) and the probable sea pen. The vagrant epifauna was dominated by arthropods (Figure 3D) that walked across the seafloor or perhaps on occasion swam close to it; some of them (e.g. *Burgessia*) may have burrowed (56). The vagrant epifauna also included the molluscs and enigmatic beasts such as *Opabinia* (Figures 1I, 2D) (156), and *Hallucigenia* (Figure 1E) (29). The polychaete *Canadia* (37) and chordate *Pikaia* (Figure 1B, D) (34, 136, 148) appear to have been well adapted for swimming; they were probably at least partially nektobenthonic. The pelagic species (Figure 3D) may have been derived from different depths and may include representatives swept in from the open ocean. The agnostid and eodiscid trilobites are generally regarded as pelagic (105). The other pelagic animals are identified on the dual basis of morphology and rarity. The carapace of *Isoxys* shows convergence with the modern pelagic ostracode *Conchoecia daphnoides;* this may indicate a similar mode of life. The abundance of gelatinous tissue in *Amiskwia* (Figures 1F, 2A) (32), *Odontogriphus* (27), and *Eldonia* (135) or marked adaptations to swimming [e.g. *Nectocaris* (28), *Insolicorypha* (37)] are taken as key features. Their rarity is a reflection of the low probability of becoming involved in benthonic turbidites. Unlike the other pelagic genera, *Eldonia* is abundant (43); while it may not have been pelagic, its restriction to a limited horizon and area (27, 135, 137, 153) suggests the specimens were trapped as a shoal.

The more impoverished Raymond quarry fauna differs somewhat in character from that of the Phyllopod bed (36). The lower diversity could be due in part to more selective fossilization; but the presence of creatures such as the infaunal worm *Banffia* (33, 136) and the epifaunal arthropod *Leanchoilia* (94, 137, 148), which are very rare in the Phyllopod bed, suggests that a different association is represented (36).

Feeding Methods

In only a few cases are identifiable gut contents known. Feeding methods are usually established by determining the likely function of the food-collecting organs. In many cases (33%) the method of feeding remains either unknown or very uncertain. Three feeding types are recognized: suspension feeders (35% of the fauna), deposit feeders (13.5%, includes swallowers and detritus collectors), and carnivores/scavengers (18.5%).

Many of the members of the sessile epifauna were suspension feeders. These animals probably exploited different water levels for food (Figure 3A), as has been demonstrated in other paleocommunities (11, 66, 67). Vagrant filter feeders included *Leanchoilia* (17); the identification of a polychaete worm in the gut of this arthropod (116) is incorrect. Pelagic suspension feeders are represented by *Eldonia, Odontogriphus* (27), and perhaps *Amiskwia* (Figures 1F, 2A) (32).

Deposit feeders include the priapulid *Fieldia,* which usually had sediment in its midgut (30), the hyolithids (74), and probably the monoplacophoran *Scenella* (E. L. Yochelson, personal communication). This feeding type has been identified with varying degrees of certainty in the arthropods *Branchiocaris* (12), *Canadaspis* (14), *Plenocaris, Yohoia* (155), *Marrella* (Figures 1H, 2E) (73, 154), and possibly *Burgessia* (56) and *Naraoia* (158). The polychaete *Burgessochaeta* may have picked food off the sediment surface with its elongate tentacles (37). A poorly known polychaete [Type A in (37)] has its gut packed with sediment.

Predators and scavengers form a significant proportion of the fauna. Gut contents of the priapulid *Ottoia* include hyolithids, often with opercula in situ, and more rarely brachiopods. The hyolithids were presumably eaten alive and their usual orientation within the gut suggests that they were hunted (30). Since hyolithids are regarded as epifaunal (74), *Ottoia* may have sought them along the sediment-water interface. That one specimen of *Ottoia* contains another individual of *Ottoia* in its gut is taken as evidence

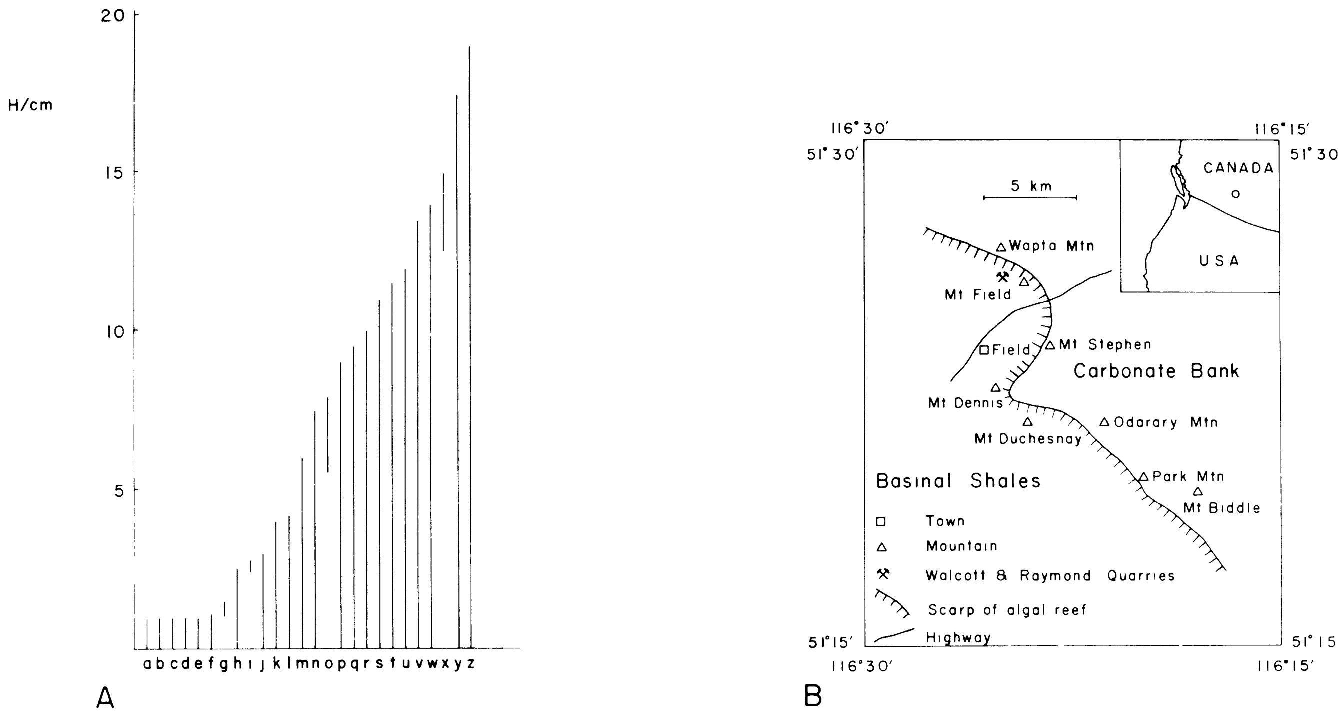
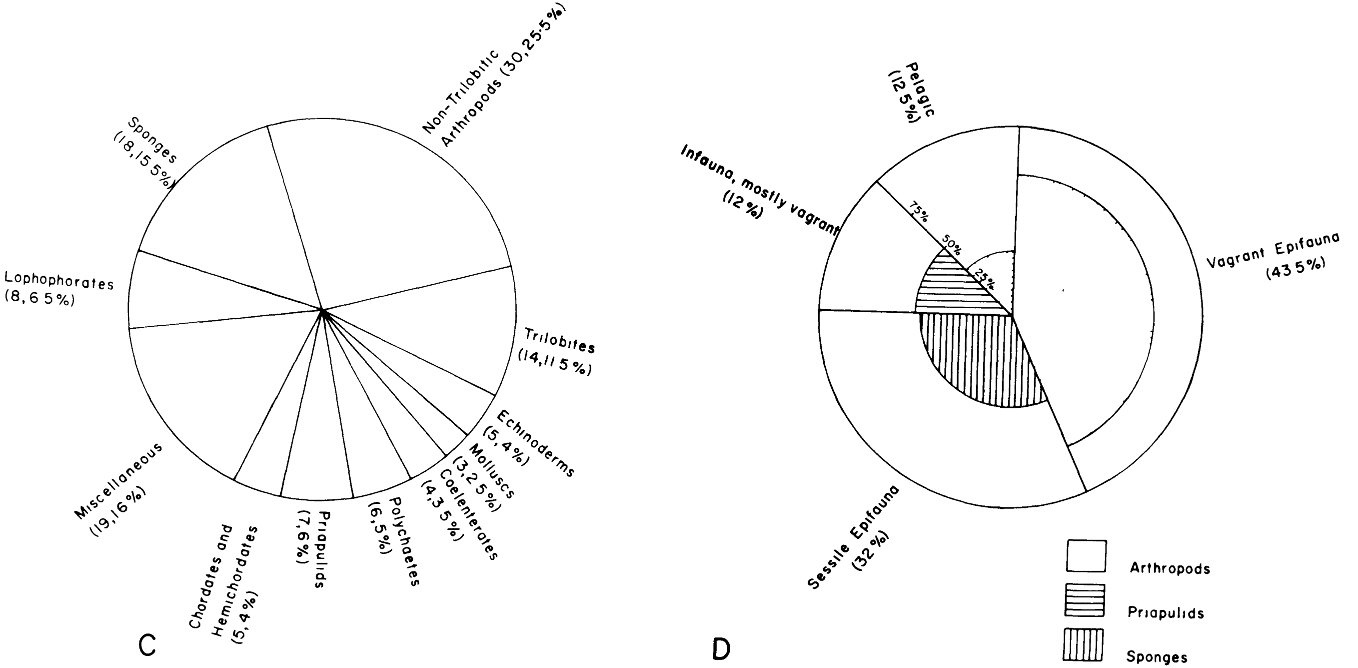


Figure 3 A: Graph to show maximum known height above substrate of food collecting units of various suspension feeders: brachiopods a–d (139, 146), sponges e,f,h,j–n,p–w,y,z (144), echinoderms g,o,x (119), phylum uncertain i (31). The sponges are assumed to have filtered water over entire length of body. Brachiopods attached to algae (143) or sponges (30) are not taken into account. Depth of insertion into sediment assumed to be minimal and species assumed to have lived vertically. a–d, various brachiopods; e, *Hazelia* (*H.*) *mammillata;* f, *Diagoniella hindei:* g, *Walcottidiscus magister;* h, *Pirania muricata;* i, *Dinomischus isolatus;* j, *Eiffelia globosa;* k, *Vauxia* (*V.*) *dignata;* l, *Takakkawia lineata;* m, *H. palmata;* n, *Corralio undulata;*



o, *Echmatocrinus brachiatus;* p, *H. delicatula;* q, *Chancelloria eros;* r, *H. obscura;* s, *V. gracilenta;* t, *V. bellula,* u, *H. nodulifera;* v, *H. conferta;* w, *V. densa;* x, *Gogia? radiata;* y, *Halichondrites elissa;* z, *Wapkia grandis.* B: locality map of the area around Field, British Columbia. Inset shows location of area with respect to western North America. C: pie diagram of composition of fauna on a generic basis. The number of genera and its approximate percentage of the fauna are given after each group. The figures given for the sponges are estimates and may be conservative. A few additional genera of nontrilobitic arthropods have been described but their validity is not certain. D: pie diagram of living habits of the fauna on a generic basis. The phylum that dominates each habitat is also shown.

for cannibalism (30). Other priapulids [*Selkirkia, Louisella* (Figures 1C, 2C), *Ancalagon*] had prominent mouth armatures and were apparently predatory (30). The prominent gnathobasic limbs of the arthropods *Olenoides* (157), *Naraoia* (158), *Emeraldella,* and *Sidneyia* (17) [which has prominent gut contents (117, 134)], were probably used for predation. There is circumstantial evidence for scavenging by ostracodes (30, 154). The frequent association of *Aysheaia* with sponges suggests that they formed the diet of this primitive arthropod (160). The armed frontal process of the enigmatic *Opabinia* (Figures 1I, 2D) probably captured food and passed it back to the mouth (156). The dorsal tentacles of *Hallucigenia* (Figure 1E) may have been used for feeding. The clustering of about twenty specimens of this bizarre beast on another worm suggests that they congregated to scavenge the corpse (29). The radula-like mouthparts of *Wiwaxia* may have been used for scavenging or grazing. That the elongate dorso-lateral spines of some specimens of *Wiwaxia* are broken off is ascribed to unsuccessful predation (S. Conway Morris, in preparation). *Nectocaris* is considered to be predatory and may have occupied an ecological niche similar to that of modern chaetognaths (28). The coelenterate *Mackenzia* may have been carnivorous, but contrary to the case for other probable Cambrian coelenterates (1) no direct evidence for predation has been noted. The body of the medusoid *Peytoia* may have been able to contract radially and bring together its prongs to grasp prey (S. Conway Morris, in preparation).

Other Aspects of Paleoecology

Of interactions other than interspecies feeding little is presently known. The crinoid *Echmatocrinus* is invariably attached to a worm tube, a hyolithid, or another hard object (119). The sponges, however, are only occasionally attached to worm tubes or brachiopods (30, 144). The specific association between the brachiopod *Dictyonina,* which settled on the elongate spicules of the sponge *Pirania,* may represent a case of commensalism (30), though brachiopods of other species are occasionally found attached. Inarticulate brachiopods are sometimes found attached to algae (143). That some species are found crowded together over limited areas may indicate gregarious habits. Examples have been noted among sponges (144), the crustacean *Canadaspis* (14), the priapulid *Ottoia,* and the possible enteropneust worm. Study of the association of species on the collected slabs might throw more light on species interaction.

Rotting and Decay

Despite the exquisite preservation of the fossils there is evidence of decay. In some species a dark stain (Figure 1H) is associated with some of the specimens (14, 29, 30, 36, 37, 56, 153–156, 158, 160). The stain comprises decay products that oozed from the body into the surrounding mud (29, 30).

Its frequent location around the anterior or posterior regions suggests that its usual points of egress were the mouth and anus. In rare cases decay has resulted in detachment of external (e.g. setae) or internal organs (e.g. intestine) (37, 148, 153, 154). Additional evidence for decay was documented in the priapulid *Ottoia,* where a gradation was demonstrated from perfectly preserved specimens, to those where the body wall has folded away from the cuticle and the internal organs are visible, to specimens that consist of collapsed and folded cuticle (30).

THE WIDER-SCALE IMPORTANCE OF THE BURGESS SHALE FAUNA

1. About 16% of the fauna cannot be placed in known phyla. Some of these creatures [e.g. *Hallucigenia* (29), *Opabinia* (156)] represent "experimental" groundplans (Figures 1E,I, 2D) that were ultimately unsuccessful. These forms may represent relicts of an earlier metazoan radiation, but the persistence of novel animals during the Paleozoic (61, 81, 82) demonstrates how scanty our knowledge is of metazoan diversification.
2. Some 80% of the fauna is soft-bodied. The low diversity of normal Cambrian faunas (see 2, 126) may be due partly to the scarcity of groups possessing readily fossilizable hard parts.
3. The pervasive idea that certain groups must have had hard parts to function effectively is negated by the existence of relatives [e.g. *Naraoia* among trilobites (158)] with fragile cuticles. The existence of "soft-bodied" trilobites (unfossilizable in normal circumstances) is postulated by Crimes (38) from study of early Cambrian trace fossils.
4. Banks (4) ascribed late Precambrian and Cambrian trace fossils to the activities of arthropods, annelids, and molluscs, rather than to Metazoa as a whole. The diversity of the Burgess Shale fauna illustrates that many other potential trace producers were present in the Cambrian and that in the absence of diagnostic features noncommital identifications are preferable.
5. As is not the case in modern marine environments, priapulids are more abundant than polychaetes in the Burgess Shale (34). The decline of predatory priapulids in favor of polychaetes may have begun in the Ordovician when jaws evolved among eunicid-like polychaetes (30). Further research should show how the Burgess Shale species occupying various ecological niches were replaced by different forms. For instance, certain Burgess Shale arthropods may have occupied niches presently taken by various crustaceans, while other larger arthropods might have approximated the role of modern benthic fish (33). Sponges were evidently the dominant suspension feeders, and other groups (e.g. brachiopods, echinoderms) were less important.

6. Descendants of some groups represented in the Burgess Shale avoided extinction by migrating into marginal niches. In contrast with modern priapulids, those of the Cambrian evidently dominated at least some infaunal assemblages (Figure 3D). The modern Priapulidae have narrow distribution and often occupy habitats unattractive to many metazoans (64). The other two families (Tubiluchidae, Maccabeidae) are meiofaunal (64, 88) and may be minaturized descendants of Cambrian priapulids. As other examples of minaturization, the entoprocts may derive from a *Dinomischus*-like form (Figures 1G, 2B) (31) and the tardigrades from an *Aysheaia*-like animal (18, 73, 160). The endoparasitic Acanthocephala, possibly derived from an *Ancalagon*-like priapulid (30), might illustrate another method of "escape" from competition.

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