Geological Survey of Canada
Miscellaneous Report 43

FOSSILS OF THE BURGESS SHALE
A National Treasure in Yoho National Park, British Columbia

S. Conway Morris and H.B. Whittington

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Cover photo

Marrella *(x5), exposed from the underside, showing the spines curving back from the head, the antennae (a), a second long appendage (b), and the many pairs of limbs on the trunk. At the back, a dark patch is visible on the rock; a stain caused by decay products leaking out of the body into the surrounding sediment.*

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Preface

The Burgess Shale was discovered and made famous by Charles D. Walcott, who recognized the importance of its unique fossils and spent the summers of 1909-1913 painstakingly quarrying and collecting. A half-century later, Walcott's large collection was still virtually the only material available for study of the Burgess Shale fauna, and it was widely believed that the fossil-bearing beds had been completely quarried away. Many of Walcott's collection and preparation methods, and the fund of biological knowledge on which he based his interpretation of the fauna, had become outmoded. The scientific need for a modern re-study of the Burgess Shale fauna and flora was evident, as was the value of new material, collected according to modern standards, if it could be obtained.

Reconnaissance by geologists of the Geological Survey of Canada indicated that some fossil-bearing beds remained at the site, and perhaps could be made to yield their treasure. Officials of Parks Canada, recognizing the scientific importance of a modern study, gave permission to re-open the quarry. Professor Harry B. Whittington, then of Harvard University, was invited to lead the paleobiological team, because of his comprehensive knowledge of the fossil groups involved and his success with innovative photographic techniques of illustration. The Geological Survey of Canada provided financial and logistical support for the quarrying effort in 1966 and 1967, and studied the geology of the Burgess Pass area to establish the environment in which this unique deposit was laid down.

The extensive results of this work are mainly published in very specialized scientific journals. This special paper, a contribution of the Geological Survey of Canada to the Centennial of the National Parks of Canada, is designed to explain the Burgess Shale, and the significance of its famous fossils, to the interested public.

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FOSSILS OF THE BURGESS SHALE, A NATIONAL TREASURE IN YOHO NATIONAL PARK, BRITISH COLUMBIA

INTRODUCTION

In Yoho National Park, near the small town of Field, British Columbia, the magnificent mountains of the Main Ranges of the Canadian Rockies are composed almost entirely of sedimentary rocks that were deposited during what is known to scientists as the Cambrian Period. In human terms, these rocks are of immense antiquity; radiometric methods of dating[1] indicate that they were deposited approximately 530 to 560 million years ago. Even though there is no ready yardstick by which we can comprehend such figures, it is worth recalling that the Earth itself is about 4600 million years old. In other words, almost 90 per cent of Earth's history had elapsed prior to Cambrian times.

Even a cursory glance at the rocks surrounding Field will reveal that they range from inclined to more or less flat lying; and it might be supposed that the flat-lying strata have not been tilted or folded since their original deposition. In fact, the rocks have undergone considerable displacement and are nowhere near the position where they were originally laid down. This is because part of the process of mountain building in the Rockies involved the thrusting and eastward transport of huge slices of rock that formerly were located far to the west of their present positions.

The sedimentary rocks are varied in composition, and even at a distance can usually be recognized from the colour of weathering. For example, the yellowish brown rocks on the lower slopes and cliffs of the surrounding mountains are predominantly sandstone, while, higher up, bluish-grey limestones and darker brown shales are distinguishable. Most if not all the Cambrian sediments of this area were deposited under marine conditions. The presence of fossil brachiopods and echinoderms in these rocks, animals that today are never found in freshwater but only in the seas, strongly suggests marine conditions during deposition. We therefore assume that the other fossils found with them are also marine creatures.

As is typical for Cambrian rocks the world over, trilobites are the most abundant fossils in these strata. Trilobites are an extinct group of arthropods (literally animals that had jointed legs), distant relatives of the modern shrimps and lobsters, that had an external shell or exoskeleton reinforced with calcium carbonate. Other kinds of fossils accompany the trilobites. The fossil brachiopods were bivalved creatures, some representatives of which still survive in some abundance and variety at various depths in the sea, all over the world. Hyolithids, an extinct group with a characteristic conical shell that could be closed by a lid-like plate called the operculum, are also abundant. Somewhat rarer in the Cambrian rocks are the remains of sponges and echinoderms (a group represented in present-day seas by starfish, sea urchins and crinoids), but these almost invariably consist of scattered spicules and plates because the soft tissues connecting them rapidly rotted after death. Indeed, the only reason these groups are preserved as fossils is because they possessed skeletal hard parts that were resistant to decay following the death of the animal. Their associated soft parts quickly decomposed and disappeared after death and, normally, paleontologists can only guess as to what such soft parts looked like.

Under normal circumstances, therefore, only the hard parts of fossils are preserved. These include the shells of bivalves and gastropods, the exoskeletons of trilobites, and the plates of echinoderms - all of which are made of calcium carbonate. However, if one looks at a modern assemblage of animals living on and in the seafloor, it transpires that, although there are indeed many species (especially snails and clams belonging to the group Mollusca) with hard parts, there are usually as many, if not more, that are either soft-bodied or have such delicate skeletons as to stand a minimal chance of preservation. While we know that the character of marine life has changed very substantially since the Cambrian, there is no good reason to think that soft-bodied animals were any less common in ancient seas than today. Indeed, the reverse may well have been true. Normally, paleontologists must be content with what the fossil record provides in the form of various skeletal remains, and only the tracks and burrows (trace fossils) left by walking (crawling) and tunnelling soft-bodied creatures hint at their former diversity. Occasionally, however, for reasons that are not well understood, the processes of decay that normally result in the destruction of soft tissues and delicate skeletons are suspended or avoided. Such examples of soft-part preservation in the fossil record are of extraordinary importance to paleontologists because they give a far more accurate insight into the original diversity of life than is normally available. A number of such soft-bodied faunas are known through the fossil record, but it is arguable whether any surpass in overall importance the amazing example located here in Yoho National Park. The fauna is of particular importance in that it is a sample of marine life early in the history of multicellular animals, only a few tens of millions of years younger than the earliest animals with preservable hard parts. The Burgess Shale fauna (and flora) occurs at two horizons, exposed in small quarries, on the west side of the ridge (Fossil Ridge) that runs between Mount Field and Wapta Mountain, about 4.8 kilometres north of the town of Field.

The fossils remaining at these quarries are irreplaceable, and the rocks containing them may yet yield further clues as to the origin of these unique deposits. For this reason, **access to the quarries is by permit only** (obtainable at the Yoho Park Administration office, in Field). The responsible visitor will report any thieves or vandals to the nearest Park Warden. **Visitors caught removing fossils or rocks from any part of the Park are liable to prosecution.**

The discovery of the Burgess Shale fossil beds seems to have been largely accidental, and the story now forms part of the folklore of paleontology. What appears to have happened is that the eminent Cambrian paleontologist, Charles D. Walcott, who was Secretary of the Smithsonian Institution in Washington, D.C., U.S.A., was riding with

[1] Radiometric methods of dating are based on the rate of decay of radioactive elements contained in rock-forming minerals.

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members of his geological expedition during an autumn day in 1909 along the trail that traverses the west side of Fossil Ridge. One of the horses stopped at a loose block deposited by an avalanche, Walcott then dismounted and noticed that the block contained soft-bodied fossils. He must have been aware immediately of the importance of his find, but it was only on his return the following year, when the intact stratum from which the block had fallen was discovered, that he realized the treasure-trove he had stumbled upon. Five seasons of quarrying, in what Walcott named the "Phyllopod bed", yielded tens of thousands of exquisitely preserved arthropods with only the most delicate of skeletons, soft-bodied worms, sponges, algae, and a wide variety of more peculiar groups, as well as typical Cambrian animals such as trilobites, brachiopods, molluscs and echinoderms, some of which also had their soft parts preserved. This material was shipped to the Smithsonian Institution where it is still available to researchers. Walcott described much of the biota, but his descriptions were preliminary and it was clear that a great deal remained to be learnt about the Burgess Shale fauna and flora, and about its origin in relation to its environment.

RECENT WORK, AND HOW THE SHALE WAS FORMED

In 1966, the Geological Survey of Canada was given permission by Parks Canada and the authorities of Yoho National Park to reopen the Burgess Shale quarries. In this and the ensuing year many more specimens were collected, and they, together with Walcott's earlier collections, provided the impetus for a systematic redescription of all the fossils. Detailed studies of the geology of the area in the post-Walcott years, by Charles Ney, D.G. Cook, W.H. Fritz, J.D. Aitken and I.A. McIlreath, have provided a fairly clear picture of the site in which the fossils accumulated. The Burgess Shale is now recognized as part of a sedimentary sequence of silts and muds (Fig. 1) deposited in relatively deep water immediately adjacent to an enormous reef-like structure that was originally composed of limestone (calcium carbonate), perhaps secreted by marine algae. The limestone has been altered chemically since deposition to the rock known as dolomite (or dolostone). The edge of this reef originally formed a vertical submarine escarpment many kilometres in length, its upper surface and rim lying under shallow, sunlit waters and the face of its cliff-like edge plunging into the gloomy depths hundreds of metres below (Fig. 2). Careful mapping and reconstruction of this reef, now dissected by erosion and faulting, led to the discovery that in some way the reef escarpment controlled the distribution of the faunas that lived on and in the muds of the adjacent deep water. As well as the Burgess Shale fauna, other prolific faunas, especially rich in trilobites, were known to exist just beside the reef. The most famous of these additional faunas are preserved in the great fossil beds (*Ogygopsis* Shale) exposed on the northwest shoulder of Mt. Stephen. However, no equivalents of the Burgess Shale with its plenitude of soft-bodied fossils had been recognized elsewhere along the reef escarpment until, with the active co-operation of the Park authorities, D.H. Collins and his colleagues from the Royal Ontario Museum (Toronto) mounted a systematic search for new soft-bodied fossil localities. To date, more than a dozen such localities have been found along a 20 km stretch of the reef escarpment. However, important as these new localities are, none rivals the Burgess Shale in the diversity of its forms and the exquisite preservation of the fossils. The Burgess Shale fauna is still the ultimate source for the greatest insights into the vanished Cambrian world.

Although we cannot explain fully why the preservation of the fossils is so exceptional, there were clearly a number of important factors. The animals were living on and in the muds at the foot of the submarine cliff (Fig. 32). Periodically, patches of the wet mud slumped downslope, forming a dense submarine cloud of mud containing the live animals that were on and in it, as well as carcasses and broken pieces of algae. This cloud travelled probably only a relatively short distance, before the fine grained mud settled and rapidly buried the animals and plants. Thus, whole animals and bits of algae were buried, and levels of oxygen at the burial site were probably very low so that rates of organic decay were correspondingly reduced. Other poorly understood physical and chemical factors also must have intervened to explain the preservation of soft parts as thin films of mineral matter. Parts of these films reflect light, as the photographs in figures 6, 16, 18, and 23 show.

THE FAUNA AND FLORA

The Burgess Shale fauna consists of over 120 species, representing various arthropods, molluscs, brachiopods, cnidarians, sponges, polychaete worms, priapulid worms, echinoderms, chordates, and a number of miscellaneous forms that are not readily accommodated in any of the major groups (phyla) of animals (Fig. 3). A considerable number of algae also occur. The species are not equally abundant; some are known from thousands of individuals, whereas others are known only from a single specimen.

THE FLORA

The flora of the Shale consists of delicate, branching remains of seaweeds or algae that are preserved abundantly in specific thin layers in the quarry that Walcott excavated. In one layer, *Marpolia* (Fig. 4) occurs as masses of broken fragments, with few other fossils and no other alga in the same layer. Other thin layers have yielded abundant broken parts of an alga in the form of a perforated sheet. Walcott described many other algal species, but all are rare; no detailed study of these fossils has been published since his work. The way the fossil algae occur, separate from one another and only rarely associated with animal fossils, suggests that they may have lived in a different environment from the animals, possibly attached to the submarine cliff, and were periodically broken off and swept down to be buried in a slumped layer.

THE FAUNA

Arthropods

Arthropods are the most abundant (in terms of specimens collected) and varied (in numbers of genera and species) of the animal fossils in the Burgess Shale (Fig. 3). Their familiar living relatives are the insects and spiders of the continents and, in the sea, crabs, shrimps and lobster. The arthropod's segmented body has a pair of jointed legs on

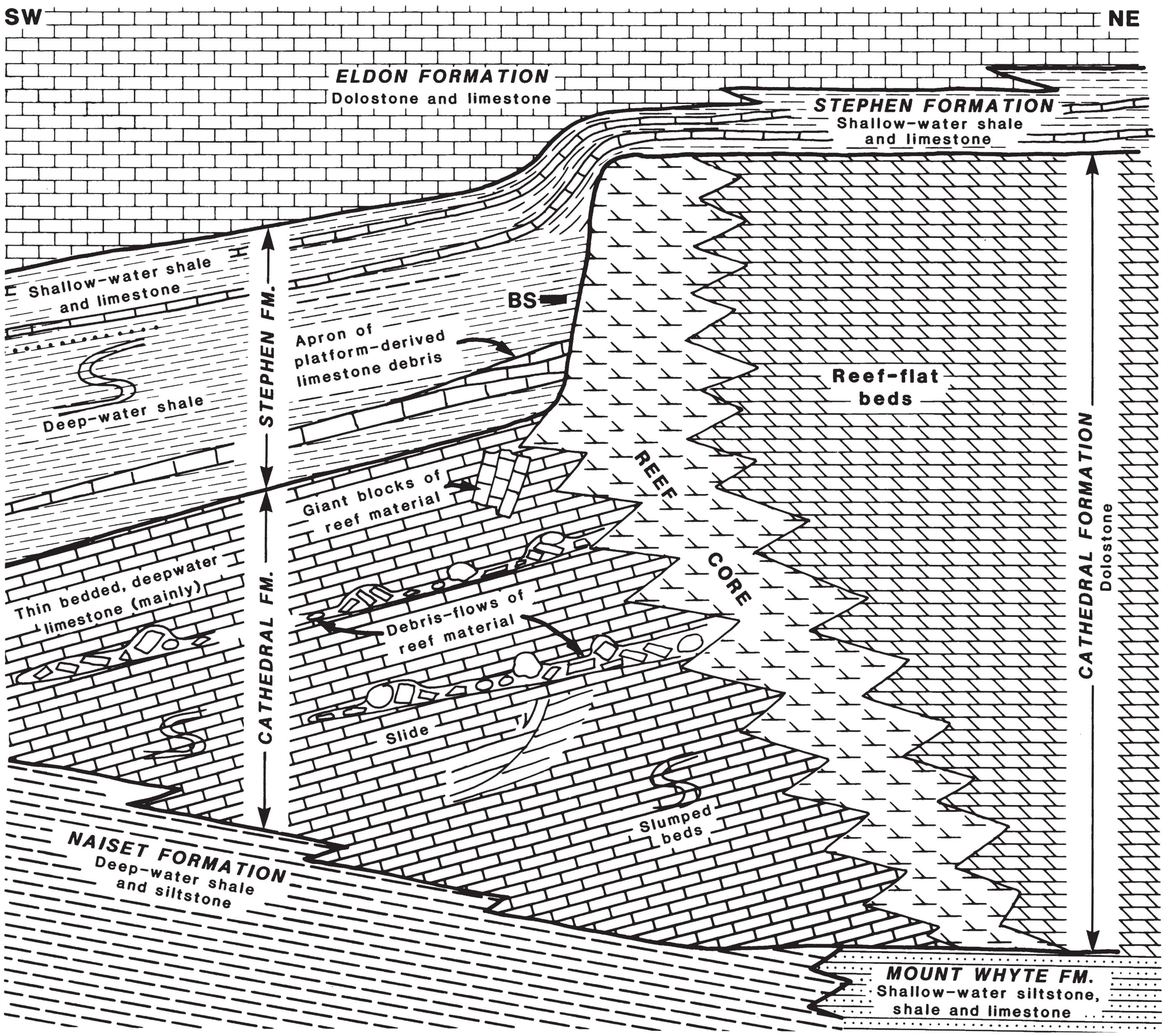

Figure 1. *A schematic cross-section of the stratigraphic sequence of sedimentary rocks deposited in the vicinity of Field, Yoho National Park.*

The approximate position of the Burgess Shale within this column is marked by a rectangle labelled BS. All formations shown are of Middle Cambrian age. (After Aitken and McIlreath, 1984, ***Geos****, vol. 13, no. 1, p. 19).*

each segment, and these legs, as well as the body, have stiffened outside coverings. This exoskeleton may be of tough, tanned, organic material, or may be reinforced with a layer of calcium carbonate, as in the claws, limbs and body covering of crabs and lobsters. A group of segments at the front of the body form a head, which may bear eyes and have specialized limbs for catching, cutting, and grinding food. The main body or trunk, behind the head, consists of a series of similar segments with paired limbs. Finally, there is a tail region which may be: a plate, formed by fused segments; or fan-like; or a spine. Trilobites [literally three lobes – hence tri-lob(e)-ite] are an extinct group of arthropods that show this tripartate division of the body .

At most places in the world where fossils can be collected from Cambrian rocks, the commonest fossils are parts of the exoskeletons of trilobites that were reinforced with calcium carbonate and were, therefore, more likely to be preserved. In the Burgess Shale, parts of trilobite exoskeletons are common; and splendid, complete exoskeletons, with the head, trunk and tail linked together, also occur (Fig. 5). Most unusual, however, is the occurrence of complete exoskeletons of *Olenoides* (Fig. 6) with the antennae and limbs in place beneath them. Because of the compaction of the body after burial, each limb is reduced to a thin, flattened sheet, and the series of limbs overlap each other like tiles on a roof.

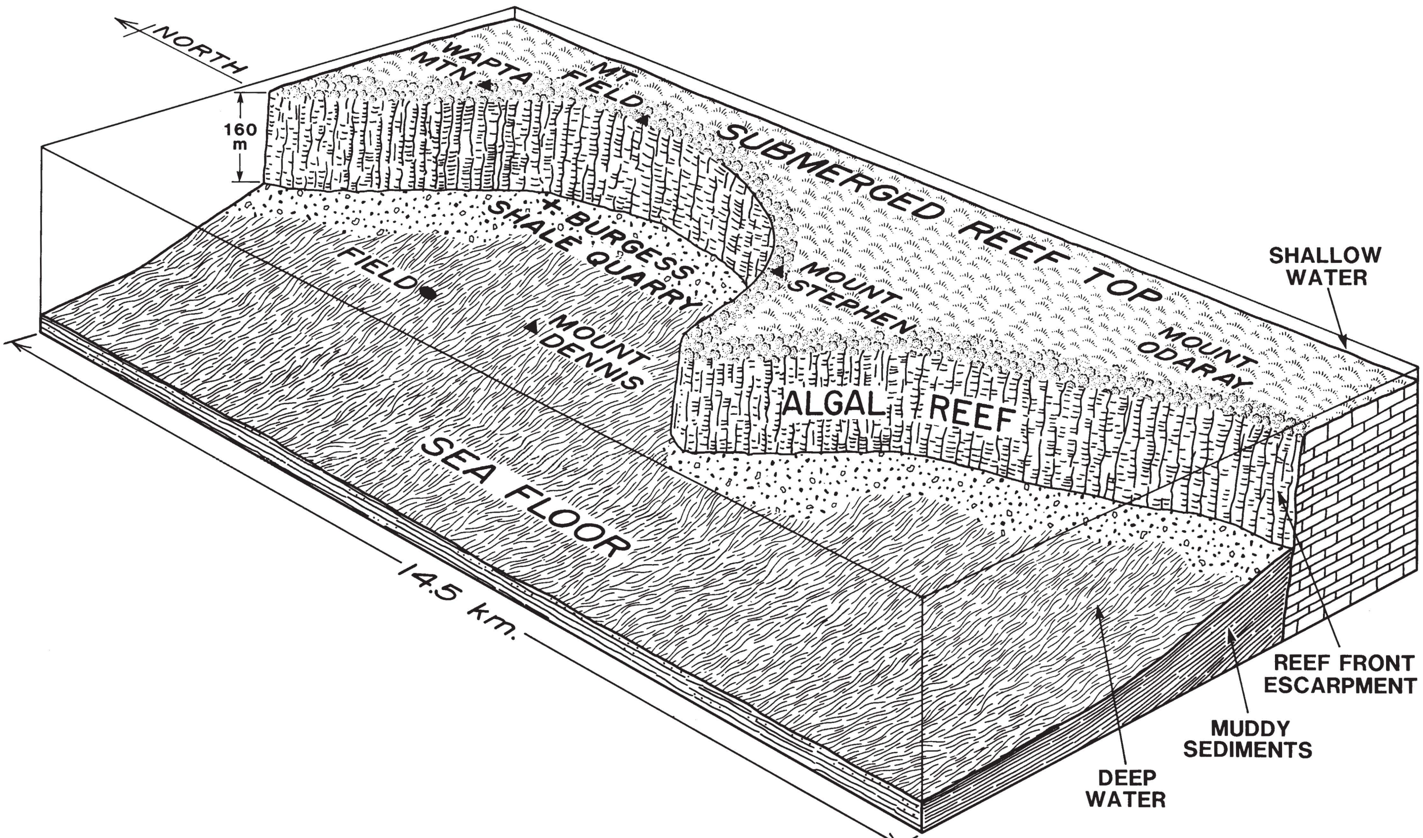

Figure 2. *A paleoreconstruction of the deeply embayed, Middle Cambrian reef escarpment that separated the shallow-water, reef areas of limestone deposition from the deep-water basin in which silts and muds (including the Burgess Shale) accumulated. The present relative locations of the Burgess Shale quarry, the town of Field, and various mountains are indicated.*

During the process of burial, mud seeped between the appendages and exoskeleton of *Olenoides*. This sediment subsequently was compressed to a thin layer of rock matrix separating the individual limbs one from another, and all the limbs from the exoskeleton. By using a tiny cutting tool, individual limbs can be exposed under the microscope. Thus, the joints in a walking leg, and the spines on the inner side and on the basal segment, have been revealed. By means of a reconstruction of the animal, it can be suggested how it walked and swam (feebly), and how food was caught by the spiny legs, torn and shredded, and passed forward to the mouth, located beneath the head.

Specimens of three other, very different, species of trilobites in the Shale have limbs preserved, but in the majority of species limbs and other soft parts are unknown.

The most common fossil in the Burgess Shale is *Marrella* (Fig. 7). Only 1 to 2 cm in length, this fossil has a conspicuous, dark, oily-looking stain, generally situated at the posterior end. Two pairs of long spines curve back over its body from the wedge-shaped head. It sensed the environment with a pair of long antennae, and the adjacent pair of feathery appendages swept food particles toward the mouth at the back of the head. Along its slim body *Marrella* had jointed walking legs, with a filamentous gill branch at the base of each leg. The dark stain was probably made by contents of the body that seeped out into the surrounding muddy matrix after burial. *Marrella* is an arthropod, but was not a trilobite, and did not have an exoskeleton stiffened with mineral matter. It is one of the 30 or more kinds of essentially soft-bodied arthropods in the Shale, none of them trilobites, that constitute an amazing and varied component of the fauna. In general, these "non-trilobites" cannot be matched with any other early Paleozoic marine animals known anywhere else in the world.

The second most common "non-trilobite" is *Canadaspis* (Fig. 8), which has a shell consisting of left and right mirror-image valves covering the head and part of the trunk, the rest of the trunk and tail projecting at the back. Careful removal of one valve has exposed limbs that are remarkably like those of some living crustaceans. Crustacea include the crabs, shrimps and lobsters of today's seas, and *Canadaspis* is their oldest known ancestor. *Waptia* also had a bivalved shell, but quite different limbs, long antennae, and conspicuous eyes (see Figure 32). The cylindrical back part of its trunk may have been muscular, permitting the bilobed tail to be flicked down, causing the animal to dart backward. A similar type of quick movement is used by living crustaceans to escape predators. *Yohoia* (Fig. 9) is much smaller, and is distinguished by a pair of limbs projecting in front of its head. Each of these limbs had an "elbow" joint and four "fingers" at the tip, and they were probably used to pick up food particles and bring them to the mouth at the front of the head. The larger and more distinctive *Leanchoilia* (Fig. 10) has a most extraordinary pair of limbs at the front; each limb is curved, and jointed at the base. Three joints carry shafts, each having a long, annulated extension that was presumably sensory. The third shaft has claws at the base of the extension. *Leanchoilia* did not have walking legs, but presumably could swim by flapping the lobes along the sides of the body. How it used the great front limbs is uncertain, but it may have rested on them when feeding on the sea bottom.

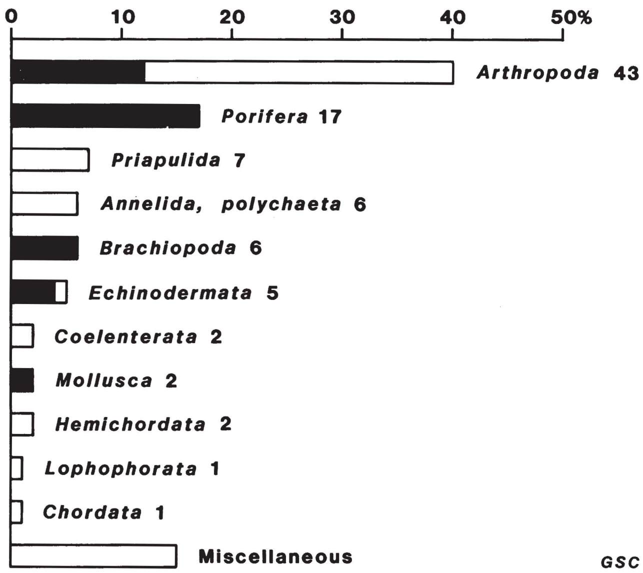

Figure 3. *The relative abundance of the major groups of animals in the Burgess Shale.*

The number of genera in each group is given, and the length of a bar shows the percentages of the total (of 107 genera) that belong in each group. The solid black portion of a bar shows the proportion of the genera in that group that had mineralized hard parts.

Sidneyia (Fig. 11) was the first of the "non-trilobites" to be described by Walcott, and was named after his son who found it. The walking legs on the trunk are remarkably like those of the living horseshoe crab, *Limulus*. The gut is preserved, and in it are broken shells of brachiopods, *Hyolithes* and trilobites, evidence that this animal could catch and crush hard-bodied prey. Two other quite different "non-trilobite" forms are *Molaria* (Fig. 12) and *Burgessia* (Fig. 13), both of which walked on the seafloor, and either fed on other tiny animals or scavenged. Each had a long tail spine, which probably served, in part, as a defensive weapon.

This brief account of some of the "non-trilobites" shows how different they were one from another in size, form and kinds of limbs. Some arthropods, like *Olenoides* and *Sidneyia*, were carnivores, actively searching for prey on and in the seafloor. Others, like *Canadaspis* and *Leanchoilia*, probably stirred up the mud and fed on scraps of organic matter on the seafloor, while smaller particles, and perhaps minute animals, served as food for *Marrella* and *Burgessia*. *Yohoia* possessed a special pair of limbs for picking up food particles and carrying them directly to its mouth. None seems to have been a strong swimmer, but some may have been able to dart away from an enemy. Thus it is clear that adaptations and modes of life were as different for individual species of these ancient animals as they are for the creatures in today's seas.

Rare but most interesting is *Aysheaia* (Fig. 14), with its thick body and short legs ending in tiny claws. Fossils of this animal show that it did not have a stiff exoskeleton, and that both body and legs were flexible. When Walcott published the first pictures of this fossil, calling it a worm, zoologists

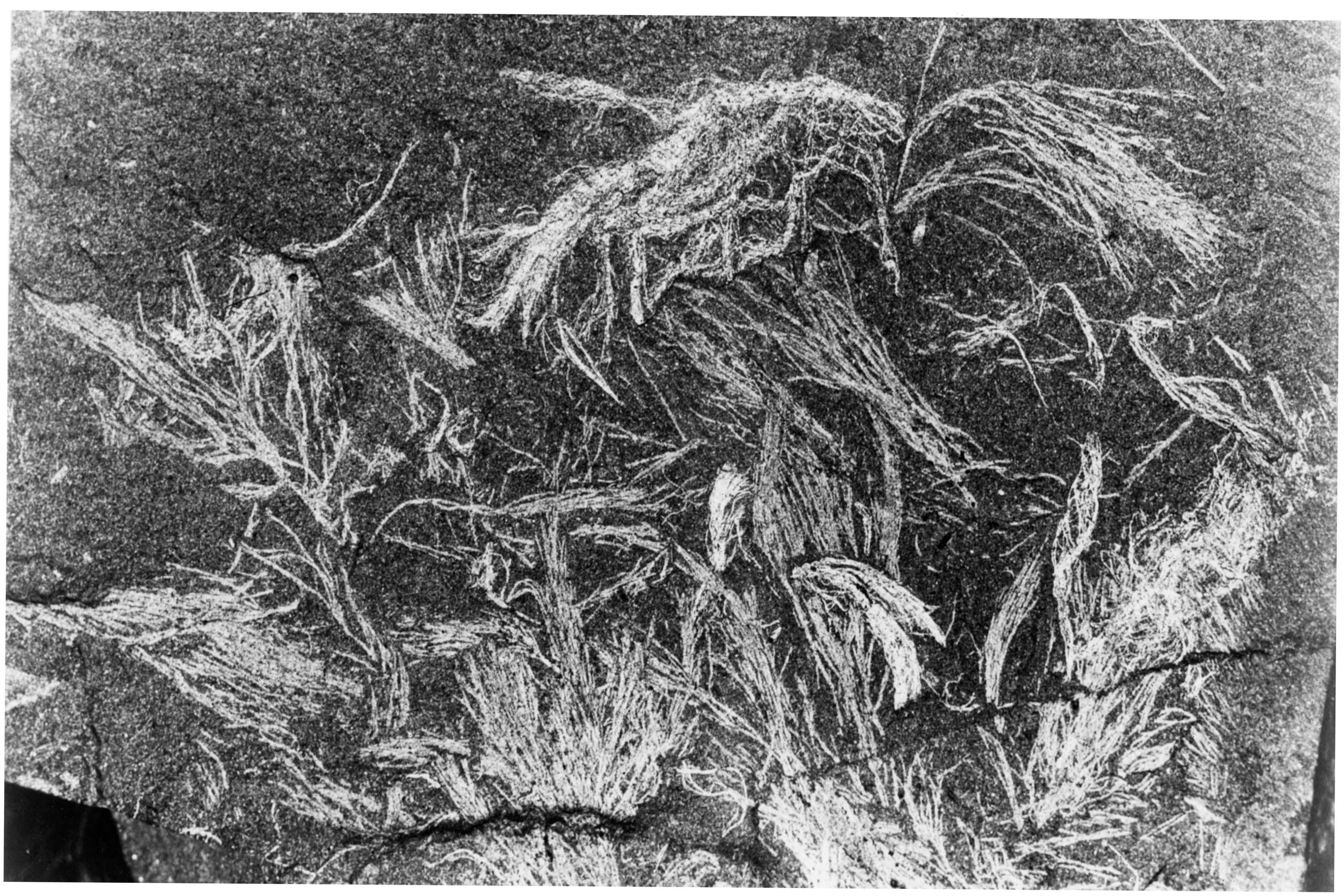

Figure 4. Marpolia *(x2.8), showing the broken fragments of this delicate, branching seaweed.*

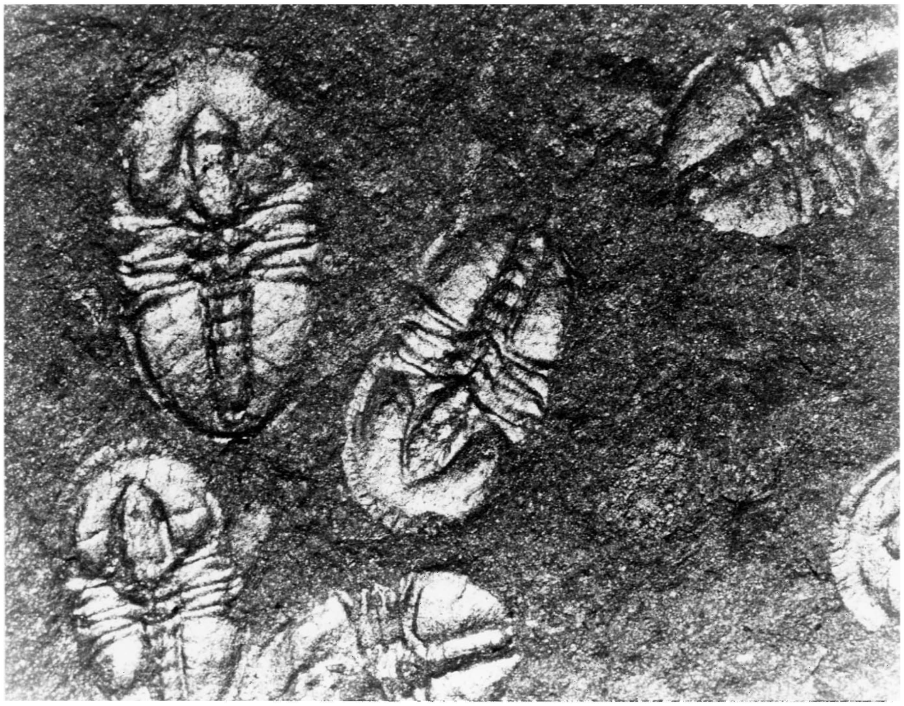

Figure 5. ***Pagetia*** *(x9.2). A group of specimens.*

Curiously, no soft parts have been identified in either this trilobite or a number of other species. ***Pagetia*** *may have been a floater or swimmer, normally living high above the seabed.*

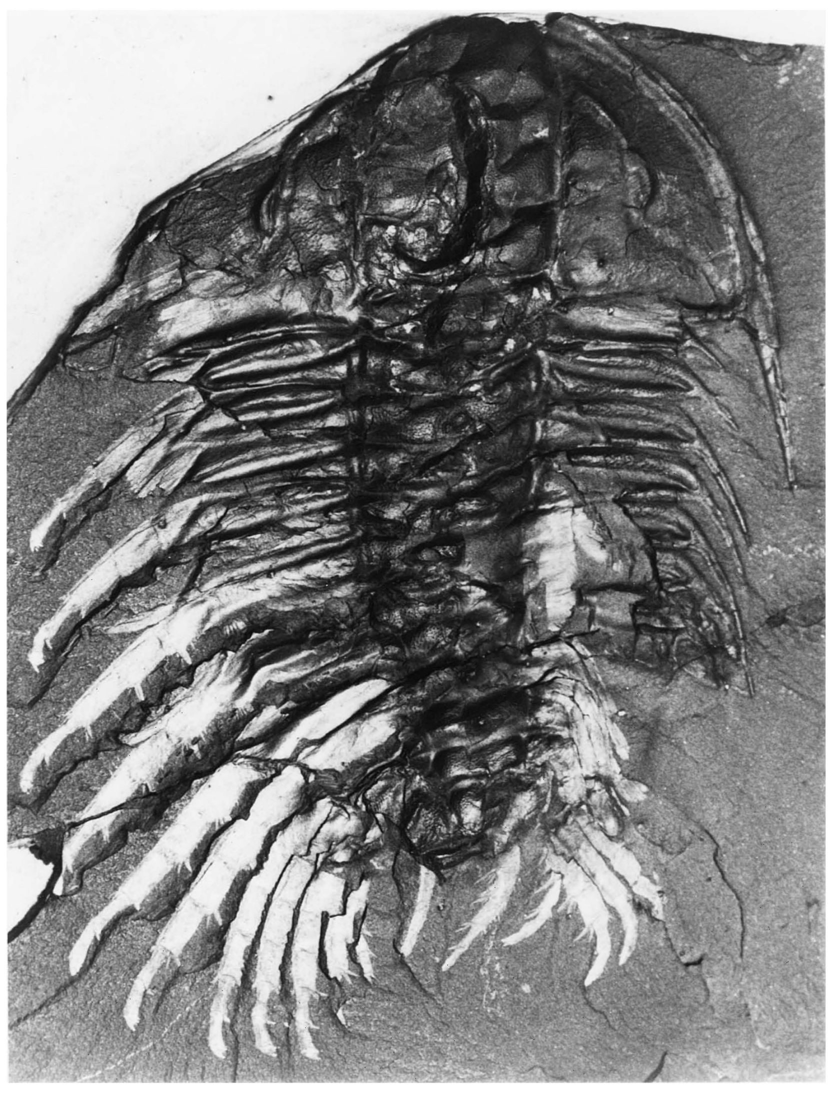

Figure 6. Olenoides *(x1.7). A complete specimen of the trilobite, showing the jointed, spiny walking legs beneath the exoskeleton.*

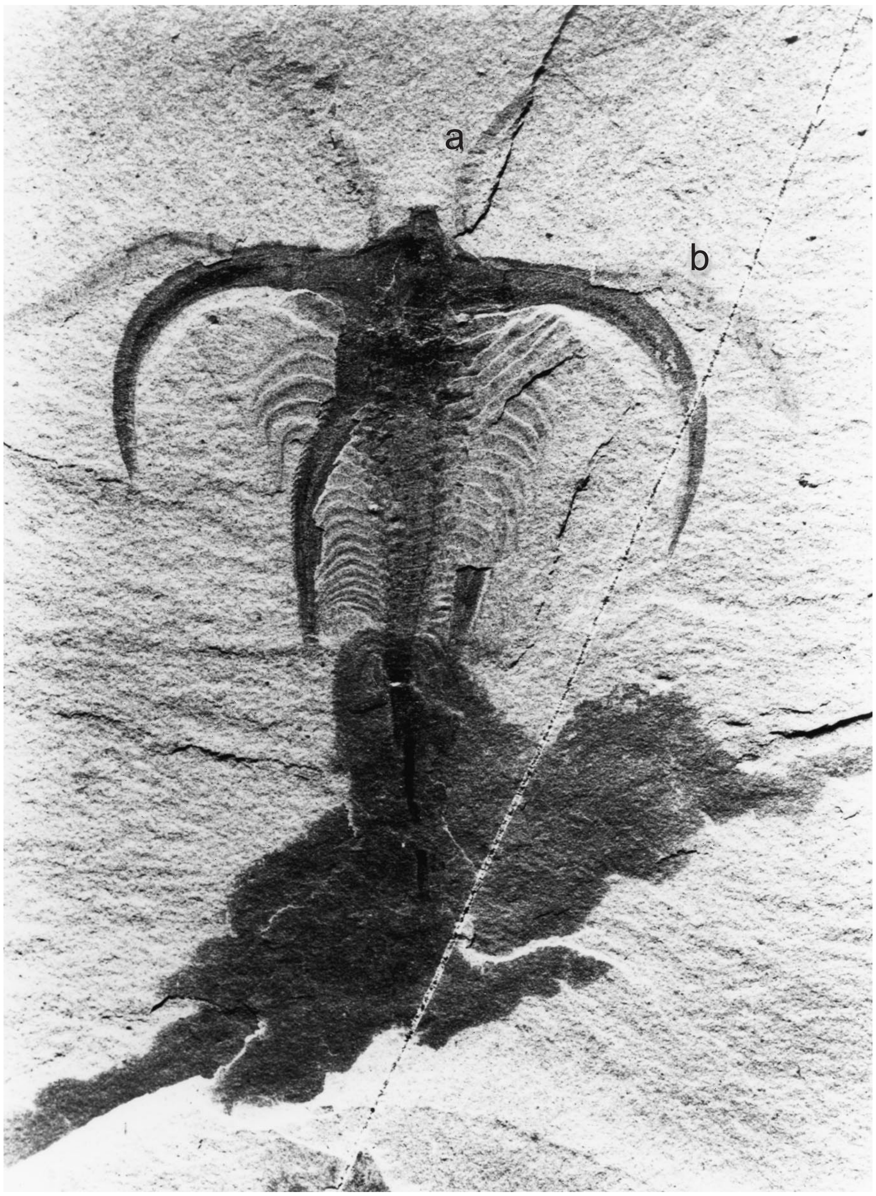

Figure 7. ***Marrella*** *(x5), exposed from the underside, showing the spines curving back from the head, the antennae (a), a second long appendage (b), and the many pairs of limbs on the trunk. At the back, a dark patch is visible on the rock; a stain caused by decay products leaking out of the body into the surrounding sediment.*

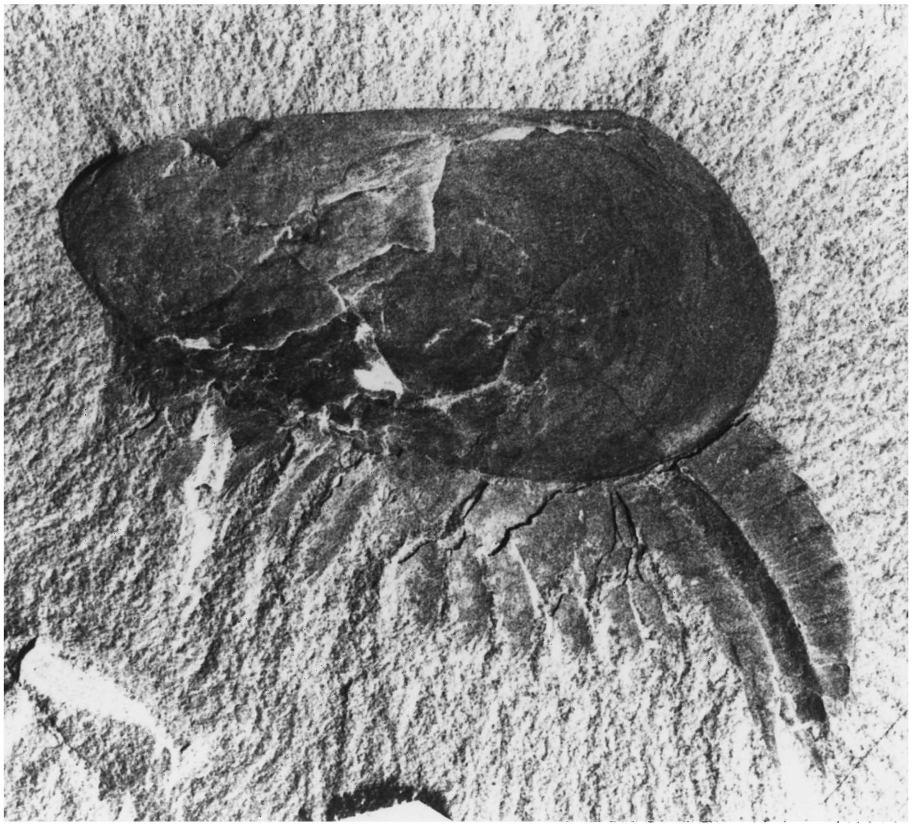

Figure 8. ***Canadaspis*** *(x2.9). The trunk and tail project from between the two valves of the shell, and parts of the limbs project below the shell. The narrow, raised strip along the trunk is the detritus-filled gut.*

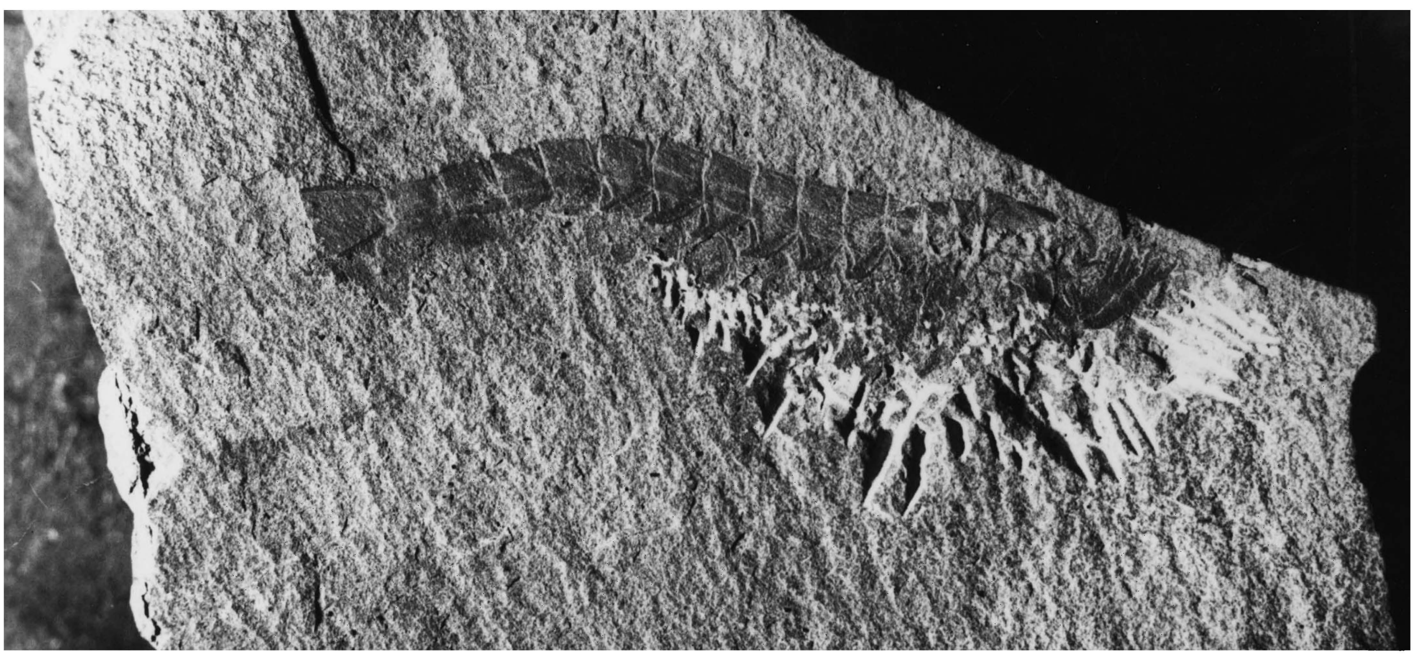

Figure 9. ***Yohoia*** *(x5.7). At the front (right side) are the bent 'arms', with four 'fingers' at the tip, used to pick up food particles. The oval tail portion is broken.*

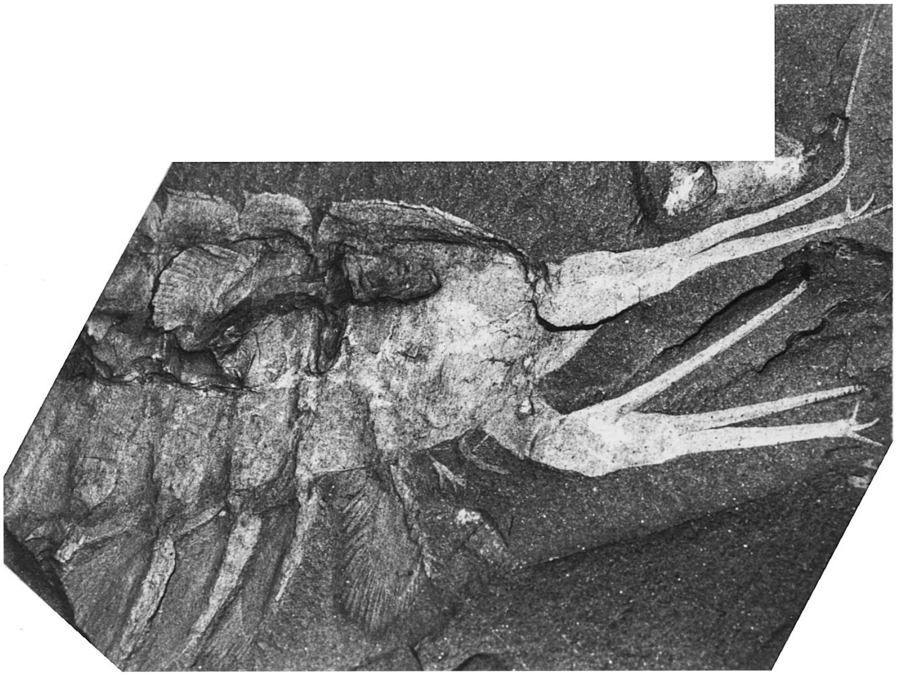

***Figure 10.* **Leanchoilia** *(x1.6). The head and a few trunk segments, showing the pair of large, branched limbs on the head. The branches had a long, annulated extension like the one at the top right. At the bottom left are the flaps with filaments, used by the animal when swimming.*

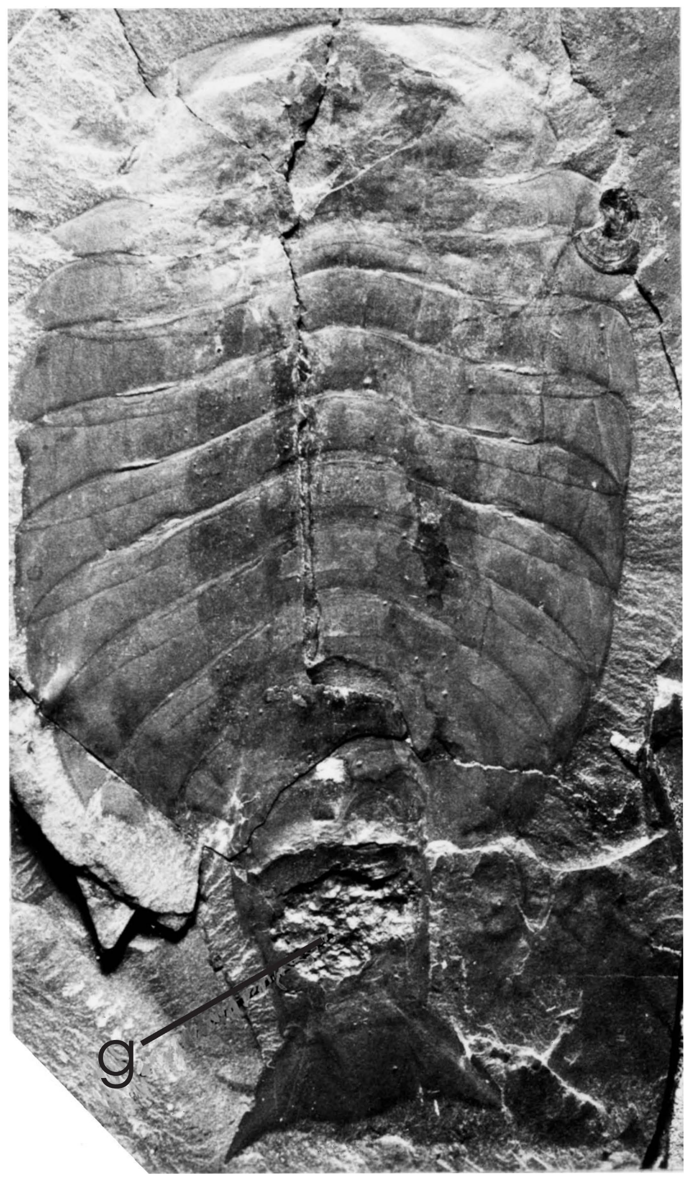

***Figure 11.* **Sidneyia** *(x1.5), showing the entire body. A patch (g) at the back has broken away to reveal fragments in the gut. Recognizable pieces of trilobites and hyolithids have been seen inside other specimens, showing that* **Sidneyia** *preyed on these and other animals with hard shells.*

Figure 12. **Molaria** *(x6.0). The entire animal is visible, with its long tail spine, and some of the limbs projecting in front of and on the left of the head.*

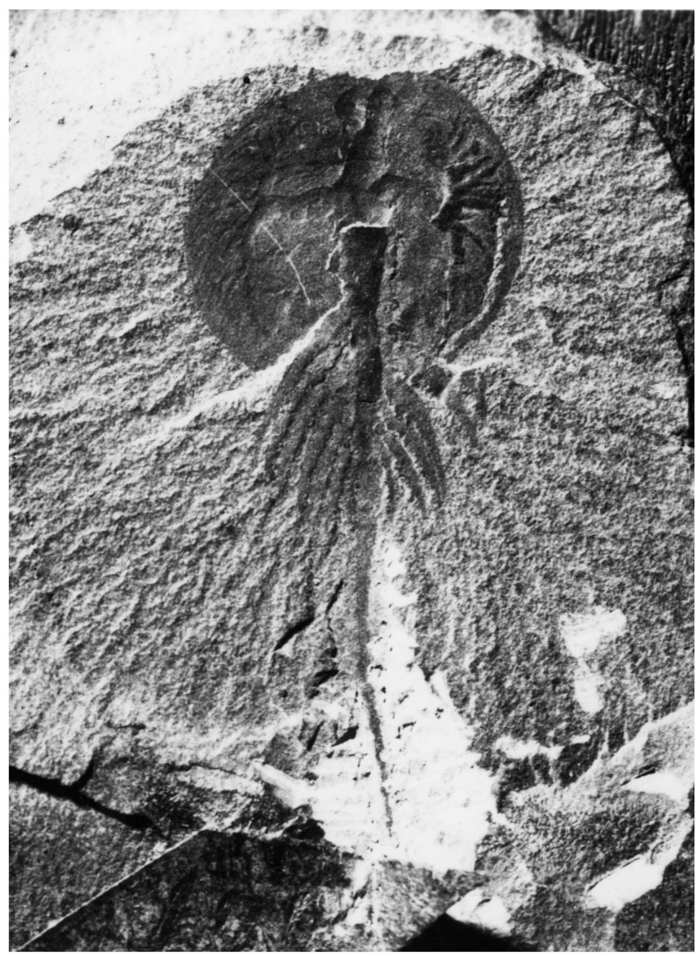

Figure 13. **Burgessia** *(x4.4), showing the circular carapace, some of the walking limbs behind it, and the long posterior spine.*

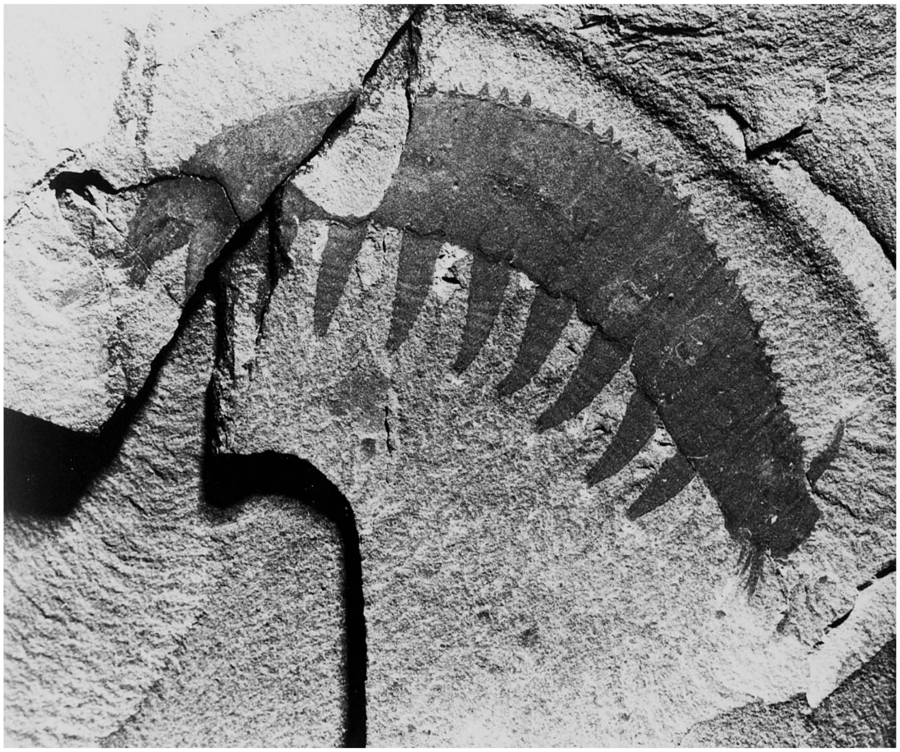

***Figure 14.* *Aysheaia* (x3.0), showing the thick body and the legs, both of which are annulated; claws are present at the tips of the legs.**

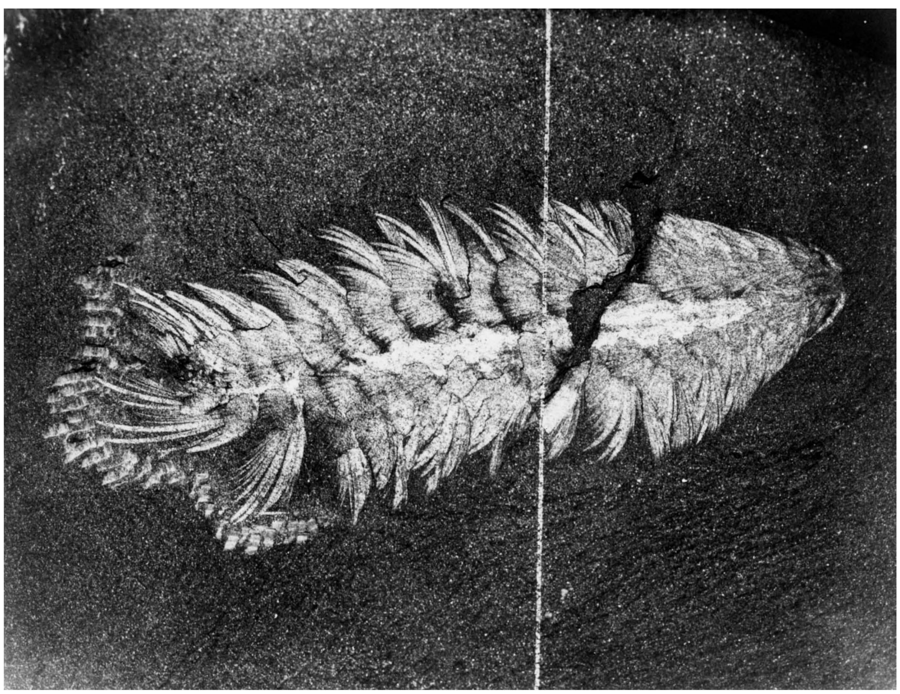

***Figure 15.* *Canadia* (x3.2). A polychaete worm, showing its prominent bundles of chaetae, and an anterior pair of small tentacles.**

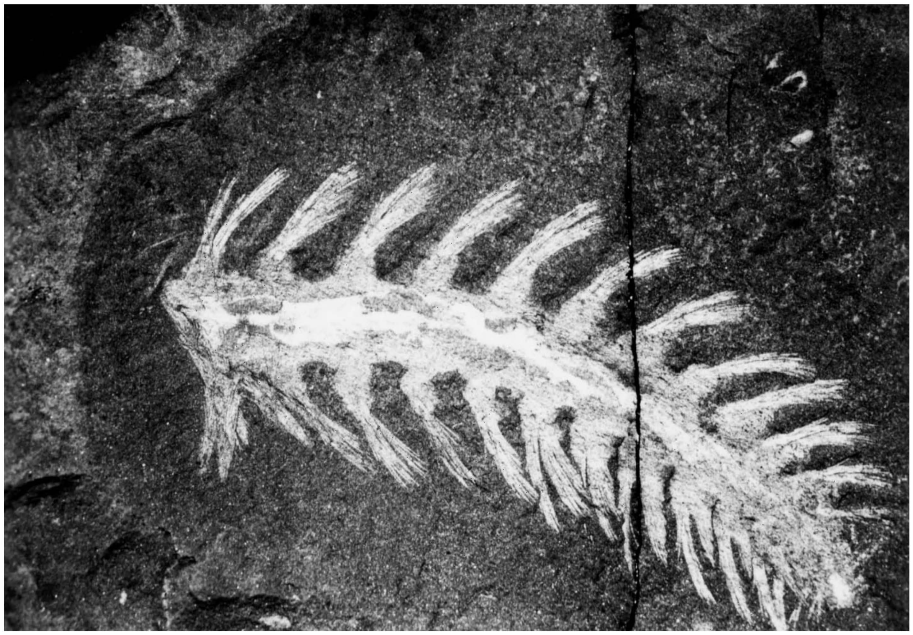

Figure 16. ***Burgessochaeta*** *(x3.7), a polychaete worm with bundles of identical chaetae on either side of each segment.*

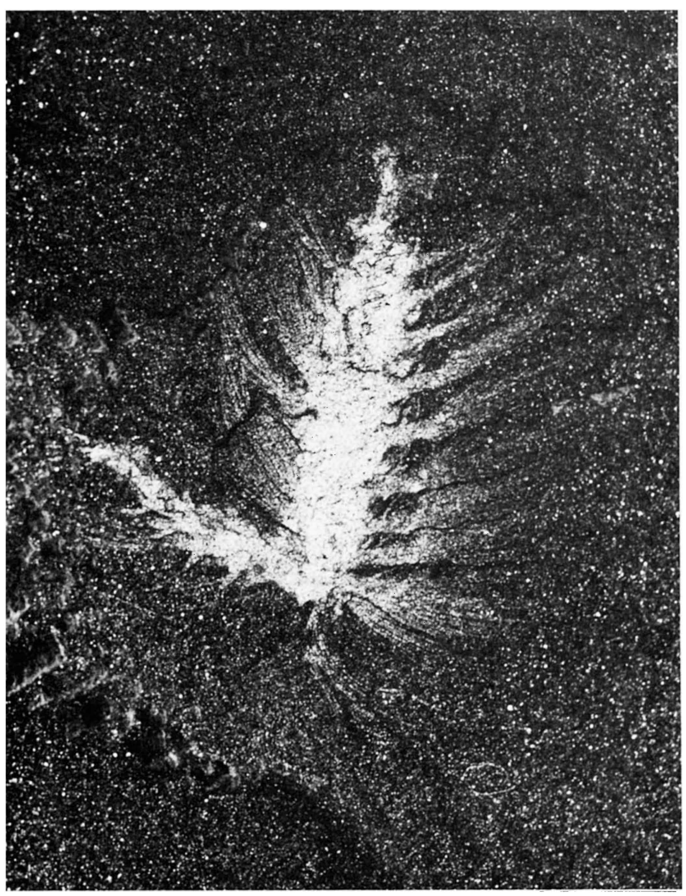

Figure 17. ***Insolicorypha*** *(x12), a polychaete worm with enormous bundles of chaetae that were evidently used in swimming.*

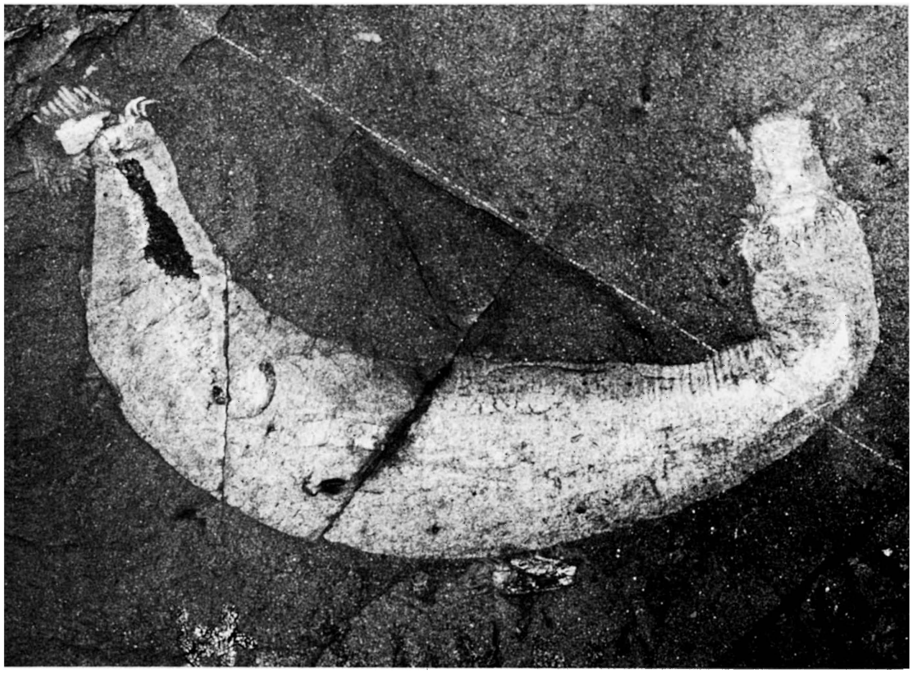

Figure 18. ***Ottoia*** *(x1.5), a priapulid worm with a spinose anterior as well as a set of hooks at the posterior end of the trunk.*

wrote at once to him pointing out how much *Aysheaia* resembled the living *Peripatus*. The latter is one of a small group of southern hemisphere land animals known as onychophores, which live amid rotting vegetation and prey on insects of various kinds. *Aysheaia* was a marine animal, and in detail shows various differences from onychophores, but it is the kind of ancestor that could have given rise to myriapods and insects. In the reconstruction of the original fauna illustrated in Figure 32, *Aysheaia* is shown as crawling on a sponge, and possibly it fed on the soft parts of sponges. This suggestion is put forward because fossils of sponges are associated with *Aysheaia*.

Polychaete worms

Soft-bodied worms account for about 12 per cent of the genera in the fauna, and one important group comprises the polychaete worms. The polychaetes have living relatives such as the rag-worm, which is common on many shorelines. These worms have segmented bodies that bear stout bristles (or chaetae) composed of the resistant organic material chitin. These chaetae are especially prominent on the Burgess Shale polychaetes, and are most prominent on *Canadia* (Fig. 15). This worm had a head bearing two elongate tentacles. It also had a stout body, the dorsal surface of which was almost entirely obscured by broad, flattened chaetae that formed an imbricate array. Arising at regular intervals from a more ventral region of the body were broad bundles of chaetae that appear to have been well adapted for propelling the worm through the water. For this reason, *Canadia* is believed to have been a swimmer, cruising above the seabed. Another abundant polychaete is *Burgessochaeta* (Fig. 16), but this worm is believed to have had a mode of life very different to that of *Canadia*, because there is evidence the former lived in the sediment. Its elongate body bore a series of chaetae that together may have helped to move the animal up and down a burrow system, while elongate tentacles at the anterior moved over the sediment in search of food particles (see Figure 32). There are a number of other polychaetes in the Burgess Shale, but one deserves special mention. This is *Insolicorypha* (Fig. 17), which is chiefly remarkable for its large fans of chaetae that were probably used in swimming. It is only known from one specimen, and may have lived well above the seabed, normally clear of the mudflows that were carrying other Burgess Shale animals to their doom.

Priapulid worms

Another group of Burgess Shale worms, the priapulids, is far less well known today, although they are abundant locally in modern marine sediments. In the Shale fauna, however, and perhaps originally in many other Cambrian assemblages, priapulids were much more abundant than polychaete worms and show a wide range of forms. Their subsequent eclipse in marine communities may indeed have been because they were displaced ecologically by the polychaete worms. The most abundant of the Burgess Shale priapulids, *Ottoia* (Fig. 18), is especially interesting because of the wealth of information that has been gleaned about its anatomy from hundreds of specimens. Externally, the spinose anterior was armed with spines to grip the sediment in which the worm lived, and with teeth to grasp food. Internally, the alimentary canal is recognizable and, even more remarkable, the remains of food, including the conical shells of hyolithids and a few brachiopods. *Ottoia* may reasonably be interpreted as a predator, but evidence from one specimen indicates that on occasion this priapulid was cannibalistic, a habit that its modern descendants have not lost. Other identified features of its internal anatomy include the remains of muscle strands; including retractor muscles that were used to withdraw the anterior part of the body while burrowing through the soft sediment. Some features of internal anatomy are more obscure, but there is good evidence of a nerve chord.

***Figure 19. Selkirkia** (x5.3), a priapulid worm that inhabited a tube, from which only the spinose anterior projected clear.*

The second most abundant priapulid is *Selkirkia* (Fig. 19), which is distinguished by the fact that it inhabited an elongate tube with only the anterior part of the body projecting. The tube was evidently made of some fairly resistant material, because empty tubes are much more abundant than examples in which the soft parts are preserved. Presumably, in the former, the soft tissues rotted away shortly after the death of the worm and the empty tubes remained as debris on the seafloor. Sometimes, an empty tube was used for attachment by bottom-dwelling creatures such as brachiopods and sponges. Some specimens of the largest of the Burgess Shale priapulids, *Louisella* (Fig. 20), grew in excess of 20 cm in length. While both *Ottoia* and *Selkirkia* have sharp, cuticular hooks at the anterior, in *Louisella* the equivalent structures appear to have been made of lobes of softer tissue. The body was flattened in the dorso-ventral plane, and on what was probably the dorsal side, there were two long rows of feathery structures that probably acted as gills. Although no modern priapulid is like *Louisella*, comparisons with various other worms suggest that this priapulid may have lived in a horizontal burrow (see Figure 32). It is believed that undulations of the flattened body drew water along the burrow and over the worm, creating a flow that aerated the gills and removed waste products.

Brachiopods

The brachiopod fossils include representatives of the two major divisions, the inarticulates, which typically have a shell composed of calcium phosphate, and articulates with a calcareous shell. The genera present are typical of the Cambrian, but in some cases show exceptional preservation. For example, the delicate chitinous setae that project around the margins of the shell are preserved in a number of specimens (Fig. 21). Examples of one type of animal living attached to another (an epizoan relationship) are rather uncommon in the Cambrian, but this example from the Shale shows brachiopods attached to the spicules of the sponge *Pirania*. Presumably, in this relatively elevated location, a centimetre or so above the seafloor, the brachiopods were able to benefit from the feeding currents set up by the sponge and obtain food that would have been unobtainable had they been resting directly on the seafloor.

Echinoderms

Echinoderm fossils are locally abundant in some Cambrian rocks, and several varieties occur in the Shale, although none is particularly abundant. Forms that occur with some frequency in many other Cambrian rocks include eocrinoids and edrioasteroids. Typically, the former group of echinoderms have a more or less globular body with elongate feeding arms, the whole supported well above the seabed on an elongate stalk. Edrioasteroids, on the other hand, were bun-shaped echinoderms that rested on the seafloor. Another echinoderm, known as *Echmatocrinus* (see Figure 32), is unique to the Shale and immediately adjacent localities. This echinoderm is of special importance as it appears to represent the earliest known of the crinoids (sea lilies), a group that subsequently came to dominate many Paleozoic and Mesozoic seabeds. In most fossil crinoids, the vital organs of the body, such as the gut and reproductive organs, were supported on an elongate stem that anchored the animal

Figure 20. ***Louisella*** *(x1.1), a priapulid worm with two rows of feathery appendages on the trunk that probably functioned as respiratory gills.*

to the seabed. In *Echmatocrinus*, however, the distinction between stem and body is much more poorly demarcated. In most other crinoids the skeleton is made of large plates of calcium carbonate that combine to form a rigid skeleton. In the Burgess Shale crinoid, however, the plates appear to have been very thin and set in a rather flexible body. *Echmatocrinus* and its relatives may have been a common component of some Cambrian seabeds, but it was only under the exceptional conditions controlling Burgess Shale deposition that their fossilization was assured.

Molluscs

Fossil molluscs are common in many Cambrian rocks; particularly the conical shells of the primitive group known as the monoplacophorans. Although poorly known today, because they live mostly in deep water, monoplacophorans are of enormous evolutionary interest because they are believed to be directly or indirectly ancestral to most of the other mollusc groups, such as gastropods and bivalves. One monoplacophoran (*Scenella*) is very abundant in the Burgess Shale (see Figure 32), but, unfortunately, no associated soft parts have been recognized.

Hyolithids

Although some paleontologists regard the hyolithids as molluscs, most regard them as a separate phylum. As in many Cambrian assemblages, hyolithids are abundant in the Burgess Shale. Some specimens are preserved with the lid-like operculum and curved struts (helens) in place (Fig. 22). As the operculum and helens normally drifted away from the rest of the shell almost immediately after death, these articulated specimens must have been buried alive by the mudflows. As was noted above, hyolithids evidently provided part of the diet of some priapulid worms and arthropods.

Cnidarians or coelenterates

This phylum, which includes such groups as the sea anemones, scyphozoan jellyfish and corals, is apparently represented in the Shale by a large, anemone-like creature with a large, sac-like body, but without discernible tentacles. Curiously, no jellyfish have been recognized, although examples have been documented elsewhere in the Cambrian.

Chordates

The absence of fossil fish from the Burgess Shale is scarcely surprising, and it is only recently that what appear to be isolated fish scales have been found in Upper Cambrian rocks. However, it seems very likely that the ancestors of these fish might be found in the Middle Cambrian or even earlier. The discovery of the primitive chordate *Pikaia* (Fig. 23) in the Burgess Shale is thus of extraordinary interest, not only because it may tell us more about the

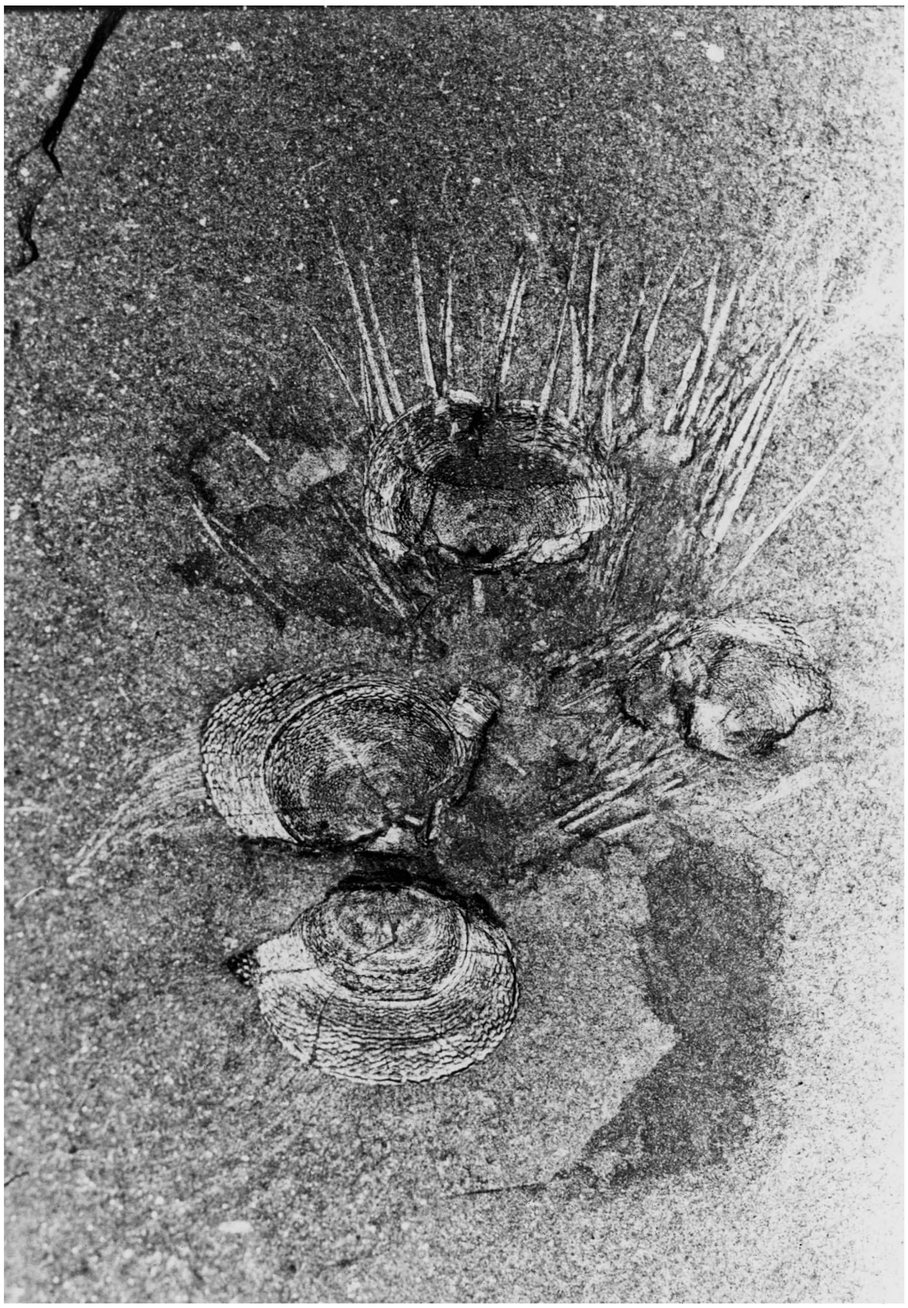

Figure 21. ***Micromitra*** *(x4.0), the subcircular shells of this brachiopod attached, as they were in life, to the sponge* ***Pirania.*** *Spicules of the sponge project from beneath the brachiopods, and the long, slim setae may be seen outside the margins of the brachiopod shells on the left and at the bottom of the picture.*

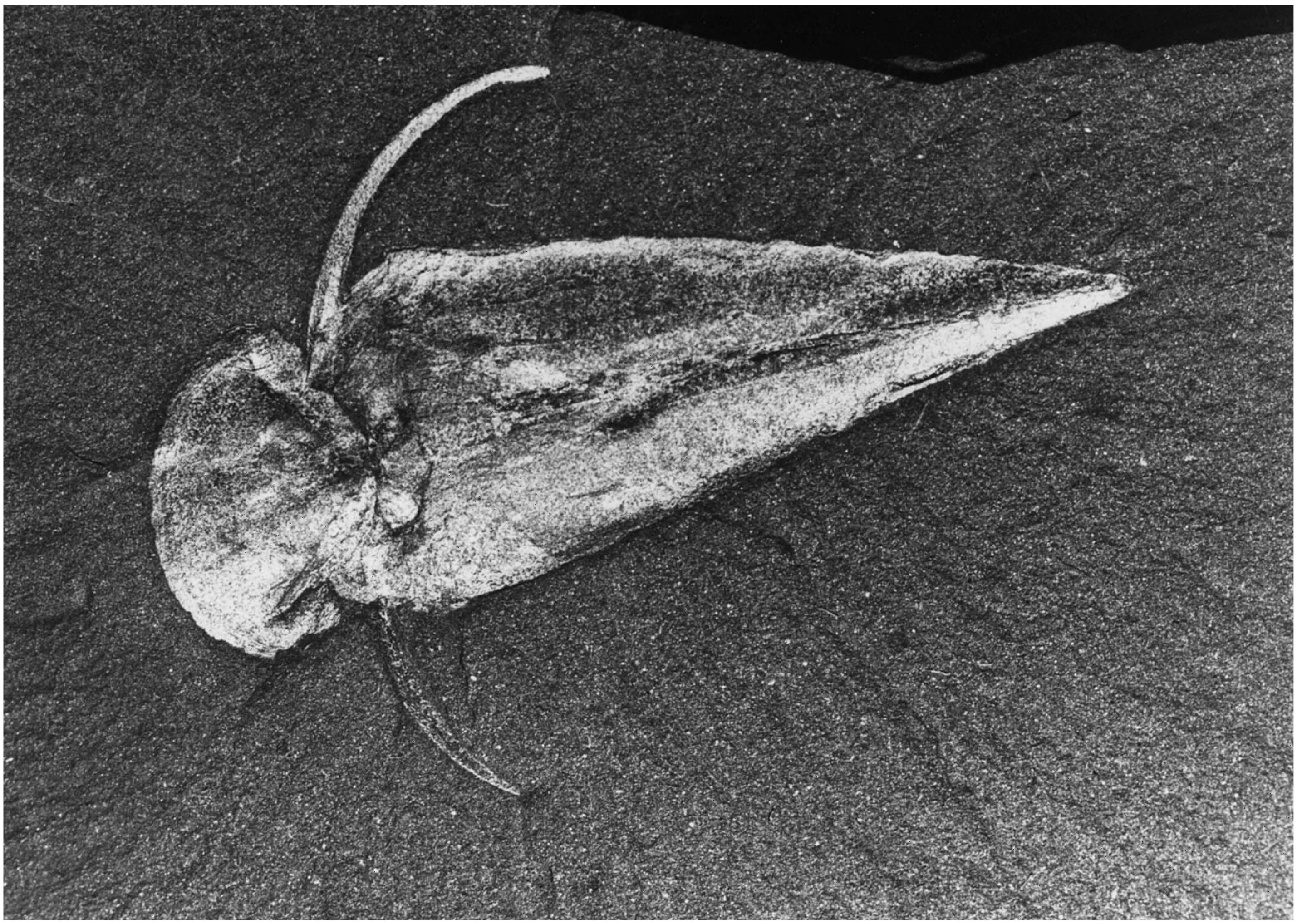

***Figure 22. Hyolithes** (x6.0). The shell is conical with a lid (at the top of the picture); between lid and shell the struts (helens), which propped it in place on the sea bottom, curve out and back.*

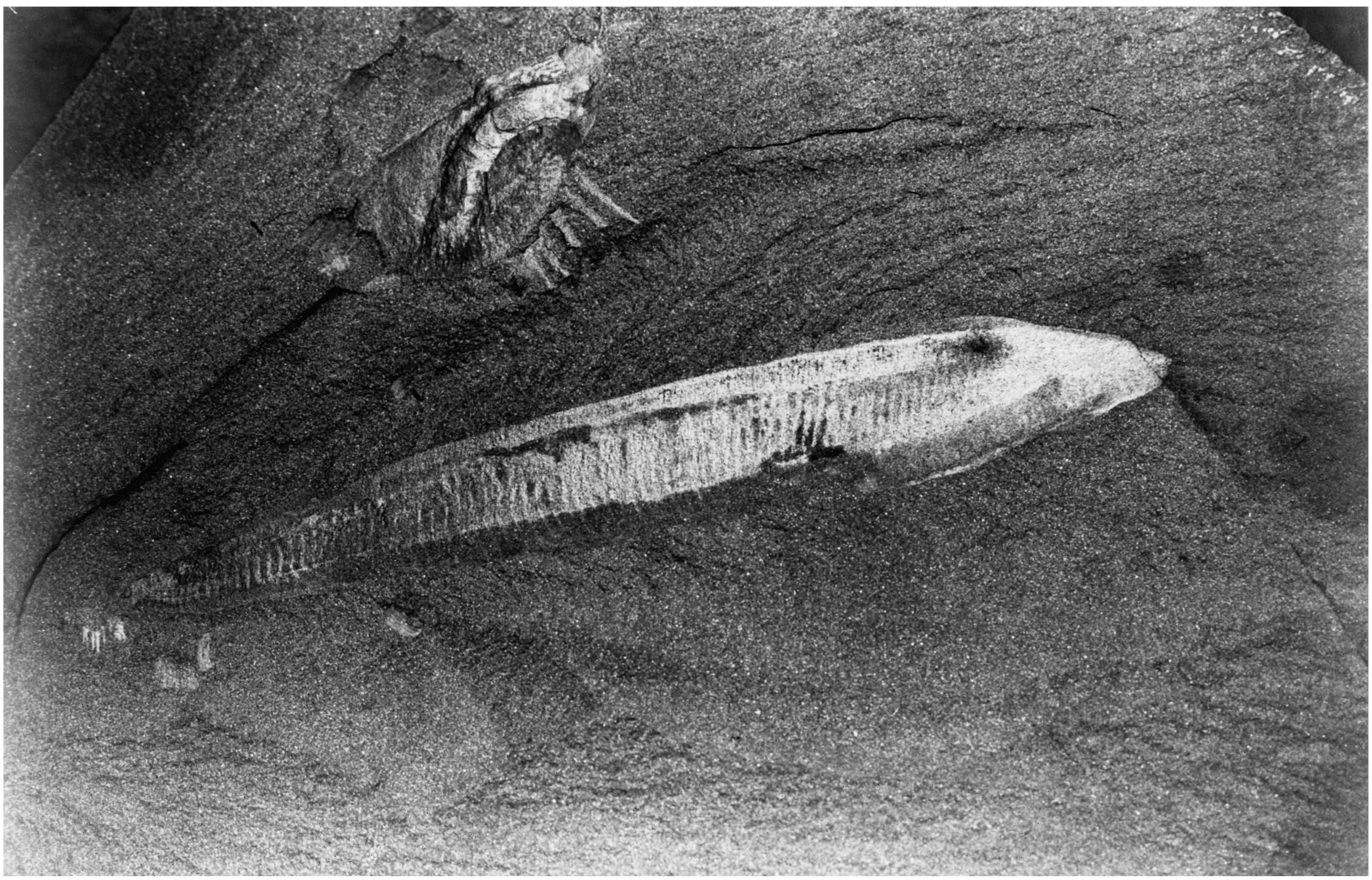

Figure 23. Pikaia** (x3.6), a primitive chordate. The prominent reflective bar on the upper side of the animal appears to represent the notochord, one of the key characteristics of this phylum. The specimen above the chordate is an example of the arthropod **Burgessia.

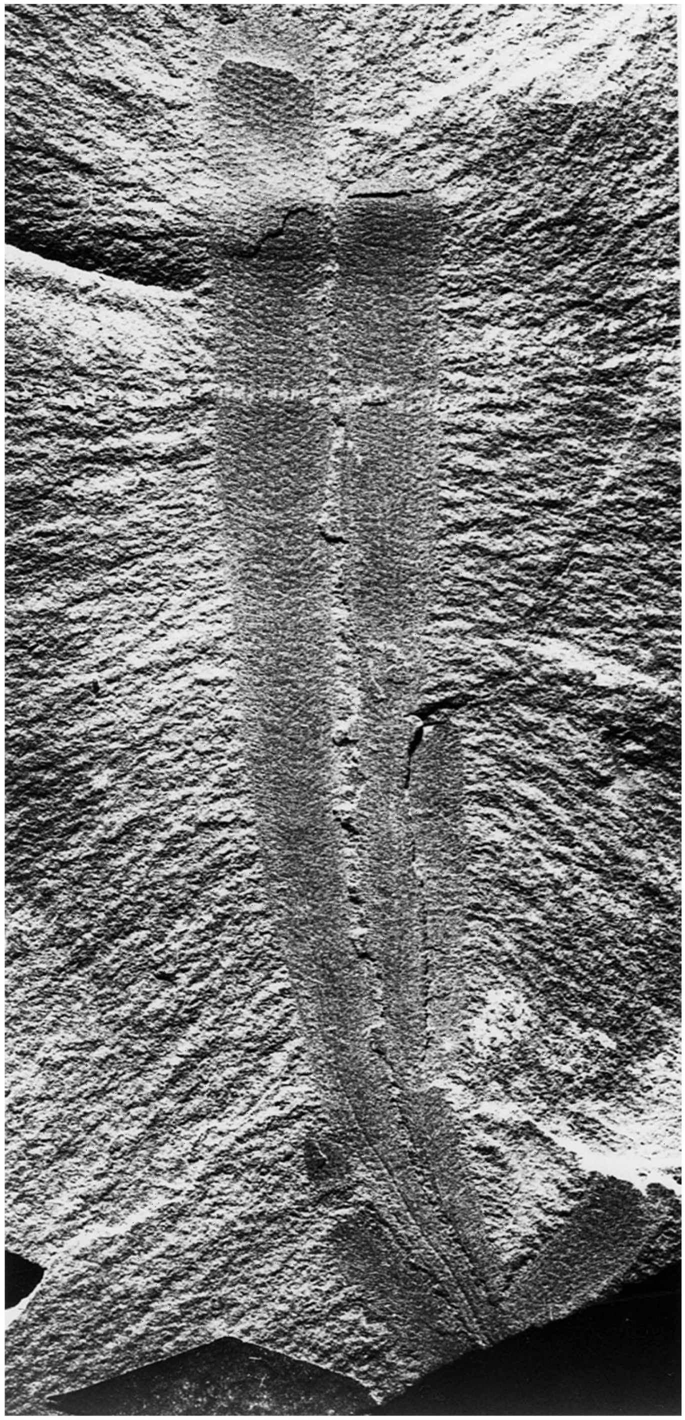

***Figure 24. Vauxia** (x2.5), a branching sponge, showing the complex network of the internal skeleton.*

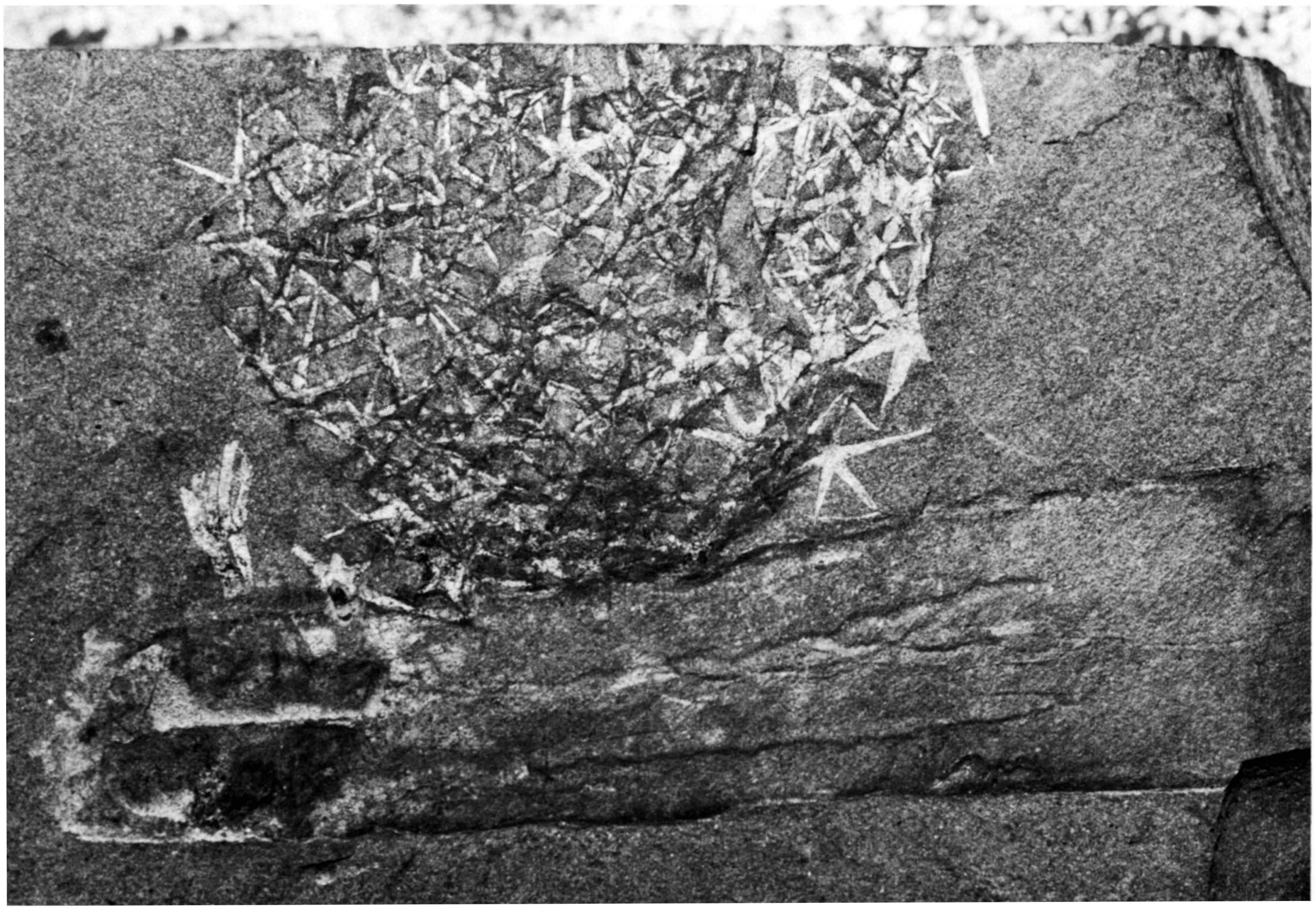

***Figure 25. Eiffelia** (x5.2), a globular sponge attached to an empty tube of the priapulid **Selkirkia** (Fig. 19), which presumably offered a convenient hard surface for anchorage.*

ancestry of fish, but because (by complex evolutionary routes) animals like *Pikaia* are thus ancestral to the amphibians, reptiles and mammals, including Man. *Pikaia* itself was a worm-like organism with a dorsal stiffening rod (the notochord, a precursor of the vertebral column) and segments arranged in a zig-zag pattern; both features also being characteristic of fish.

Sponges

Sponges are the second most varied group of fossils that occur in the Burgess Shale, and were the dominant animals attached to the seafloor. The most common of these is the branching form of *Vauxia* (Fig. 24), each branch showing a complicated network of strands. These strands appear to have been composed of spongin, the tough, flexible organic material that forms the skeleton of the present-day commercial sponge. Sponges of the past, like those living today, were conical, cylindrical, vasiform or globular in shape, and may, like *Vauxia*, have been branched. Passages through the walls were lined with cells that had minute, whip-like processes; the movement of these processes drew water through the walls and forced it out through a central cavity and opening. Minute food particles were captured from the water as it passed through the walls. The internal skeleton supported the walls, and may have been composed of spongin, or a framework of spicules made of calcium carbonate or opaline silica. Examples of sponges that had a skeleton of the latter type are *Pirania* (Fig. 21), *Eiffelia* (Fig. 25), and *Choia* (see Figure 32). Above its base *Pirania* had a central hollow stem, to which bunches of spicules were attached. *Eiffelia* had a globular shape and, like *Pirania*, sometimes attached itself to the tubes of *Selkirkia* (Fig. 19). *Choia* was also globular, but had long spicules projecting radially from it, which propped it in position on the seafloor.

***Figure 26. Opabinia** (x2.5). Long flaps hang down below the segmented body, and parts of the fins project upward at the back. On the top of the head region, three of the five eyes are visible, and the process, with its spines at the tip, curving up from the front of the head.*

Miscellaneous animals

All the animals described so far can be placed in known major groups or phyla, each according to its distinctive bodyplan. Although the various species in the Burgess Shale that can be placed in a particular phylum may be very different from their descendants alive today, there is usually no difficulty in recognizing the underlying bodyplan. There are, however, quite a large number of species with such a unique anatomy that it seems impossible to place them in any known phylum.

The unique animal *Opabinia* (Fig. 26) had a segmented body, each segment bearing a lateral flap, on the outside of which was a laminar gill. *Opabinia* could swim over the sea bottom using the flaps, and on its head it had a cluster of five compound eyes and a median, flexible process with grasping spines at the tip. Fins at the back stabilized and guided the animal as it cruised in search of food, seized it with the grasping spines, and brought it to the mouth located at the back of the head. It had no jaws or other mechanism for squeezing or grinding food, and may, therefore, have fed on small, soft-bodied animals or fragments of organic detritus.

One of the earliest descriptions of a soft-bodied animal from western Canada was made in 1892 (long before Walcott discovered the Burgess Shale), based on a spiny, jointed limb (Fig. 27). It had never been found attached to a body, and was thought to be either the trunk and tail of a *Canadaspis*-like animal, or one of a pair of limbs from the trunk segments of some otherwise unknown arthropod. On the basis of the limb, the animal was named *Anomalocaris*. It was a great surprise to find, when studying a single specimen obtained by the Geological Survey of Canada field party, a pair of the same limbs attached to the front of the animal (Fig. 28a, b). The head of the specimen is elongated, and has a pair of large, compound eyes. There are a series of flaps, graduated in size, overlapping along the sides of the body; undulations of these flaps enabled the animal to swim (see Figure 32, No. 24). On the underside of the head, at the front, a circle of toothed plates surround the mouth, a quite formidable jaw structure. An isolated specimen of this circlet of plates, stiffened but not mineralized, was found by Walcott, and has long been thought, because of its four-fold symmetry, to be the flattened impression of a jellyfish, but now it is known to be part of the animal *Anomalocaris*, the name originally given to the isolated limb. The diameter of the jaw plates, and length of the front pair of limbs, show that *Anomalocaris*

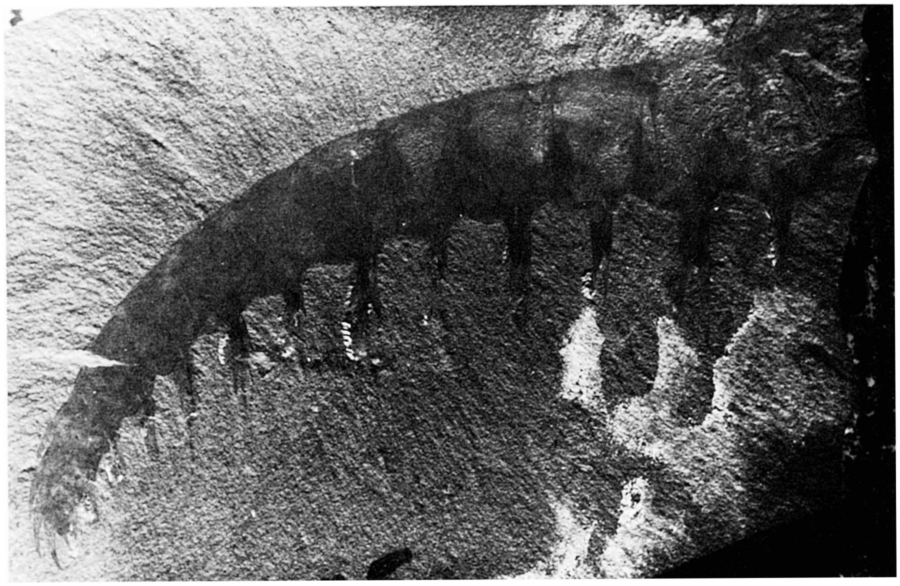

***Figure 27. Anomalocaris** (x1.1). An isolated, segmented limb, showing the spines on the inner side and at the tip.*

reached a length of at least half a metre, and thus was the largest known Cambrian animal. It must have been a predator, preying on other Burgess Shale animals, probably even on the trilobites with their mineralized exoskeletons.

The animal *Wiwaxia* (Fig. 29) is interesting because, although it cannot be placed in a known phylum, it does have certain similarities to the molluscs, which may mean that at some very remote stage they shared a common ancestor. *Wiwaxia* was very largely covered with scales, while on either side of the upper surface of the limbs an elongate row of spines arose. The arrangement of the spines strongly suggests that they were designed to deter attack and, indeed, in some cases a spine snapped off, suggesting it successfully thwarted unwelcome attention by a predator. An unusual feature of *Wiwaxia* is the way in which the size of the scales and spines matched the growth of the animal. For various reasons, it is clear that, once a scale (or spine) had been formed, it could not have increased in size as the animal continued to grow. In principle, *Wiwaxia* could have inserted new sets of scales between the older rows, so as to keep itself well encased in a protective layer, but what appears to have happened is that the scales were moulted at regular intervals and reformed at a larger size in order to match continuing growth. Moulting, that is the shedding of an external skeleton, is characteristic of groups such as arthropods. *Wiwaxia*, however, has no other similarities to the arthropods and so this method of size increase must have evolved independently. This animal probably moved across the seafloor on a muscular foot-like structure, scraping up organic particles and debris with a feeding apparatus.

Wiwaxia also is especially interesting to paleontologists for scientific reasons that extend far beyond the Burgess Shale. This is because scales belonging to related animals have been found in a wide variety of Lower Cambrian rocks. These scales occur scattered and isolated, with no evidence of other body parts, because at no other locality have exceptional conditions of preservation been discovered like those responsible for the fossilization of the Burgess Shale fauna. However, by using the complete specimens of *Wiwaxia* from the Burgess Shale, we can reconstruct the likely appearance of their Lower Cambrian relatives, and thereby document a particularly obscure part of early animal evolution.

Another unusual creature was *Dinomischus* (Fig. 30), the body of which was supported above the seafloor by an elongate stalk that was anchored in the muds of the seafloor by a bulbous holdfast. *Dinomischus* probably captured minute particles of food suspended in the seawater with the aid of plate-like structures that encircled the top of its body. Quite a number of unrelated groups of animals have anatomies that are arranged so as to keep a cup-like body with attached feeding organs well clear of the seabed on a long stem, but in no case is it possible to demonstrate a convincing relationship between these groups and *Dinomischus*.

There are a number of other miscellaneous animals in the Burgess Shale, but surely the most peculiar of all is the aptly named *Hallucigenia* (Fig. 31). This bizarre creature consisted of an elongate trunk supported by seven pairs of unjointed spines. On the opposite side of the trunk a row of seven tentacles arose, while behind them there was a cluster of small tentacles. Each of the larger tentacles ended in a bifid, snapper-like structure, and may have been used to grasp food. At the anterior end the trunk may have expanded into a head-like structure, while posteriorly the trunk bent, first upward and then forward. *Hallucigenia* is so peculiar that it is difficult to know what to compare it with; it might even be part of a larger animal that broke up before fossilization. However, a unique specimen appears to show many individuals of *Hallucigenia* clustered on and around a decaying corpse, perhaps this strange animal was a scavenger that moved across the seabed on its sharp spines.

Several other Burgess Shale animals are no easier to classify in known phyla, and also are included in the category Miscellanea. Nearly all of these peculiar animals are only found in the Burgess Shale, and are only available to paleontologists because of the unusual conditions of preservation. As with other components of the Burgess Shale

Figure 28a. Anomalocaris.

An incomplete specimen (x1.1) of the whole animal, showing the right limb, and a portion of the left limb, in place. The lobes overlap along the sides of the tapering body, the tip of which is broken off.

Figure 28b. Anomalocaris.

An enlargement (x1.7) of the front portion of the same specimen, photographed submersed in water, to show the limbs.

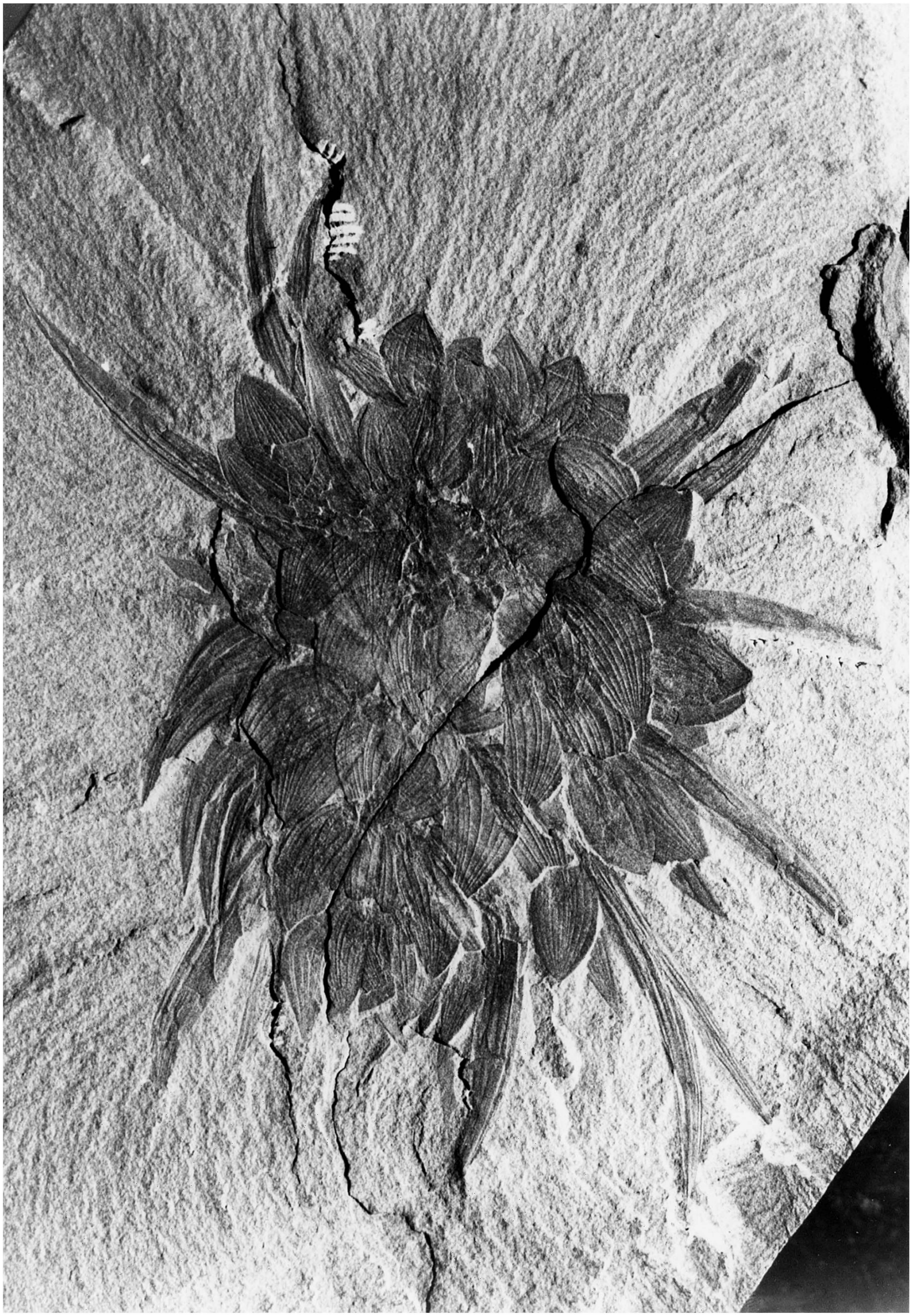

Figure 29.* *Wiwaxia *(x3.8). A view of the dorsal surface, which was covered with scales and also bore a row of spines along each edge; these spines evidently helped to deter attacks by predators.*

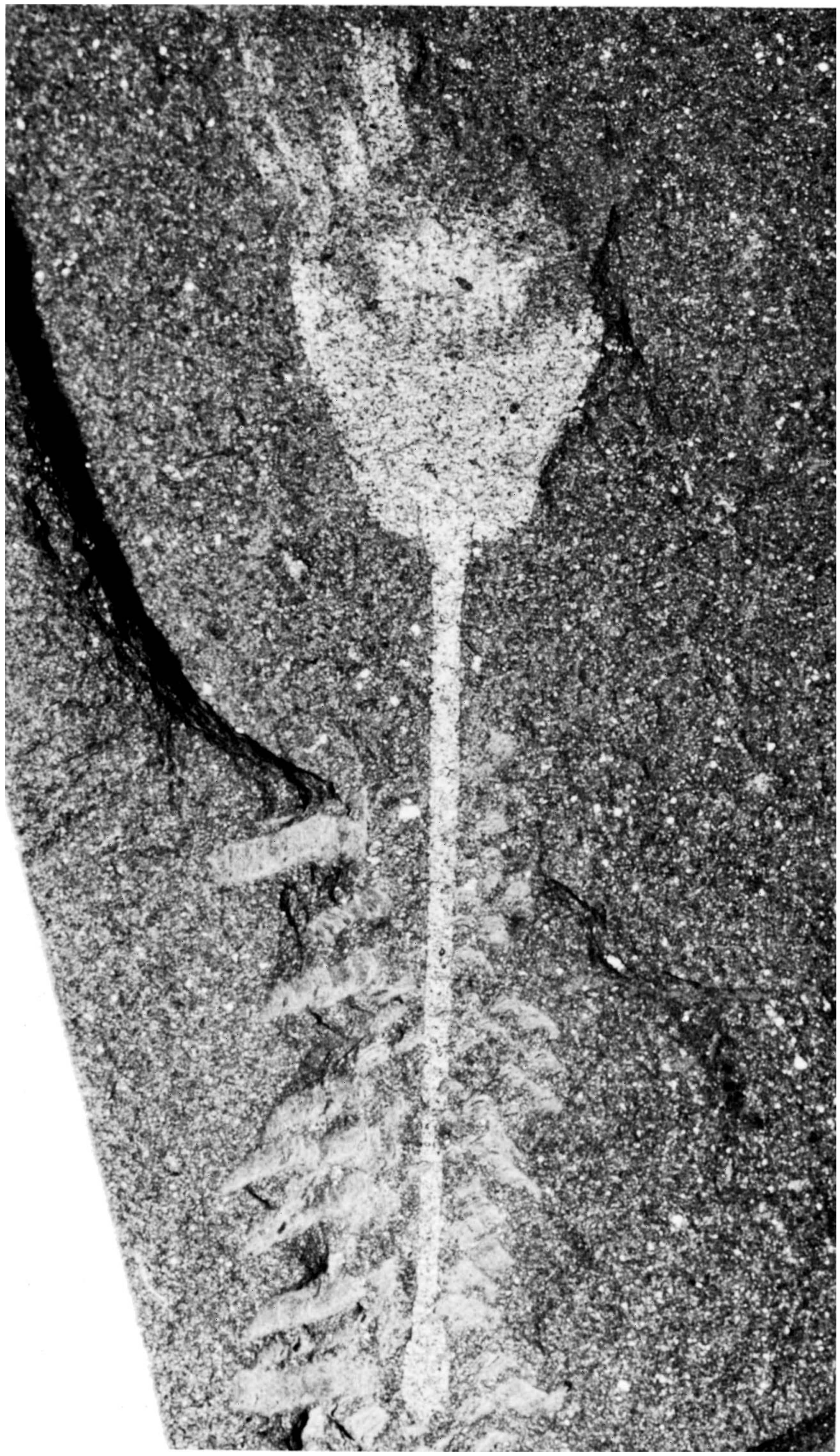

Figure 30. ***Dinomischus*** *(x9.3), a cup-shaped body with an elongate stem that kept the animal clear of the seabed. The pointed structures on the upper part of the cup may have been used in feeding.*

Figure 31. ***Hallucigenia*** *(x13.0). This bizarre creature supported its trunk on seven pairs of stilt-like spines. The tentacles that arose from the dorsal surface of the trunk are also visible.*

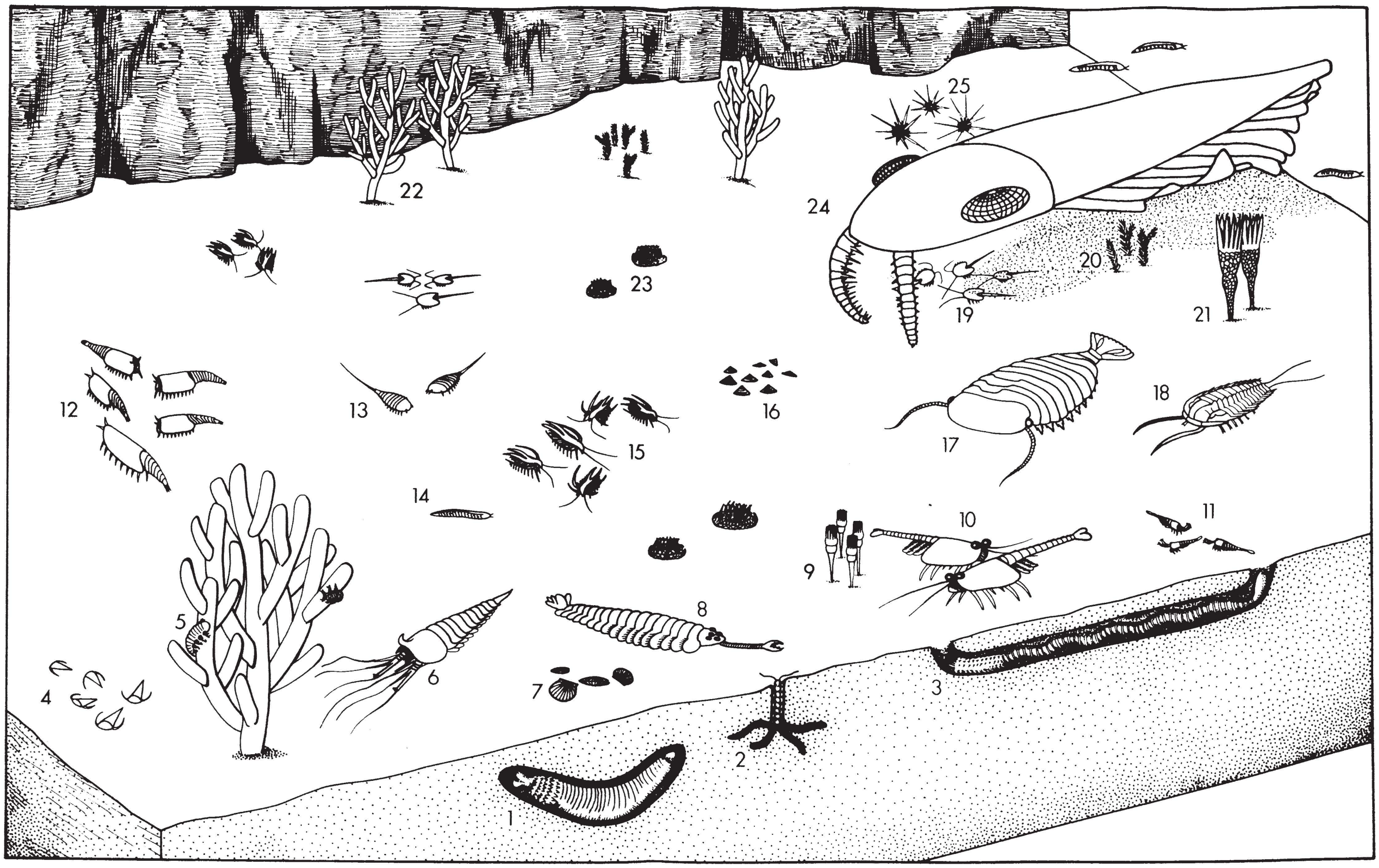

Figure 32. *Restoration of some of the Burgess Shale species living on, above, and in the muddy sediments being deposited at the foot of the submarine cliff (in background). The animals have been numbered from left to right in successive rows across the drawing, beginning with the vertical section in the foreground. The animals shown comprise: branching and globular sponges (**Vauxia**, 22, **Choia**, 25, **Pirania**, 20); the articulate brachiopod **Nisusia** (7); the monoplacophoran mollusc **Scenella** (16); **Hyolithes** (4); two priapulid (**Ottoia**, 1, **Louisella**, 3) and one polychaete (**Burgessochaeta**, 2) worms; various arthropods, [the trilobite **Olenoides**, 18; the non-trilobites **Sidneyia**, 17, **Leanchoilia**, 6, **Marrella**, 15, **Canadaspis**, 12, **Molaria**, 13, **Burgessia**, 19, **Yohoia**, 11, **Waptia**, 10, and **Aysheaia**, 5 (crawling on the sponge **Vauxia**, 22)]; the echinoderm **Echmatocrinus** (21); and the chordate **Pikaia** (14). Miscellaneous animals shown are **Opabinia** (8), **Dinomischus** (9), **Wiwaxia** (23), and the giant **Anomalocaris** (24). The animals are drawn to show their approximate relative size.*

fauna, many of them may have been far more widespread originally, but, in the absence of special preservational conditions, they failed to be fossilized elsewhere. Knowledge of such forms is important because they throw new light on the early evolution of animals. It has long been realized that most and possibly all of the animal phyla evolved during the Cambrian. What has been less widely appreciated is that, in this period of major diversification of the animals, many other bodyplans appeared that failed to survive to the present day.

As information on the many species within the Shale has grown, and we know more clearly where and how the Shale was formed, so it has become possible to visualize the setting in which the animals and plants lived (Fig. 32). One of the major results of recent work has been the realization that all other main ecological groupings, identified in modern marine faunas in terms of life and feeding habits, are recognizable in the fossils of the Shale. It must be stressed, however, that the living positions in our reconstruction in Figure 32 are hypothetical, because transportation of the fauna has not only destroyed any tracks and burrows made by the animals, but has also mingled organisms that formerly were widely separated in their habitat. However, it appears reasonably certain that some creatures lived within the sediment, including those that may have simply lived in burrows (e.g. the polychaete *Burgessochaeta* and the priapulid *Louisella*) and those that may have burrowed more actively (e.g. the priapulid *Ottoia*). Other animals were more or less restricted to the surface of the sediment. They included many of the arthropods (e.g. *Canadaspis*, *Marrella*, *Olenoides*, *Sidneyia*, and *Yohoia*) that walked on the seabed, probably raking the sediment in search of food, and other more bizarre forms such as *Hallucigenia*. Other creatures were anchored to the seafloor, including the various echinoderms, sponges, and the peculiar *Dinomischus*. More rarely, one animal lived on another; for example, the brachiopods attached to sponges. Above the seafloor there were organisms that swam, perhaps only a few centimetres clear of the sediment or, in other cases, much nearer the surface of the sea. Animals that seem to have possessed organs that were suited to swimming included some arthropods (*Leanchoilia*), polychaetes (*Canadia*, *Insolicorypha*), chordates (*Pikaia*), and the enigmatic *Opabinia* and *Anomalocaris*.

Feeding styles also show a wide range of types. Many animals sought minute food particles in the sediment, grubbing up patches of sediment or sweeping its surface. Examples of such deposit feeders include many arthropods (e.g. *Marrella* and *Yohoia*) and polychaete worms (*Burgessochaeta*). Other creatures filtered the seawater to trap food particles suspended in the water. All the sponges, brachiopods and echinoderms in the Shale appear to have been suspension feeders, which, by rising to different heights above the seabed, were able to exploit different levels in the water for food. Perhaps the greatest surprise in terms of feeding habits of the Burgess Shale animals is the number of predators. This information is particularly important because, until recently, it was thought that levels of predation in the Cambrian were low; evidence from the Burgess Shale shows that this was not so. In some cases, a predator can only be identified by the likelihood that a ferocious-appearing feeding apparatus was indeed designed to trap and kill other animals; two such examples are the trilobite *Olenoides* and the bizarre fossil *Anomalocaris*. In other instances, however, the gut contents prove unequivocally that an animal was a predator. Examples of hyolithid and brachiopod remains in the alimentary tract of the arthropod *Sidneyia* and the priapulid worm *Ottoia* have already been mentioned. The example of hyolithids eaten by *Ottoia* is of special significance because, once the shells had passed through the gut, there would have been no direct evidence, such as scratch marks or crushing, that the hyolithids had suffered predation. Many of the hyolithids found scattered over the surfaces in the Shale also may well have passed through the guts of priapulids and other worms.

THE SCIENTIFIC SIGNIFICANCE OF THE BURGESS SHALE

It should be apparent that the Burgess Shale fauna throws a unique light on the biology and ecology of a wide variety of Cambrian animals, many of which are not known in rocks at any other localities. How can we be sure that the Burgess Shale is not just a freak fauna, a sideshow that, however amazing the preservation of the fossils, has little to do with the mainstream of Cambrian evolution? Several arguments suggest that the uniqueness of the Burgess Shale fauna is because of its preservation rather than original faunal composition. To begin with, soft-bodied fossils are known from a variety of other Cambrian rocks, and faunas with especially rich soft-part preservation have been found in the immediate vicinity of the Burgess Shale. Furthermore, even when soft-bodied fossils are not preserved, Cambrian trace fossils hint at the former presence of worms and other creatures. Another important line of evidence is that practically all the Burgess Shale fossils with hard parts, for example trilobites and brachiopods, are widespread in other Cambrian rocks. Indeed, if all the soft-bodied fossils are excluded from consideration, then the impoverished residue of shelly species in the Burgess Shale would provide an assemblage identical to many other Cambrian fauna, and not in any way exceptional or indicative of a peculiar environment.

It appears, therefore, that the Burgess Shale fauna is uniquely typical of the actual Cambrian faunas, whereas assemblages from other rocks are severely biased in favour of those creatures with hard parts. The Burgess Shale thus gives us unusually complete insights into the true diversity of forms actually present, including what appear to be many phyla that have since become extinct. It also provides similar insights into the ecology, especially with regard to feeding habits. Study of the Burgess Shale has emphasized the important role of predators, as well as the varied types of animals feeding on organic particles suspended in the water, or on particles on and in the mud of the sea bottom.

The importance of the Burgess Shale to paleontological and evolutionary studies is difficult to exaggerate. Without it, our knowledge of Cambrian life would be sadly impoverished. It is all the more fitting that this superb fauna should occur in the magnificent setting of Yoho National Park, and that the quarry it came from is justifiably designated as one of Canada's World Heritage Sites.

APPENDIX
(N.C. Ollerenshaw)

GEOLOGICAL TIME SCALE

Age in millions of years	Era	Period	Geological event	Biological event
0.004	CENOZOIC (Recent life)	QUATERNARY		
1			Great Lakes formed	Man appears
1.5–2		TERTIARY		
26				
34				
55			LARAMIDE OROGENY Rocky Mountains formed	First primates
65	MESOZOIC (Middle life)	CRETACEOUS		Age of the dinosaurs
136		JURASSIC		First mammals; First birds
190–195		TRIASSIC		
225	PALEOZOIC (Ancient life)	PERMIAN	APPALACHIAN OROGENY Appalachian Mountains formed	
280		PENNSYLVANIAN		First reptiles
		MISSISSIPPIAN		
345		DEVONIAN		First insects
395		SILURIAN		
430–440		ORDOVICIAN		First fish
500		CAMBRIAN	BURGESS SHALE DEPOSITED	Invertebrates flourish
570	PRECAMBRIAN – PROTEROZOIC	HADRYNIAN		Very simple organisms
995		HELIKIAN		
		APHEBIAN		
2600	PRECAMBRIAN – ARCHEAN			

GSC

GLOSSARY

Algae: plants, almost exclusively living in water, and ranging from single-celled forms to large seaweeds.

Anterior: situated toward or at the front or head of an animal.

Arthropod: an invertebrate animal belonging to the phylum Arthropoda, characterized by jointed limbs and segmented bodies; examples are trilobites, crustaceans such as crabs, and spiders.

Articulates: brachiopods (marine shelled animals) belonging to the class Articulata, and having shells consisting of two halves (or valves) joined by "teeth" and sockets along a hinge.

Bifid: divided into two equal parts by a cleft or notch in the middle.

Biota: all the living organisms in an area, including both flora (plants) and fauna (animals).

Bivalved: having a shell divided into two separate parts (or valves).

Brachiopod: a solitary, marine, invertebrate animal with a shell consisting of two parts or valves, and belonging to the phylum Brachiopoda.

Cambrian: the name given to a specific geological unit or division in a sequence of divisions called the "geological time scale" (see Appendix above) and covering the time period from approximately 500 to 570 million years ago, during which a system of sediments or precipitates (since consolidated into rocks) were deposited.

Carapace: a shield covering the head and part or the whole of the body in crustacean arthropods.

Chaeta (or seta): a slender, typically rigid, bristle or hair (plural chaetae/setae).

Chitin: an organic material or compound (amorphous polysaccharide), a common constituent of various invertebrate animal skeletons (trilobites for example).

Chordate: an animal belonging to a grouping (or phylum) of animals with a bony spinal column or notochord.

Cnidaria or Coelenterata: a phylum of multicellular invertebrate animals, such as sea anemones, corals or jellyfish, characterized by having stinging cells and tentacles.

Dorsal: the back or upper surface of an animal.

Dorso-ventral plane: a plane at right angles to the longitudinal axis of an animal, running from the dorsal to the ventral side.

Echinoderms: marine animals such as starfish, sea cucumbers, and crinoids, characterized by radial symmetry and a skeleton formed of plates of calcite with a reticulate structure.

Ecology: the relationships between organisms and their environment, the relationships of organisms to each other, and the study of these relationships.

Escarpment: a long cliff or steep slope separating surfaces at two different levels (elevations).

Exoskeleton: a skeleton that is located on the outside of the soft parts of the body, as a shell or armour.

Fauna: all the animals in an area, or sequence of rocks, or an environment, or living during a given period of time.

Flora: all the plants in an area, or in a sequence of rocks, or an environment, or living during a given period of time.

Formation: a name used by geologists to define a sequence of similar rock strata or beds, ranging in thickness from less than one metre to more than one thousand metres, and commonly prefixed by a geographic name – for example, the Cathedral Formation, named after Cathedral Mountain.

Gastropod: a type of mollusc, typically with a single shell in the form of a spiral; for example a snail.

Genus: a category in the system of classification used by scientists to organize a grouping and hierarchy for plants and animals. A family is divided into genera, a genus is divided into species.

Helen: a strut on a hyolithid shell that forms a long, narrow, curved structure projecting laterally from the junction of the cone (main shell) and the operculum (lid).

Hyolithid: an invertebrate animal, possibly a mollusc, with a tapering shell that is triangular or circular in cross-section; the shell has a lid (operculum).

Inarticulates: brachiopods (marine shelled animals) belonging to the class Inarticulata and having shells consisting of two halves (or valves), held together by muscles only, without hinge "teeth" or sockets.

Invertebrate: an animal belonging to the Invertebrata, a grouping of animals without backbones.

Mollusc: an invertebrate animal belonging to the group designated the phylum Mollusca, which includes gastropods, pelecypods (clams etc.), and cephalopods.

Notochord: a flexible, elastic rod acting as a supporting or stiffening structure in an animal's body, ancestral to and a precursor of a backbone in a vertebrate animal.

Operculum: a lid or cover.

Paleontologist: a scientist who studies life in past geological time through the fossilized remains of animals and/or plants.

Paleoreconstruction: the development of a model of what something or some environment looked like at the time it actually existed in the geological past.

Phyllopod: literally 'leaf-foot', a leaf-shaped appendage of a crustacean arthropod.

Phylum: a category in the classification of animals; a phylum is a section of the animal kingdom and is itself divided into classes; the plural term is phyla.

Priapulid: any of a small group of wormlike marine animals belonging to the class Priapulida, and which commonly have one or two appendages at the tail end; up to several inches in length.

Process: a branch or appendage projecting from the main body.

Reef: a prominent bank or ridge built up above the level of the surrounding seafloor by reef-building organisms such as corals, sponges and bryozoans.

Seta: see chaeta.

Species: the fundamental unit in the hierarchy of classification; a population of individuals, either animal or plant, that can interbreed and produce fertile offspring; there are usually a number of species in a genus.

Trilobite: an extinct marine arthropod with an exoskeleton divided longitudinally into a convex median and paired lateral lobes (three in all); belonging to the class Trilobita; Cambrian to Permian.

Ventral: the lower or abdominal part or surface of an animal, opposite the back or dorsal side.