The Animals of the Burgess Shale

The fossils of a rock formation in western Canada are a rich sample of an animal community in the mid-Cambrian. Some of the animals are ancestors of those living today; others are unique and bizarre

by Simon Conway Morris and H. B. Whittington

By far the most numerous fossils representing the first abundant life on the earth are the hard parts of various marine animals without backbones: shells and similar fragments of external skeleton. This makes for a lopsided fossil record. For example, of the 30 or so phyla of animals living today more than half are made up of species with few hard parts or none. As a result the descent of these phyla remains largely undocumented by fossil evidence.

Fortunately the situation is not completely lopsided. A few geological deposits have been discovered that as a result of exceptional circumstances contain exquisitely preserved fossils of animals that are partly or entirely soft-bodied. Here we shall describe one such deposit: the Burgess Shale of western Canada. The great age and the rich variety of the marine invertebrates in the Burgess Shale make it perhaps the best-known of all such deposits. In addition to describing the Burgess Shale fauna we shall attempt to reconstruct the kind of underwater environment these organisms inhabited early in Paleozoic times: some 530 million years ago.

In the fall of 1909 the Secretary of the Smithsonian Institution, Charles Doolittle Walcott, was searching for fossil-bearing rock formations in British Columbia. Following a footpath that ran across the western slope between Wapta Mountain and Mount Field in the southern part of the province, Walcott literally stumbled over a block of shale that had fallen onto the path from the slope above. Examining the easily split rock, he was astonished to find the fossil impressions of a number of soft-bodied organisms preserved in its layers. In a letter to a colleague in Toronto dated November 27, 1909, he dryly reported that he had spent "a few days collecting ...in the vicinity of Field and found some very interesting things."

Walcott returned to the spot the following year to search upslope for the shale stratum that had been the source of his fallen rock. His search was successful: he found two fossil-bearing shale exposures separated by a vertical distance of some 70 feet. He did shallow quarrying in both; the lower exposure proved to be the richer of the two. He shipped back to the District of Columbia thousands of fossil specimens that he removed from what he called his Phyllopod Bed. (The term, little used by paleontologists today, refers to certain fossil arthropods, or joint-legged animals, that are probably ancestral to living crustaceans.)

As Walcott's own work and decades of study by others have shown, the fossils of the Burgess Shale include a great abundance of marine invertebrates: more than 120 species. Some of them belong to the Phylum Porifera: the sponges. This phylum of primitive animals is the only one in the subkingdom of parazoans, a category higher than the subkingdom of the one-celled protozoans but lower than the subkingdom of the many-celled metazoans. Perhaps 10 other species represent metazoan phyla that were unknown before they were found in the Burgess Shale; they are not present elsewhere in the fossil record. The scores of other species that lack hard parts can be assigned to one or another phylum of metazoans with living relatives as follows:

Coelenterates: the phylum that includes such living marine animals as jellyfishes, sea pens and corals. The Burgess Shale coelenterate species number perhaps four.

Echinoderms: the phylum that includes, among others, starfishes, sea cucumbers and crinoids, or sea lilies. At least four species of Burgess Shale echinoderms are recognized.

Mollusks: the phylum that includes, among others, oysters and clams, squids and octopuses and the primitive chitons (of the Class Amphineura). Three Burgess Shale molluscan species are recognized.

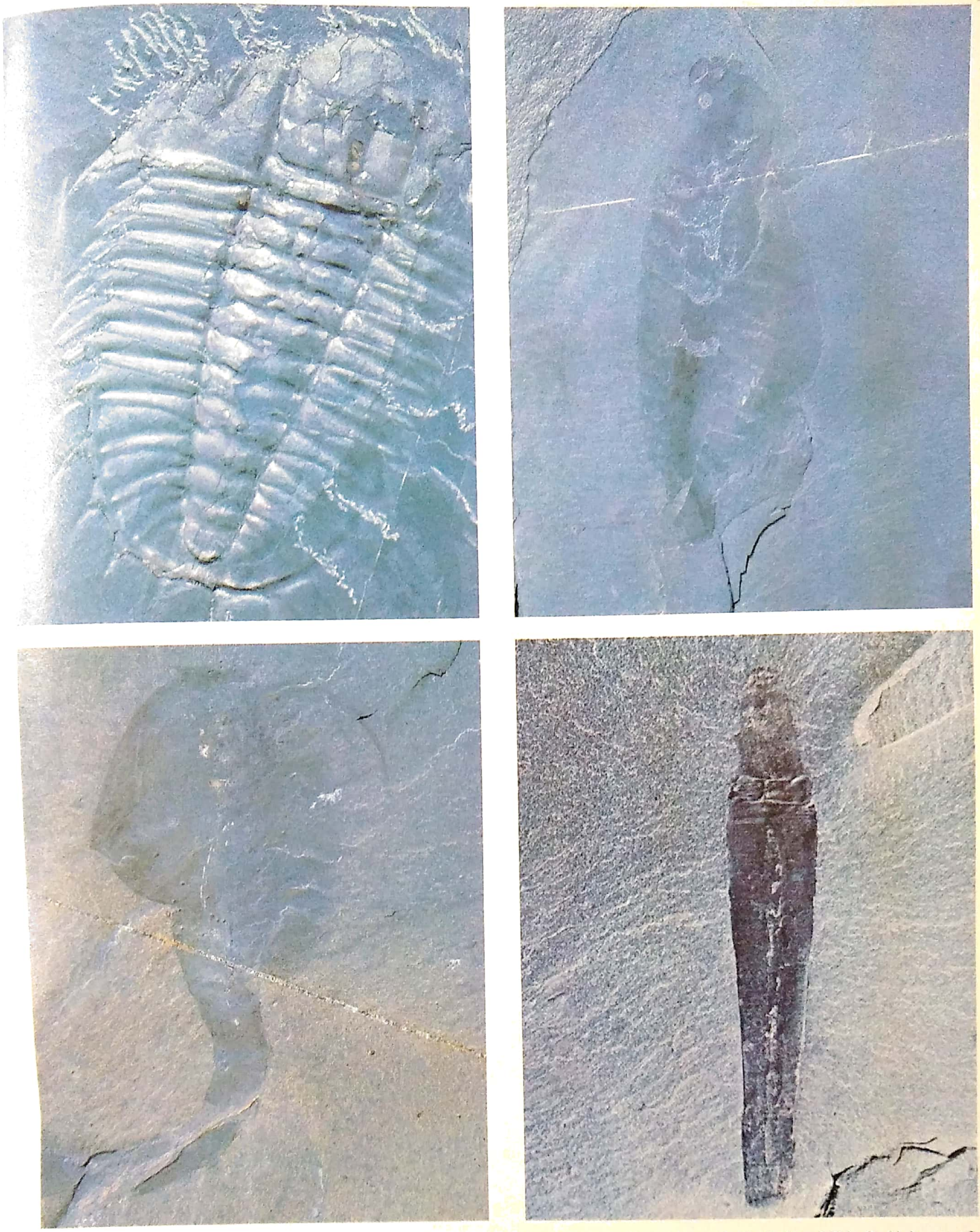
Arthropods: the phylum that includes, among a great many others, lobsters, shrimps, crabs and barnacles (all of the Class Crustacea) and the less familiar terrestrial animal *Peripatus* (a member of the Class Onychophora). The Burgess Shale arthropods include several representatives of the long extinct trilobite class, a peripatus-like animal that was aquatic rather than terrestrial, and about 30 other species of arthropods.

Priapulids: a minor phylum of unsegmented marine worms. The living genus, *Priapulus,* gives the phylum its name. Seven species of these now obscure bottom burrowers flourished in the Burgess Shale muds.

Annelids: the phylum that includes earthworms, leeches and a less familiar but very large class of marine worms, the polychaetes. The annelid phylum is represented in the Burgess Shale by six species.

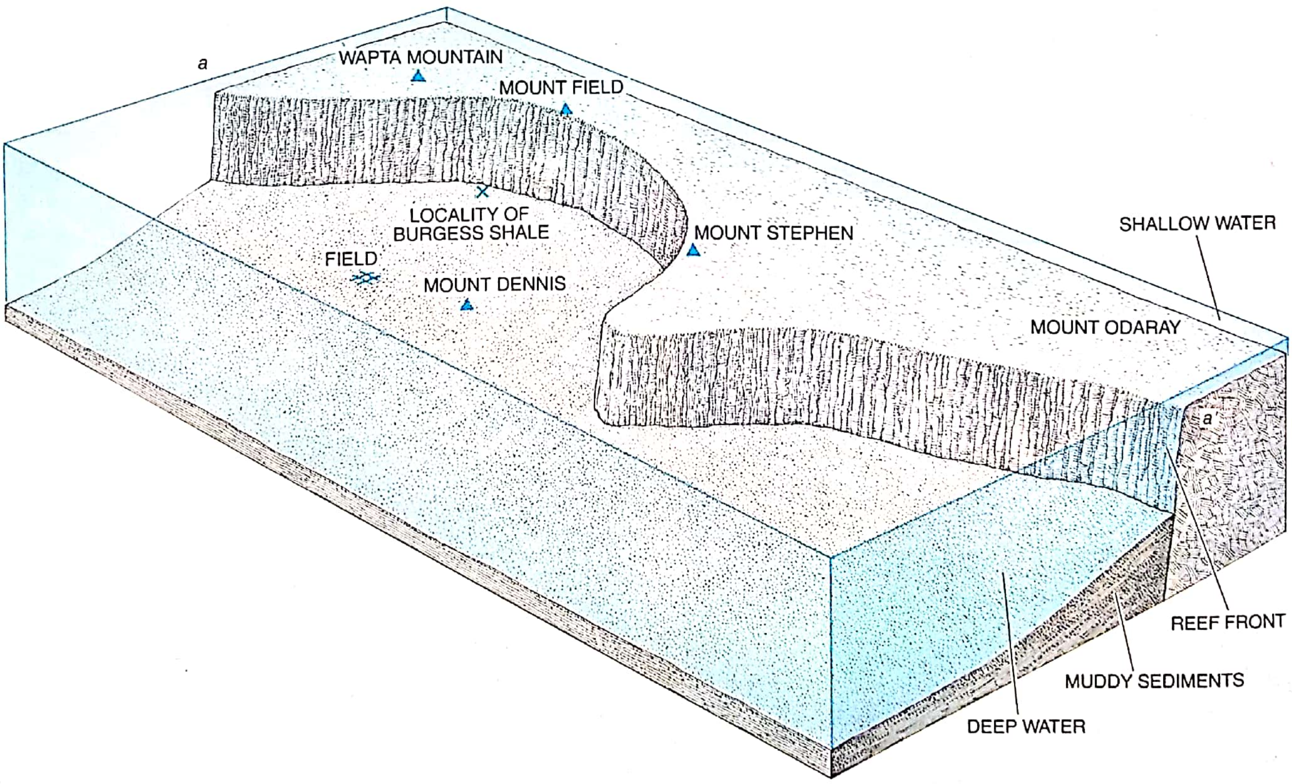
Finally, we find among the Burgess Shale fauna one of the earliest-known invertebrate representatives of our own conspicuous corner of the animal kingdom: the chordate phylum. Among its living representatives (other than vertebrates) are the sea squirts and the peculiar marine animal *Amphioxus.* The chordates are represented in the Burgess Shale by the genus *Pikaia* and the single species *P. gracilens.*

Such a remarkably preserved soft-bodied fauna, representing eight known and 10 or more previously unknown phyla that flourished in the Middle Cambrian, is by itself of great interest to students of the fossil record. In addition to this intrinsic interest, however, the Burgess Shale invertebrates, with their specialized adaptations, have an even wider importance in clarifying the early evolution of the animal kingdom. The only earlier-known soft-bodied animals are representative of late Precambrian time, 700 to 600 million years ago and therefore at least 70 million years earlier than Middle Cambrian times. These are the Ediacara animals, first discovered some 30 years ago in the Ediacara Hills of southern Australia and recognized since then in a number of other places throughout the world. The Ediacara



FOUR ANIMALS that lived in the ocean in Middle Cambrian times, some 530 million years ago, are seen in these fossils. At the top left is a trilobite, *Olenoides,* one of the many animals whose anatomy has been preserved in remarkable detail in the silts that solidified to form the Burgess Shale of British Columbia. The specimen is 5.5 centimeters long. Unlike most arthropods, or joint-legged animals, *Olenoides* had unspecialized limbs. At the top right is another Burgess Shale arthropod, *Waptia.* When this bottom-feeding animal was extended, it was four centimeters long. At the bottom left is *Opabinia,* one of about 10 animal species found in the shale that belong to previously unknown phyla. It had five eyes and steered its seven-centimeter body with a vertical tail fin as it swam close to the sea floor in search of food. At the bottom right is one of the many unsegmented marine worms that inhabited the sea floor. It is *Selkirkia,* one of the priapulid phylum. With its projecting proboscis it measured five centimeters. A successful group in the Cambrian, priapulid worms are now rare.

LOWER QUARRY, named the Phyllopod Bed by Charles Doolittle Walcott of the Smithsonian Institution, who first sampled the Burgess Shale, shows patches of winter snow. The view looks south. This and a higher shale exposure were requarried for fossils in 1966–67.

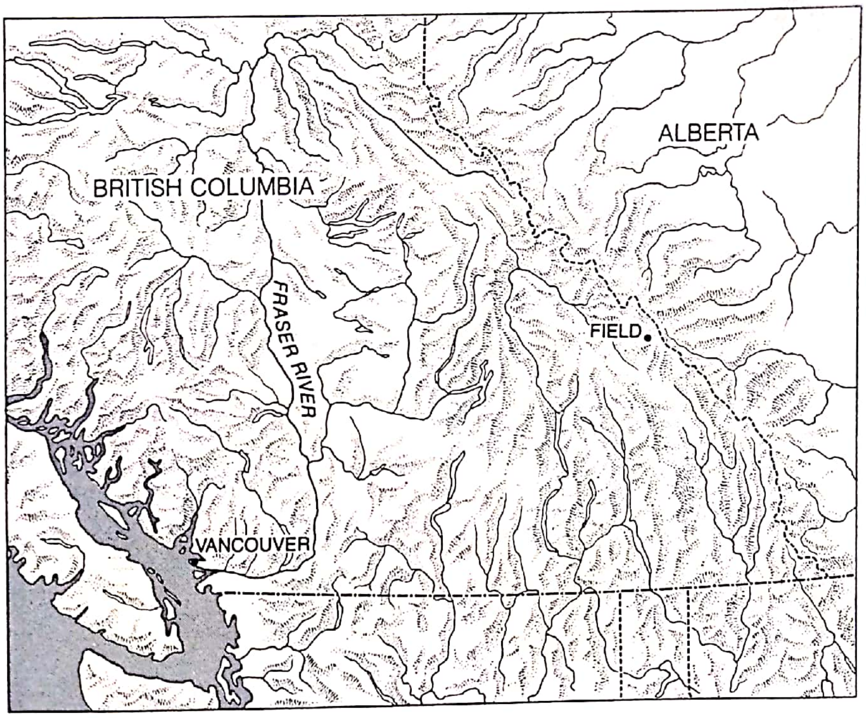


BURGESS SHALE OUTCROP, marked by the colored X in this block diagram of the Middle Cambrian seascape, is a small portion of an extended sea-bottom deposit of silts accumulated at the foot of a deeply embayed algal reef that rose vertically some 530 feet above the shallowest silts. The reef did not rise above sea level but was covered by shallow water. The vertical scale in the block diagram is exaggerated by a factor of five, and the distance (*a–a'*) from north to south along the reef is some nine miles. Later uplift and dissection gave rise to the peaks of the Rockies along the border of Alberta and British Columbia, indicated by colored triangles. The reconstruction of the sea floor and the reef is based on the work of I. A. McIlreath of Petro-Canada, one recent investigator of the unique formation.

fauna stands in marked contrast to the Burgess Shale fauna both in the kinds of animals represented (chiefly coelenterates) and in these earlier animals' limited range of specialization.

The event that separates the impoverished Ediacara fauna from the Burgess Shale fauna is an explosive evolutionary diversification of multicelled animals that took place near the beginning of Cambrian time. The fossils of the Burgess Shale thus give us a unique glimpse into the results of this sudden metazoan adaptation relatively soon after it occurred.

In spite of the work done by Walcott and others significant gaps remain in what is known about the Burgess Shale paleoenvironment and how its fauna was preserved. A fuller appreciation of these gaps stimulated a reinvestigation of the site by the Geological Survey of Canada, beginning more than a decade ago. The authorities of the Yoho National Park in British Columbia and the Parks Canada administration in Ottawa granted special permission to collect material from the shale outcroppings. Walcott's quarries were reopened in 1966 and 1967 under the direction of J. D. Aitken of the Geological Survey of Canada. Both the new material collected during these two seasons and a part of the great Burgess Shale collection amassed by Walcott some 60 years earlier then came to us at the University of Cambridge for analysis.



BURGESS SHALE FORMATION is situated some 350 miles northeast of Vancouver near the town of Field, B.C. The fossil-rich formation was found accidentally by Walcott in 1909.

What kind of environment did the Burgess Shale fauna inhabit? Studies done by I. A. McIlreath of Petro-Canada and W. H. Fritz of the Geological Survey of Canada show that the animals lived on or in a muddy bottom where sediments had accumulated at the base of a gigantic reef. This structure, made up of material secreted by algae, rose vertically for hundreds of feet from a deep-water basin that was gradually being filled with sediments. Scattered outcrops of the reef front can still be traced for miles across British Columbia. The bottom waters of the basin were apparently limited in circulation, rich in hydrogen sulfide and poor in oxygen. The various invertebrates flourished where the muddy sediments were banked high enough against the reef to be clear of the stagnant bottom waters, about 530 feet below sea level.

The reef-front sediments were not stable. Studies of the shale by D. J. W. Piper of Dalhousie University show that periodic slumping resulted in the flow of mud into the deeper anaerobic waters of the basin. These flows wiped away all the surface tracks and subsurface burrows made by the Burgess Shale fauna. Because the animals trapped in the torrents of mud died during or shortly after their burial they could not leave new traces. This means that the way of life of each species must be deduced from a study of their organs of locomotion and from comparisons with living invertebrates of the same kind.

At the same time the catastrophic burials, in anaerobic deposits of fine silt where scavengers could not survive, greatly favored the preservation of the animals' soft parts. As the mud gradually compacted and became hard rock the buried carcasses were flattened and the soft parts were transformed into thin films of calcium aluminosilicate. In general the films are rather dark, but certain parts of most specimens are preserved as highly reflective areas.

Paradoxically, although the animals' soft parts are wonderfully preserved, signs of rotting after burial can often be detected. Many specimens are associated with a black-stained area, a result of the body contents of the carcass seeping out into the surrounding mud. In extreme cases the fossil of a worm consists only of a hollow bag of cuticle because practically all the animal's internal organs have been destroyed by decay. In some worms a subtler indication of decay is the pulling away of body-wall muscles from the cuticle.

Burial in a mud flow has other important effects. For one thing, many of the animals came to be buried at all angles; the shale bedding has therefore preserved them in a variety of orientations that reveal much more of the animals' anatomy than simple horizontal burial does. For another, the fluid sediments that penetrated between the appendages of animals such as arthropods and polychaetes during the turbulent flow of silt were eventually reduced to thin layers of shale. Judicious work with a microchisel enables one to remove these fine layers, thereby revealing further details of a specimen's anatomy that would otherwise remain hidden.

The composition of the Burgess Shale fauna upsets the conventional notion of what makes up a typical assemblage of Cambrian animals. The fossils found at most Cambrian localities are the exoskeletons of such arthropods as trilobites, the shells of various members of the brachiopod phylum and of such echinoderms as the extinct plate-shelled Eucrinoid class. Animals such as these account for barely 20 percent of the invertebrate genera in the Burgess Shale. Is it justified, then, to regard the Burgess Shale assemblage as the Cambrian norm, at least with respect to the fauna of deeper waters, and to view the other Cambrian faunas as being skewed by the selective fossilization of animals with hard parts?

Since the Burgess Shale represents a single environment that has been frozen for a split second of geologic time, no firm answer can be given to the question. Several factors nonetheless suggest that the Burgess Shale fauna was not untypical of Middle Cambrian times. The scattered occurrence of species similar to those from the Burgess Shale in other Cambrian rocks hints at the existence in this period of a widespread soft-bodied fauna. Furthermore, in some Cambrian fossil assemblages certain rather peculiar species were able to flourish because access by sea to the area of deposition was limited. The Burgess Shale, on the other hand, lay at the edge of the open sea and would have been exposed to colonization by marine larvae floating in from other areas. This circumstance adds weight to the hypothesis that the Burgess Shale fauna approaches the Cambrian norm.

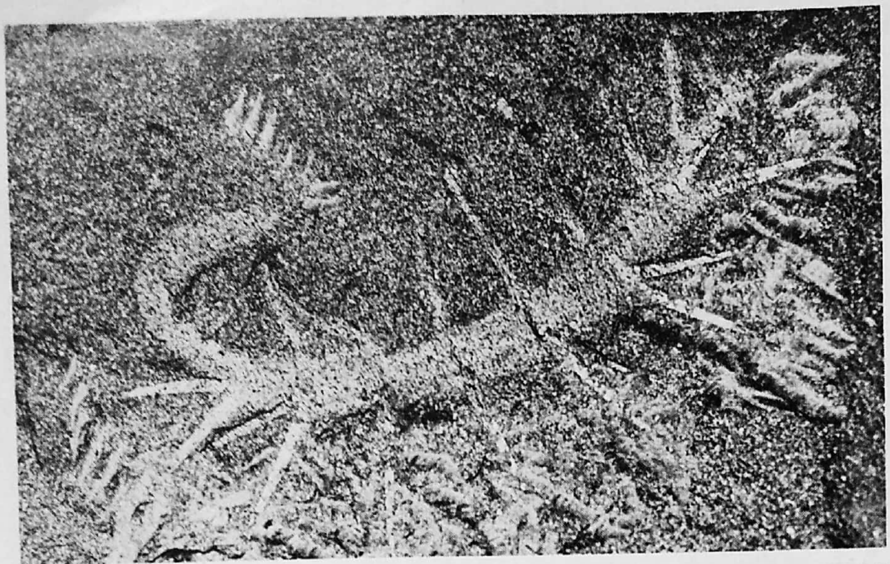
In this connection it should be noted that representatives of certain modern invertebrates that have almost certainly had a long geological history are absent from the Burgess Shale. No species of the platyhelminth phylum, the flatworms whose living members include flukes, tapeworms and planarians, are present. There are also no species of another worm phylum, the Nemertea, which includes the modern proboscis worm, and none of still another, the sipunculid phylum. It may be that such worms are not represented because the reef-front environment was not suitable for them.

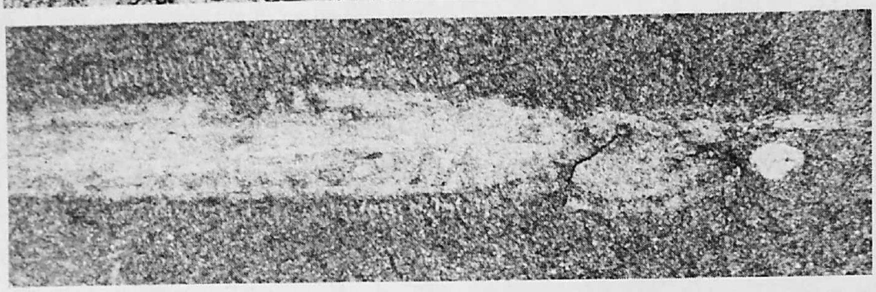
Most of the species found in the Burgess Shale can be placed in the ecological framework of a bottom-dwelling marine community that thrived on the muddy sea floor between intervals of slumping. The mud supported an active group of burrowing invertebrates, with priapulid worms predominant. Attached to the sea floor and growing to various heights were a variety of sponges representing at least 15 genera; they fed on food particles suspended in the water. Actively patrolling the sea-floor surface or plowing through the mud in search of food were many species of arthropods. Certain brachiopods occupied a peculiar niche: they attached themselves to the elongated spicules of one of the sponges, *Pirania*. For the brachiopods the advantages are obvious: they lived somewhat above the turbid waters of the sea floor and could capture food particles such as the sponges fed on at these higher levels.

In addition to this community of fixed and mobile surface dwellers and burrowers a number of free-swimming species inhabited the waters along the reef front. Of these animals there are only tantalizing glimpses, in the form of rare specimens buried by chance in the slumped sediments. The different members of this pelagic fauna probably lived at different depths; some among them may have been species swept into the reef-front area from the open sea.

At most Cambrian fossil localities the mineralized exoskeletons of trilobites, the most familiar of all Paleozoic arthropods, are in the majority. In the Burgess Shale, however, trilobites—with one exception—are comparatively unimportant. The exception is *Olenoides*, which is of great significance because in several specimens the appendages have

UNDERWATER SCENE where silts slope down from the face of the great reef and the Burgess Shale fauna lived is shown in an idealized reconstruction. No attempt has been made to show the animals in numbers proportional to their fossil abundance. The fauna are identified by number, starting at the bottom left; only about a fifth of the species fossilized in the shale are shown. Most of the immobile animals of the sea floor are sponges: *Pirania* (*12*), seen with brachiopods attached to its spicules; *Eiffelia* (*22*); the gregarious *Choia* (*25*); a gracile species of *Vauxia* (*5*), with a more robust species at the top right, and *Chancelloria* (*27*). Three other immobile animals are *Mackenzia* (*21*), a coelenterate; *Echmatocrinus* (*16*), a primitive crinoid, seen attached to an empty worm tube, and *Dinomischus* (*17*), one of the Burgess Shale species that represent hitherto unknown invertebrate phyla. The burrow-dwelling animals are *Peronochaeta* (*1*), a polychaete worm that fed on food particles in the silt; *Burgessochaeta* (*2*), a second polychaete that captured food with its long tentacles; *Ancalagon* (*4*), a priapulid worm possibly ancestral to some modern parasites; *Ottoia* (*7*), another priapulid, seen at the center feeding on the mollusk *Hyolithes* (*6*) and at the right burrowing; *Selkirkia* (*8*), a third priapulid, seen here in a burrow front end down, and *Louisella* (*9*), a fourth priapulid that inhabited a double-ended burrow and undulated its body to drive oxygenated water over its gills. *Peytoia* (*10*) is a free-swimming coelenterate shaped like a pineapple ring. The sea-floor-dwelling mollusks in addition to *Hyolithes* are *Scenella* (*23*), its soft parts hidden under "Chinese hat" shells, and *Wiwaxia* (*24*), with its covering scales and defensive spines, seen here plowing a trail through the silt. Among the many arthropod genera of the sea floor are *Yohoia* (*3*), with its distinctive grasping appendages; *Naraoia* (*13*), an atypical trilobite that retained some larval characteristics; *Burgessia* (*14*), with its long tail spine; *Marrella* (*15*), which may have swum just above the sea floor; *Canadaspis* (*20*), an early crustacean, and *Aysheaia* (*26*), a stubby-legged animal suggestive of the living land dweller *Peripatus*. Other representatives of new phyla seen in addition to *Dinomischus* are *Hallucigenia* (*18*), one preparing to feed on a dead worm and two others approaching it, and *Opabinia* (*19*), seen here grasping a small worm with its single bifurcated appendage. Finally, seen swimming alone at the top left, is *Pikaia* (*28*), the sole representative of the chordate phylum in this Middle Cambrian fauna. *Pikaia* probably used its zigzag array of muscles to propel itself above the sea floor. The phylum of chordates includes the subphylum of vertebrates, which evolved later.





been preserved in detail. *Olenoides* had a pair of slender antennae in front and a pair of cerci, or antennalike structures, in back. The limbs along the length of the animal, up to 16 of them, were all similar in construction. The coxa, a large unit closest to the body, carried a battery of ferocious-looking spines. Attached to the coxa were two appendages; one was a filamentous gill and the other was a walking leg. *Olenoides* could seize and shred soft food, such as small worms, and pass the fragments along to its mouth. The forward antennae and the rear cerci no doubt supplied the animal with information about both food and potential predators. The fact that the primitive limbs of this trilobite are all similar is in marked contrast to the arrangement in many fossil and living arthropods whose limbs are variously modified and specialized.

About 40 percent of the Burgess Shale fauna consists of arthropods. Both in the number of species and the number of individual specimens the soft-bodied representatives of the phylum outrank the hard-shelled trilobites. Many of these "nontrilobites" have had their appendages preserved in remarkable detail; some of them must have been effective predators and scavengers. The most abundant is *Marrella,* an arthropod with a wedge-shaped head that bore two pairs of long hornlike spines curving to the rear. *Marrella* sensed the sea-floor environment with a pair of antennae and swept food particles toward its mouth with adjacent feathery appendages. Its score or more of side limbs were jointed, and a filamentous gill branched from each limb.

The next most abundant of the nontrilobites is *Canadaspis.* All but the hind part of its body was concealed by a double shell. Careful removal of this covering reveals the underlying appendages, which are remarkably like those of certain living crustaceans. Still another arthropod was one of the larger predators of the sea floor. This is *Sidneyia,* an animal whose distinctive limbs recall those of the living horseshoe crab, *Limulus.* It has been possible to identify some of the gut contents of *Sidneyia* as being fragments of brachiopod shells, evidence

UNIQUE ANIMALS of the Burgess fauna include the four seen in the photographs at the left. At the top is *Hallucigenia,* shown in the illustration on the preceding two pages. Second from the top is *Nectocaris,* a streamlined animal with conspicuous fin rays. At the bottom left is *Amiskwia,* a gelatinous worm with prominent fins. At the bottom right is *Dinomischus,* the stalked animal also shown reconstructed on the preceding two pages. Each of these species and six or more others represent hitherto unknown phyla of invertebrates.

that this arthropod was able to crush hard-bodied prey.

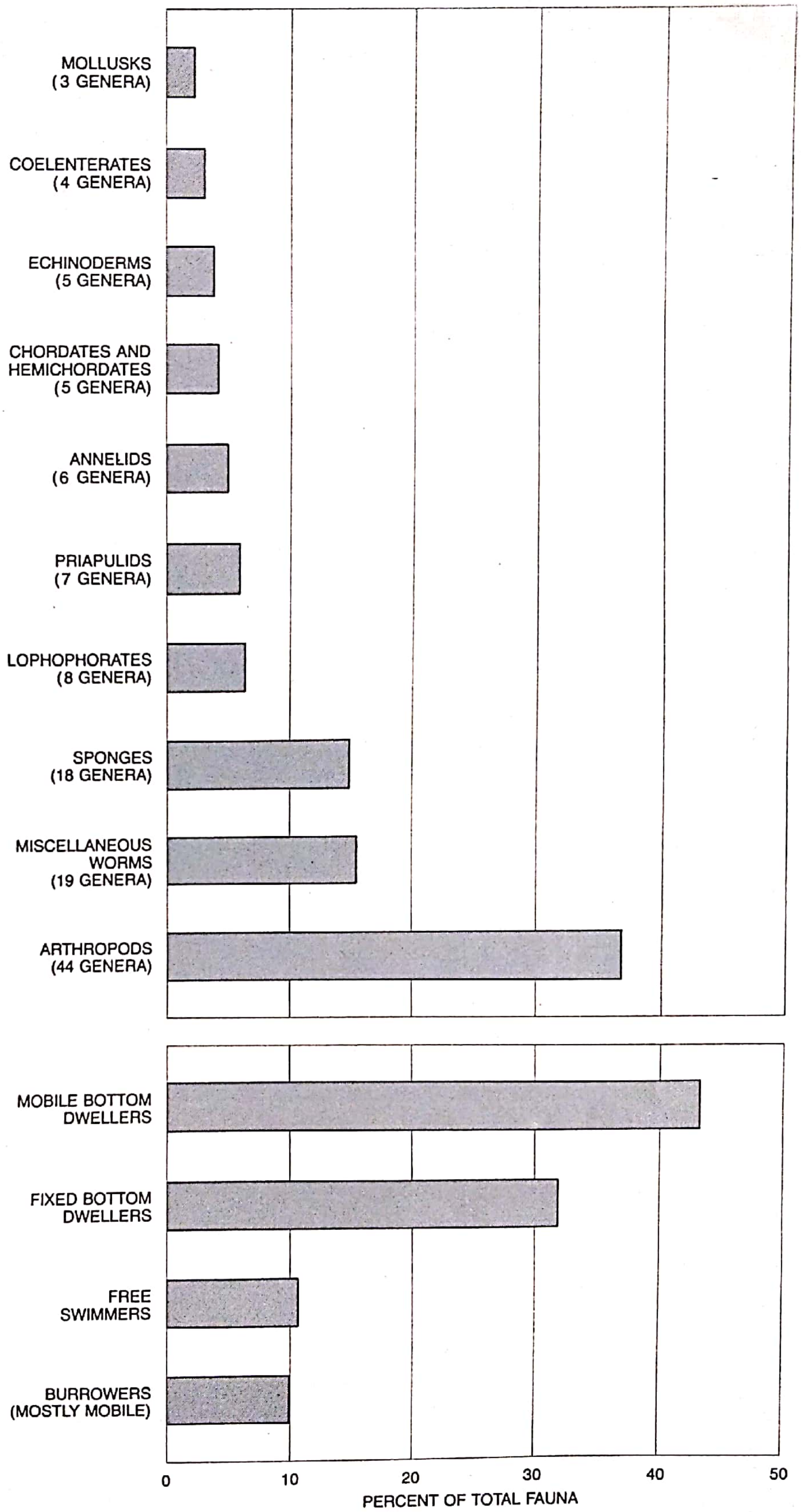
Sidneyia was not the largest of the Burgess Shale arthropods. The shale contains the impressions of isolated large limbs; if they are in proportion, they may have belonged to an animal as much as a meter long. The name *Anomalocaris* has been assigned to these fossils, which possibly represent one of the largest of all Cambrian invertebrates.

The most interesting of all the Burgess arthropods is *Aysheaia*, an animal with a pudgy body and stubby limbs. When Walcott first published a photograph of this fossil half a century ago, a number of zoologists wrote to him to point out how much this Middle Cambrian invertebrate resembled *Peripatus*, an animal with eight genera of relatives (comprising two families) in the small class of onychophores within the arthropod phylum. *Peripatus* was a land animal and *Aysheaia* was a marine form; nevertheless, *Aysheaia* surely represents the kind of ancestor that could have given rise to such living arthropods as myriapods and insects.

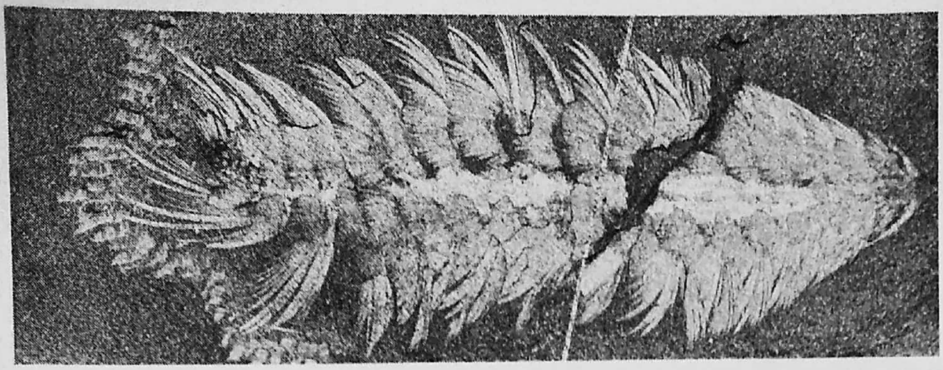
Although some of the nontrilobite arthropods in the Burgess shale, such as *Aysheaia*, are reminiscent of later forms, most of them cannot be placed in any recognized group. They have no obvious relatives either among the other Burgess Shale species or among the arthropods of later times. Because they exhibit a surprisingly wide array of anatomical features, indicating a high degree of specialization, they are evidence of a hitherto unsuspected adaptive radiation of arthropods in Cambrian times. It appears that the numerous stocks that arose during this period of rapid evolution were mostly unsuccessful. It is interesting to note that the animals that were to become dominant in later geological history generally have only a minor position in the various Cambrian faunas; a hypothetical observer would have been hard-pressed to predict just which groups had the flexibility necessary for long-term biological success.

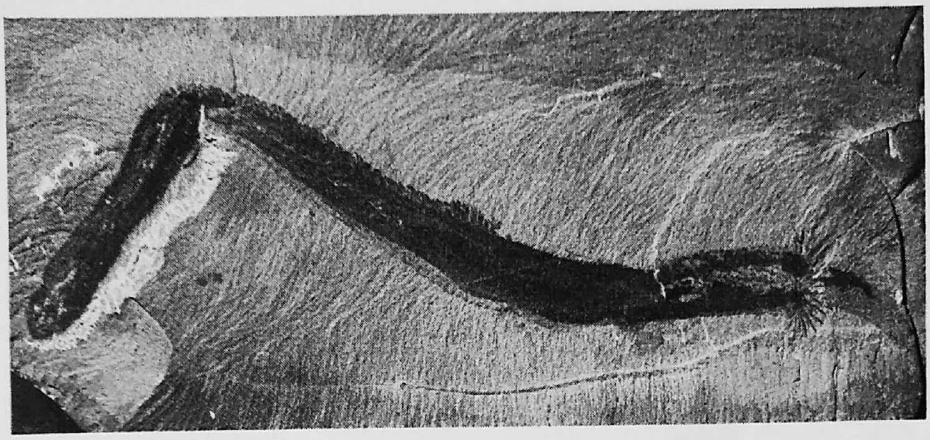
Of the Burgess Shale animals other than arthropods the representatives of six phyla are particularly noteworthy. Among the echinoderms the class of holothurians, the group that includes the sea cucumbers, was once thought to be widely represented. Now only one animal, *Eldonia*, is so classified. Unlike the great majority of the species in its class, *Eldonia* had a jellyfishlike body and a pair of oral tentacles. These animals probably swam through the water in shoals, using their tentacles to capture food. Another Burgess Shale echinoderm, the sea lily *Echmatocrinus*, is the earliest crinoid in the fossil record; as might be expected, it shows a number of primitive features.

The species of the coelenterate phy-



BURGESS SHALE GENERA currently number 119. The percent of the total assigned to various phyla is indicated in the upper part of this bar chart. Nearly 40 percent of the total are arthropods; only 14 of the 44 arthropod genera are trilobites. Worms other than priapulids and annelids (19 genera) and sponges (18 genera) make up another 30 percent of the total; mollusks are the most poorly represented. In terms of habitat, as the lower set of bars indicates, more than 40 percent of the Burgess Shale animals wandered the sea floor and more than 30 percent were rooted in the silt. Most of the burrowing animals also moved freely, although some remained fixed. Burrowers were slightly outnumbered by animals that swam above the sea floor.





TWO PHYLA OF WORMS in the Burgess Shale fauna are the familiar annelids and the less common priapulids. A typical Burgess Shale annelid is *Canadia,* a polychaete worm (*top*); its setae, bundles of fine bristles that were organs of locomotion, are preserved in detail. A typical priapulid worm (*bottom*) is *Louisella,* also reconstructed in illustration on pages 114 and 115.

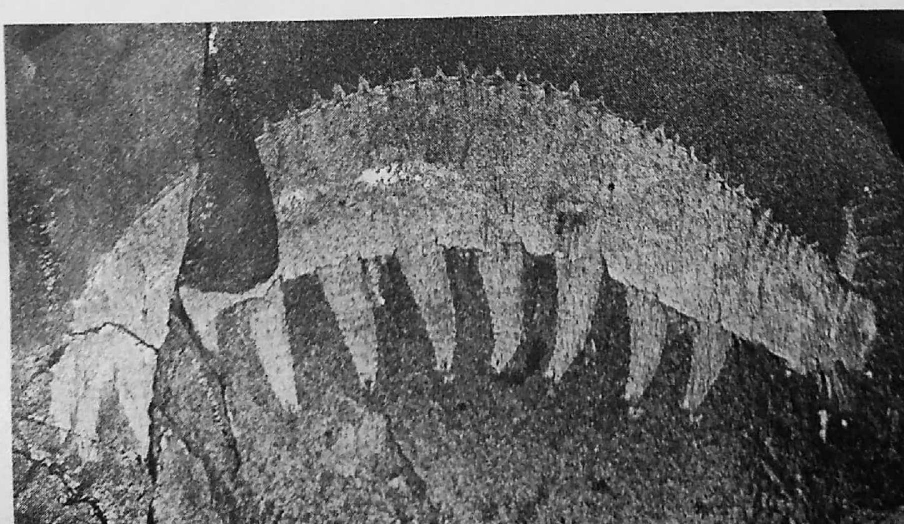
lum are among the most primitive of the metazoans. For example, in the late Precambrian fossil assemblage from the Ediacara Hills the coelenterates predominate. In contrast, the several Burgess Shale coelenterates, some resembling jellyfishes and others resembling sea pens, seem to have played a rather limited role in the community. On the other hand, the Burgess Shale sponges, the most primitive of all the animals present, were prominent members of the community. They were abundant and varied in form; some species grew on the sea floor in thickets.

The various Burgess Shale "worms" were mainly assigned by Walcott to the annelid phylum in general and to the class of polychaetes in particular. It is now realized that many of them belong to other phyla. Nevertheless, it is among the polychaete worms that some of the most spectacular examples of soft-body preservation are to be found: the setae, or bundles of fine bristles, that were these animals' organs of locomotion have been particularly well preserved as bright, reflective films in the shale. One of the polychaetes, *Canadia,* apparently did not live in a burrow but spent much of its time swimming close to the sea floor. Another, *Burgessochaeta,* was probably a more typical burrower, taking refuge in the muddy bottom and searching for food around the burrow entrance with its long tentacles.

Today the priapulid phylum is of interest only to a handful of specialists. These worms, however, were an important group in Cambrian times, and two priapulids present in the Burgess Shale are particularly noteworthy. One of them, *Ottoia,* is the most abundant of the group. It has been preserved in such detail that muscles are clearly visible and the gut content of some specimens can be analyzed. *Ottoia* fed on two kinds of shellfishes: brachiopods and hyolithids. The hyolithids, possibly members of the mollusk phylum, had a conical shell that was capped by a protective operculum, or lid, when the animal was fully withdrawn. The teeth of *Ottoia* were not strong enough to break open the shell, and so the hyolithids were swallowed whole and their soft parts were digested as the shells passed through the priapulid's gut unscathed. These shellfishes were not *Ottoia's* only food. A unique specimen contains within its gut the remnants of another worm of the same species, showing that (as with some living priapulid worms) *Ottoia* could be cannibalistic.

Parasitologists take considerable interest in another Burgess Shale priapulid. It is *Ancalagon,* which may be ancestral to the living group of spiny-headed worms, the Acanthocephala, that seem to have been parasites for millions of years. These parasitic worms have no gut and absorb nourishment through their body wall while they are lodged in the intestine of their host. If evolution is hypothetically reversed and the worms are reendowed with the organs necessary for a free-living existence, the reconstructed animal is remarkably like *Ancalagon.*

Two other supposed worms, once considered to be polychaetes, are *Wiwaxia* and *Pikaia.* The body of *Wiwaxia* was covered with large scales. Long spines that curved upward and outward along the animal's back evidently were protection against predators. That the spines actually were protective is indicated by the fact that in some specimens of *Wiwaxia* they have been snapped off. An inhabitant of the sea floor, *Wiwaxia* nourished itself by scraping off fragments of food with a rasping organ. The rasp resembles the radula, or horny



ANCESTRAL ARTHROPOD with a striking resemblance to the living onychophore *Peripatus* is this remarkably preserved invertebrate, *Aysheaia.* Cambrian arthropods such as *Aysheaia* could have been ancestral to such living members of that phylum as the myriapods and insects.

toothed tongue, of certain living mollusks. Is *Wiwaxia* a primitive mollusk? If it is, the details of its remarkably preserved anatomy will throw new light on the early evolution of this highly successful phylum of invertebrates.

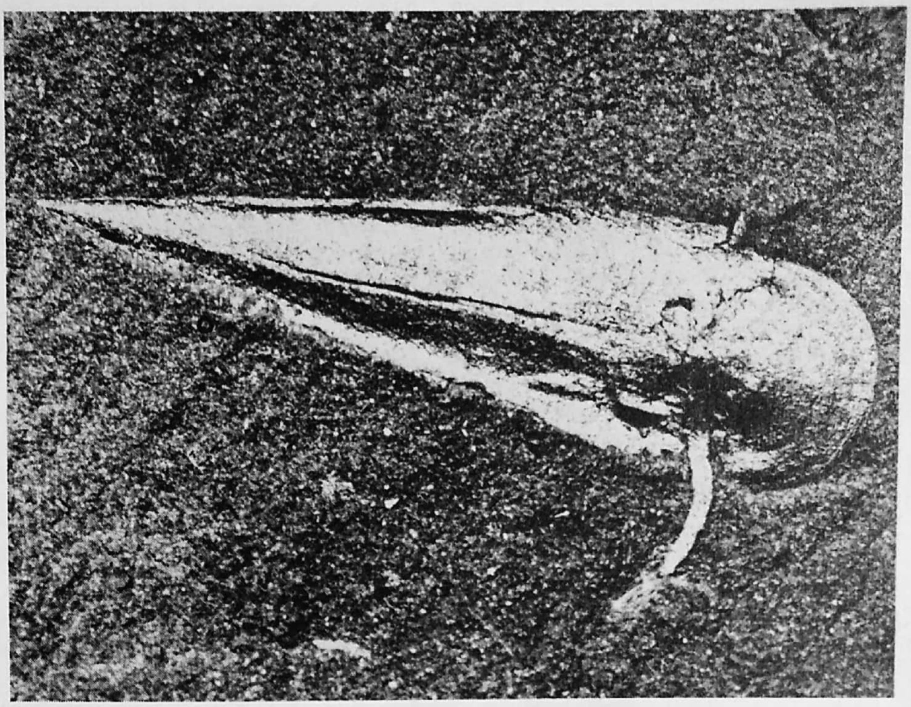
What about *Pikaia*, formerly considered a polychaete worm? Some 30 well-preserved specimens show a prominent rod along the animal's back that appears to be a notochord, the cartilagelike stiffening organ that gives the chordate phylum its name. In addition to this key anatomical feature the blocks of muscle in *Pikaia* form a zigzag pattern that is comparable to the musculature of the primitive living chordate *Amphioxus* and of fishes. Although *Pikaia* differs from *Amphioxus* in several important respects, the conclusion that it is not a worm but a chordate appears inescapable. The superb preservation of this Middle Cambrian organism makes it a landmark in the history of the phylum to which all vertebrates, including man, belong. There are possible instances of even earlier chordates from Lower Cambrian formations in California and Vermont but none is as rich in detail.

Perhaps the most intriguing problem presented by the Burgess Shale fauna is the 10 or more invertebrate genera that so far have defied all efforts to link them with known phyla. They appear to be the only known representatives of phyla whose existence had not even been suspected. Their origins must lie in Precambrian obscurity, where the initial metazoan diversification began. The peculiarity of these novel animals is exemplified by the aptly named *Hallucigenia*.

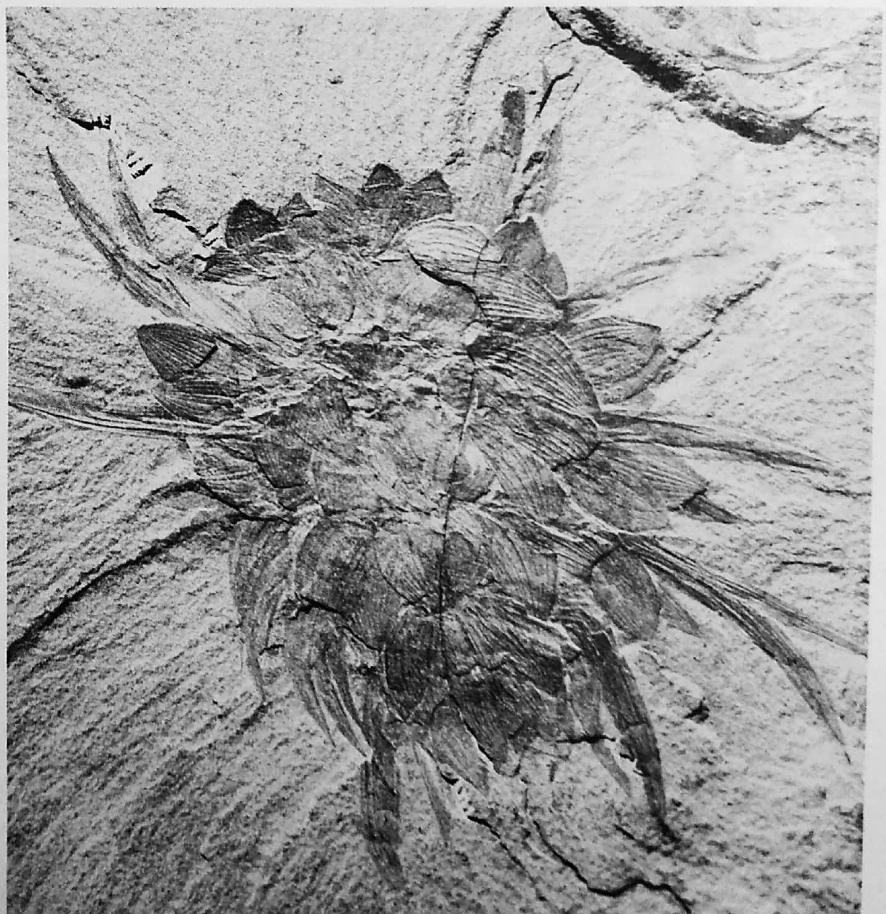
This animal propelled itself across the sea floor by means of seven pairs of sharply pointed stiltlike spines. Seven tentacles arose from the upper surface of the animal's body; at the end of each tentacle was a pair of strengthened tips. Did the tentacles gather food? If they did, did each tentacle act as an individual mouth with a direct connection to the animal's alimentary canal? There are more questions than answers, but a valuable clue to the animal's behavior is preserved in a specimen from a Harvard University collection. There one can see more than 15 individual *Hallucigenia* associated with a large worm. There seems little doubt that, having detected the carcass of the worm, these odd animals had congregated to scavenge it.

Compared with *Hallucigenia* a second unique animal, *Opabinia*, seems almost orthodox. Its five eyes were arranged across its head, so that it was probably able to avoid predators with ease as it swam close to the sea floor, steering itself with a vertical tail fin. *Opabinia* fed by capturing prey with a grasping organ that projected forward.

Alternative approaches to problems



MOLLUSK REPRESENTATIVE, *Hyolithes*, **had a cone-shaped shell that was capped by a protective lid. One of the burrowing worms,** *Ottoia*, **preyed on these mollusks but was not able to break the shell open. The worm digested** *Hyolithes'* **soft parts and excreted its shell.**

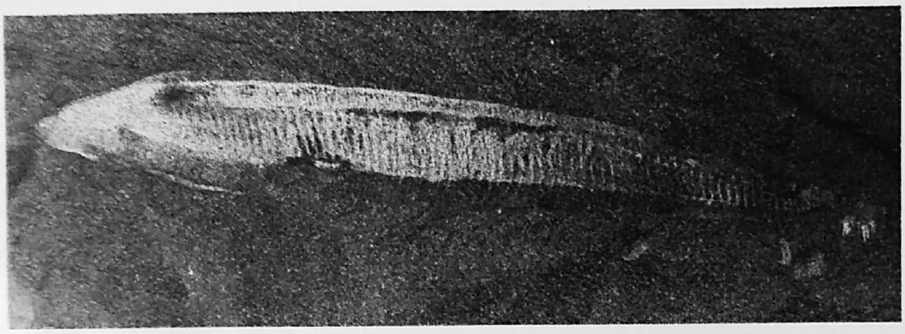


PROBABLE MOLLUSK, *Wiwaxia*, **with its cover of large scales and array of long protective spines, was first placed among the polychaete worms of the Burgess Shale. Its rasplike feeding organ, similar to a mollusk's radula, suggests that it belongs to the molluscan phylum instead.**

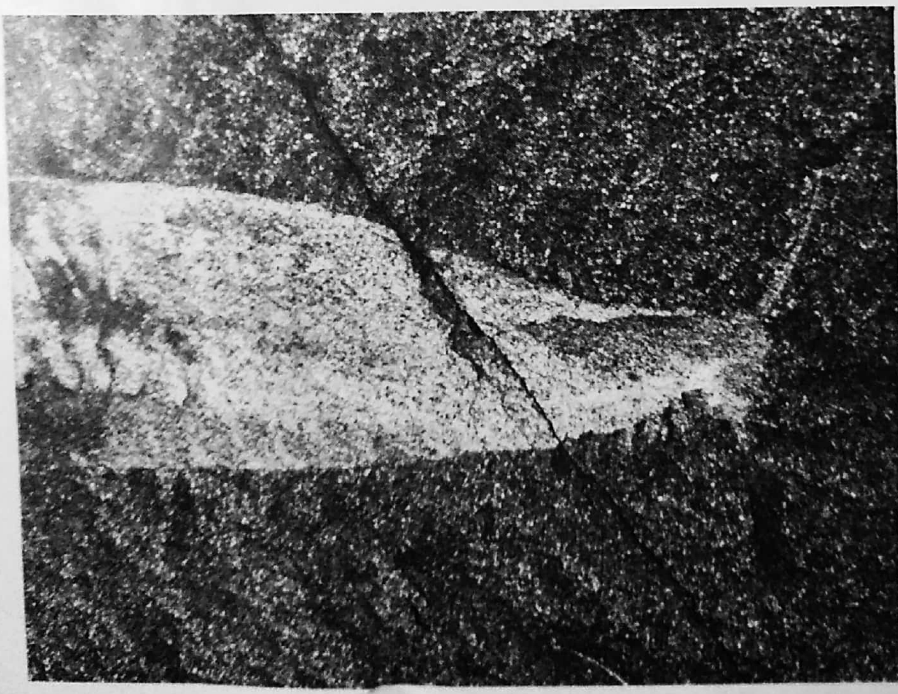
of functional design are evident among these unusual invertebrates. For example, for a worm with a fluid-filled body cavity one problem is that muscular contraction in one part of the body will distort the shape of the rest of the body. In annelid worms the problem has been solved by dividing the body cavity into a series of watertight compartments. *Banffia*, a unique Burgess Shale worm, developed an alternative solution. The stiffened front half of its body was separated from the more saclike back half by a prominent constriction at the midpoint. The constriction appears to have damped the hydrostatic fluctuations set up by the locomotor muscles of the animal's front half, thereby minimizing the distortion of its unstiffened back half.

Some representatives of new phyla have been preserved by the dozen. Others, particularly the free-swimming inhabitants of the higher water levels that would seldom be trapped by slumping mud, are quite rare. One such animal is the worm *Amiskwia;* judging by its prominent fins, it was probably quite an active swimmer. Another animal, *Nectocaris*, a fast-swimming predator, had enormous eyes and evidently propelled its streamlined body by rapid lateral flicks of its body. Prominent dorsal and ventral fins, stiffened by numerous fin rays, helped to keep the animal stable as it was swimming.

Conodonts, or "cone teeth," are enigmatic fossils that resemble tiny teeth; they are found in formations ranging in age from the latest Precambrian to the Triassic, a span of almost 400 million years. Although they look like teeth, they cannot have acted as such because they show no signs of wear. What soft-bodied animal had conodonts and for what purpose has long been an unanswered question. Another rare pelagic invertebrate preserved in the Burgess Shale, *Odontogriphus*, may be that animal. The tentacular feeding apparatus of the animal, another unique representative of a hitherto unknown phylum, incorporates a set of minute conical objects that appear to be conodonts. Since conodonts cannot have acted as teeth, the hypothesis has been advanced that they were some kind of support for the feeding tentacles. Was the feeding apparatus of *Odontogriphus* and of animals like it the source of the conodonts so copiously distributed throughout the Paleozoic and the earliest Mesozoic fossil record? Possibly so.



STIFFENING ROD, or notochord, runs partway along the back of the early chordate *Pikaia*. The animal's head, seen in more detail in the illustration below, is at the right. The pattern of its musculature resembles that of fishes and of the living primitive chordate *Amphioxus*. A reconstruction of this free-swimming chordate appears in the illustration on pages 114 and 115.



FRONT END of *Pikaia* is seen enlarged in this photograph, making visible the animal's pair of sensory tentacles and behind them a short row of small appendages. Earlier Cambrian formations preserve the remains of possible chordates, but none compare with *Pikaia* in detail.

As more is learned about the Burgess Shale fauna the picture of Cambrian life will gain a new perspective, particularly with respect to the explosive evolution of the metazoans. For example, the wide range of arthropods, with their distinctive and different groupings of anatomical characteristics, is already such that a single phylum seems too small to hold them all. The adaptive radiation of the Cambrian invertebrates can be seen as the initial response to the availability of a very wide variety of marine ecological niches. Hence many Cambrian animals seem to be pioneering experiments by various metazoan groups, destined to be supplanted in due course by organisms that are better adapted. The trend after the Cambrian radiation appears to be the success and the enrichment in the numbers of species of a relatively few groups at the expense of the extinction of many other groups.

An additional possibility is suggested by the Burgess Shale fauna itself. Some groups of major stature in Cambrian times, such as the priapulid worms, may have fared badly against later competitors and only escaped extinction by migrating into marginal niches that were either unattractive or unavailable to other metazoans. One such manifestation of movement into a marginal niche is the scaling down of body size. This miniaturization may well be how some priapulids managed to survive. An alternative escape route is to become parasitic; the priapulids that appear to have given rise to the parasitic spiny-headed worms could be an example of the alternative. In any event the Burgess Shale fauna affords both a marvelous glimpse of evolution in action during this brief interval of Middle Cambrian times and a stern reminder of how impoverished and distorted the fossil record is. The study of these soft-bodied animals illuminates many hitherto unsuspected aspects of the history of life.