4

Burgess Shale: Cambrian Explosion in Full Bloom

James W. Hagadorn

THE MIDDLE CAMBRIAN BURGESS SHALE IS ONE OF THE world's best-known and best-studied fossil deposits. The story of the discovery of its fauna is a famous part of paleontological lore. While searching in 1909 for trilobites in the Burgess Shale Formation of the Canadian Rockies, Charles Walcott discovered a remarkable "phyllopod crustacean" on a shale slab (Yochelson 1967). Further searching revealed a diverse suite of soft-bodied fossils that would later be described as algae, sponges, cnidarians, ctenophores, brachiopods, hyoliths, priapulids, annelids, onychophorans, arthropods, echinoderms, hemichordates, chordates, cirripeds, and a variety of problematica. Many of these fossils came from a single horizon, in a lens of shale 2 to 3 m thick, that Walcott called the Phyllopod (leaf-foot) Bed. Subsequent collecting at and near this site by research teams led by Walcott, P. E. Raymond, H. B. Whittington, and D. Collins has yielded over 75,000 soft-bodied fossils, most of which are housed at the Smithsonian Institution in Washington, D.C., and the Royal Ontario Museum (ROM) in Toronto.

Although interest in the Burgess Shale fauna has waxed and waned since its discovery, its importance has inspired work on other Lagerstätten and helped galvanize the paleontological community's attention on soft-bodied deposits in general. For example, work on the Burgess Shale has stimulated work on the older Chengjiang fauna (Chapter 3), as well as a number of other Burgess Shale–type localities from around the world (Chapter 5).

In the first descriptions of the Burgess fauna, Walcott placed most of the new taxa (over 110 species) within existing taxonomic groups.

Among other reasons, this was largely because his specimen analysis was based on examination of unprepared single shale slabs. Because many specimens are oriented obliquely to bedding planes, folded over on themselves, and/or contain shale intercalated between carcass segments, subsequent dissection and analysis of part–counterpart slabs allowed more detailed morphological reconstructions and hence more accurate taxonomic assignments (Whittington 1971a). Together with reexcavation of original collecting sites and documentation of new collection sites, reexamination of Burgess Shale specimens using these techniques has yielded a variety of new interpretations about these organisms and provided more accurate phylogenetic, paleoecological, and environmental information about Middle Cambrian marine life.

The fauna of the deposit includes both relatively common skeletonized forms and an abundance of soft-bodied forms seldom preserved in typical Cambrian paleoenvironments. This conservation Lagerstätten is thus unique because it provides the most comprehensive view of a typical benthic paleocommunity during the Cambrian explosion. Early in its history, this deposit was recognized as exceptional (Walcott 1911b), not only because it was the first documented example of a nearly complete Cambrian paleocommunity, but because at that time the Cambrian represented the oldest accepted record of animal life. Faunas from these strata are preserved in fine-grained obrution deposits that were transported via fluidized flows into a poorly oxygenated basin or trough adjacent to a major carbonate escarpment. Rapid burial, low oxygenation, and early diagenetic clay replacement of carcasses allowed the preservation of a variety of soft- *and* hard-bodied organisms representing most major marine phyla, as well as several morphologically distinctive organisms of uncertain taxonomic affinity.

Geological Context

The Burgess Shale is an informal name for two fossiliferous shale members of the Burgess Shale Formation, which are well exposed near the town of Field, British Columbia (Figure 4.1). Over the past 100 years, the vast majority of the Burgess Shale biota has been collected from two quarries, known as the Walcott and Raymond quarries, both of which are located along the western slope of a ridge between Mount Field and Mount Wapta, in the southern portion of Yoho National Park.

During the Cambrian, three continuous but laterally interfingered lithofacies belts were deposited along the passive margin of the North American Cordilleran margin: the inner detrital belt, the middle carbonate belt, and the outer detrital belt (Palmer 1960; Robison 1960). The Burgess Shale occurs along the margin of the outer two facies belts, and thus the stratigraphic framework for the Burgess Shale includes se-

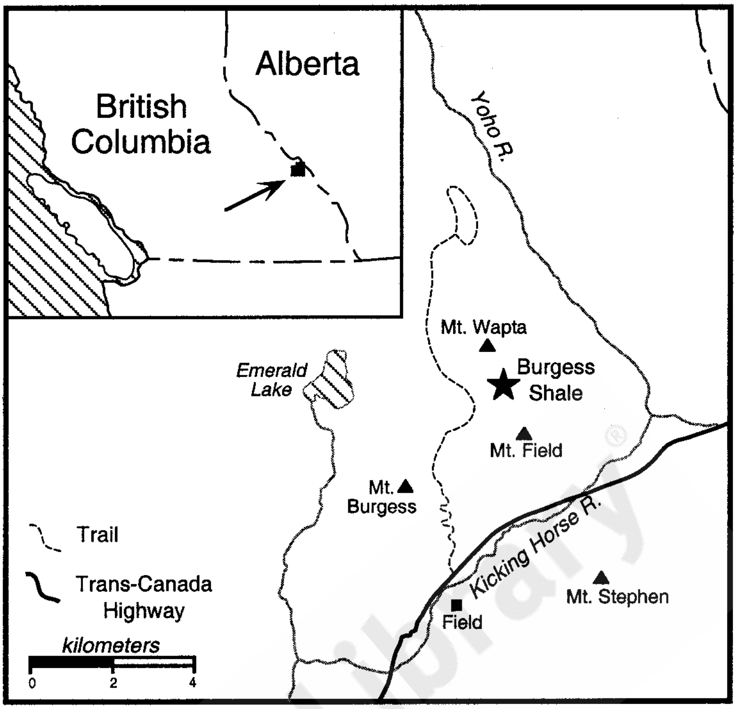

FIGURE 4.1 Part of Yoho National Park, British Columbia, Canada. The star indicates the location of the Walcott and Raymond quarries. (Modified from Whittington 1985)

quences deposited in both settings (Stewart 1989). In the Mount Field region, the margin of the carbonate belt was delineated by a nearly vertical carbonate escarpment composed of a massive, approximately 250 m thick sequence of thin-bedded reef-flat dolomites—these constitute the Cathedral Limestone Formation (Aitken 1971; McIlreath 1974, 1977; Aitken and McIlreath 1984) (Figure 4.2). Beyond the outer edge of this escarpment, deep-water slope limestones and platform-derived carbonate debris accumulated in what is known as the Takakkaw Tongue (Aitken 1997). Above the Takakkaw Tongue is the Burgess Shale Formation consisting of 10 members, most of which are dominated by shales (Fletcher and Collins 1998) (Figure 4.2). Above the four lowest members of the Burgess Shale Formation are the Walcott Quarry Shale Member and the Raymond Quarry Shale Member (Figure 4.2). Although a few soft-bodied fossils occur in the basal shales of the overlying Emerald Lake Oncolite Member, the vast majority of soft-bodied fossils occur in the Walcott Quarry and Raymond Quarry Shale Members. For the purposes of this chapter, the name Burgess Shale is used to denote localities in the Yoho National Park region that occur in the stratigraphic interval encompassing these two members, unless otherwise noted. The Burgess Shale Formation is approximately 350 m thick, and its upper-most member, the Marpole Limestone Member, both caps the underlying nine members in the Burgess Shale Formation and is laterally equivalent with the Cathedral escarpment-capping Waputik Member of the Stephen Formation (Fletcher and Collins 1998) (Figure 4.2). Both the Burgess Shale and Stephen Formations are capped by the laterally extensive limestones of the upper Middle Cambrian Eldon Limestone Formation (Walcott 1908a, 1908b) (Figure 4.2).

The presence of similar assemblages of *Glossopleura* zone trilobites in the Takakkaw Tongue and the Cathedral Limestone Formation suggests coeval deposition (Fritz 1971; Aitken and McIlreath 1984; Fletcher and

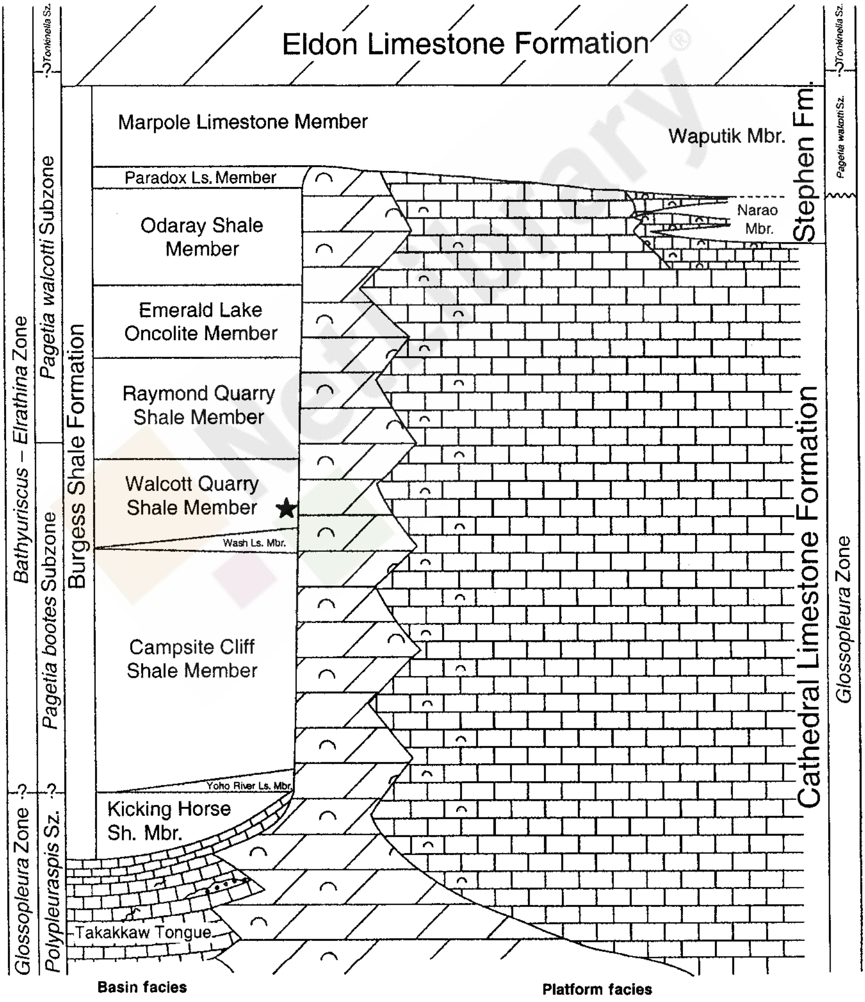

FIGURE 4.2 Stratigraphic context for exposures of Middle Cambrian strata in the Mount Field region. Walcott's original "Phyllopod Bed" is indicated with a star. (Modified from Fletcher and Collins 1998; after original from Fritz 1971 and Aitken and McIlreath 1984)

Collins 1998). Although the basal member of the Burgess Shale Formation contains *Glossapleura* zone trilobites, the remainder of the unit and the adjacent Stephen Formation contain Middle Cambrian *Bathyuriscus-Elrathina* zone trilobites (Walcott 1908a, 1908b, 1917, 1927, 1928; Rasetti 1951), also suggesting coeval deposition of these units. More important, this co-occurrence corroborates lithostratigraphic evidence that significant paleobathymetric disparity existed in this environment during deposition of the Burgess Shale Formation (Fritz 1971; McIlreath 1974, 1977; Aitken and McIlreath 1984; Fletcher and Collins 1998).

PALEOENVIRONMENTAL SETTING

Burgess Shale faunas were deposited in a relatively deep (~200 m below sea level) outer shelf setting, tens of meters oceanward of a massive cliff-like carbonate bank (Aitken 1971; Whittington 1971a; Piper 1972; McIlreath, 1977; Aitken and McIlreath, 1984) (Figure 4.2). During initial deposition of the shales of the Burgess Shale Formation, this carbonate bank extended at least 160 m above the muddy seafloor. Although originally interpreted to reflect an intact reef margin (Aitken and McIlreath 1984), Stewart, Dixon, and Rust (1993) reinterpreted this cliff face as a headwall formed through platform margin collapse. Within the immediate area of the Burgess quarries, strata of the Takakkaw Tongue record post-truncation deposition of associated smaller carbonate debris from this platform into an outer shelf setting (Rasetti 1951; Collins and Stewart 1991). After drowning of the platform, finer-grained siliciclastic sediments built up in the basin, eventually blanketing the surface of the platform.

The fauna of the Burgess Shale includes allochthonous and autochthonous assemblages of pelagic and benthic organisms that were likely transported from near the base of the escarpment into a localized depression or trough by a series of high-density fluidized flows (Whittington 1971a, 1971b; Piper 1972; Allison and Brett 1995). In the Walcott quarry, soft-bodied fossils are preserved in a wide variety of orientations with respect to bedding, and many are compressed at high angles to bedding or exhibit folding of carcasses, suggesting entrainment in a localized flow. The presence of seafloor slumping and graded bedding corroborates this evidence, suggesting transport of faunas (Piper 1972). Some have argued that initiation of these flows was mediated by biological activity (Hecker 1982) or high sediment organic content (Keller 1982). Although the distance of transport of this allochthonous assemblage is debated, Conway Morris (1979a, 1986) estimated maximum transport distances of 0.9 to 1.8 km. Experimental taphonomic studies corroborate the possibility of a far-traveled soft-bodied fauna (Allison 1986; Briggs and Kear 1993), and the presence of photosynthetic algae in the deposit suggests a minimal transport estimate for pelagic forms of 70 m (Briggs, Erwin, and Collier 1994). Individual beds are graded and may possess skeletal remains at the base, including a wide variety of skeletonized and soft-tissue compressions, foldings, and orientations (Walcott 1912a; Whittington 1971a; Piper 1972; Conway Morris 1977d, 1986). The absence of evidence for amalgamation or recycling in the rhythmically layered shales of this deposit further suggests that each layer in the Burgess Shale may represent an individual transport event, and thus paleoecologic inferences (outlined later) drawn from myriad layers in this deposit are constrained by an unknown duration of time-averaging. Although the soft-bodied faunas from the Walcott Quarry Shale Member were almost certainly transported, some fossils from the Raymond Quarry Shale Member were likely deposited *in situ* or suffered minimal transport. For example, trace fossils in the Raymond Member were not transported (Allison and Brett 1995), and some sponges exhibit evidence of burial while their bases were still rooted in the sediment (Collins 1996b).

On a larger scale, strata exposed along the northwest–southeast-trending Mount Wapta–Mount Field ridge closely parallel an important facies change in this region. The schematic diagram in Figure 4.2 illustrates the lateral intersection of the Burgess Shale Formation with the carbonate strata of the Cathedral Limestone Formation. The coarsely crystalline Cathedral Formation carbonates were likely deposited in a shallow, well-oxygenated tropical setting, along the eastern margin of Laurentia (Robison 1976; Scotese et al. 1979; Whittington 1981b). If Cambrian conditions are analogous to modern conditions, then the Burgess Shale may have been accessible to high levels of faunal migration typical of tropical settings, suggesting that the deposit may represent maximum diversity levels for deeper-water tropical Cambrian facies (Conway Morris 1986). Isotopic analyses of bulk organic and carbonate carbon in Burgess Shale fossils seem to corroborate these hypotheses (Butterfield 1990a).

TAPHONOMY

The unique taphonomic and paleoenvironmental conditions of the Burgess Shale are of special importance because they allowed paleontologists to obtain their first view of a typical Cambrian community—in the process, revealing that these communities, much like modern settings, were dominated by soft-bodied forms as well as the more typically preserved mineralized forms. The Burgess Shale fauna includes forms with both mineralized and nonmineralized skeletons, including benthic and pelagic assemblages of faunas and floras that likely inhabited both outer shelf and platform margin settings. These faunas consist of animals living at the site of the deposit, as well as animals and algae that lived nearby and were trapped in a fluidized flow. In addition to living specimens, flows likely entrained a host of discarded or postmortem skeletal elements of trilobites, brachiopods, monoplacophorans, and hyolithids (Whittington 1971a; Piper 1972; Conway Morris 1977d, 1986).

The hard and soft parts of the fauna are largely preserved flat on bedding planes, laid out or squashed in a variety of orientations, although some are oriented at an oblique angle with portions of their appendages intersecting different levels of strata. After quarrying, specimens are usually preserved as part and counterpart on split slabs. Although some of the fossils may have lain on the seafloor for a relatively long time, as evidenced by scattered skeletal fragments, most of these organisms were likely buried rapidly within the fluidized flow. The absence of escape structures, even though the fauna includes effective burrowers such as priapulids (Conway Morris 1977d), and the lack of coiling or osmotic shrinkage in the annelids and arthropods (*sensu* Dean, Rankin, and Hoffman 1964), suggest that Burgess Shale organisms may have been stunned or killed before burial (Conway Morris 1986). Evidence of post-burial decay varies from complete preservation of internal organs to absence of all soft parts. The degree of decay is visible in some specimens by the presence of a squeezed-out intestine and dark stain near the posterior of the organism (Whittington 1971b). This stain is visible as a pyrite patina (Allison and Brett 1995) and is inferred to represent body contents that seeped out into the surrounding sediment during the initial stages of decay.

Although soft-bodied specimens do contain evidence of kerogenized organic carbon films, and some organic-walled fossils have been extracted from the deposit (e.g., *Wiwaxia*), most of the soft tissues have been replaced by hydrous aluminosilicates together with minor pyrite (Conway Morris 1977d; Whittington 1980b; Butterfield 1990a; Orr, Briggs, and Kearns 1998). Soft-bodied fossils are typically preserved at the tops of fining-upward beds, which are commonly laminated and capped with organic detritus (Allison and Brett 1995). Whereas the exact mechanism for this unique soft- and hard-part preservation is still poorly understood, it has been hypothesized to result from the combination of rapid burial and mortality mentioned earlier (Whittington 1981b; Conway Morris 1986), replacement of tissues by clays during early diagenesis (Orr, Briggs, and Kearns 1998; but see Butterfield 1990a; Towe 1996), deposition of this flow in an anoxic environment (Whittington 1985; Allison and Brett 1995), and proximity to structurally resistant geomorphic features (Collins, Briggs, and Conway Morris 1983).

Although the mechanism for replacement of soft tissues by clay minerals is not well constrained, replacement may have been catalyzed by bacteria, by variations in the composition of the decaying tissues, and/or by variations in pore-water chemistry (Orr, Briggs, and Kearns 1998). Another preservation catalyst for this Lagerstätte was the locally fluctuating bottom-water oxygenation. For example, evidence for anoxia in sediments and overlying waters is common in the soft-tissue-rich Walcott Quarry Shale Member and includes rarity of pyrite framboids, even dispersal of pyrite, and absence of trace fossils and shell beds. Where soft-tissue preservation is more sporadic higher in the deposit (e.g., Raymond Quarry Shale Member), higher benthic oxygenation levels are suggested by low-diversity shell beds, complex burrows, and pyritic organic remains (Allison and Brett 1995). Finally, soft-tissue preservation is also mediated by geologic and geomorphic factors. In particular, well-preserved fossils are typically found only in the shales immediately adjacent to the Cathedral Limestone Formation, largely because strata adjacent to this massive carbonate escarpment were shielded from penetrative deformation and development of intense cleavage during subsequent orogenic and metamorphic events (Aitken 1971; Collins, Briggs, and Conway Morris 1983; Aitken and McIlreath 1984).

Mineralized skeletal elements of the Burgess assemblage, such as calcareous skeletal elements, have mostly been replaced or coated by silicates or framboidal pyrite, whereas phosphatic or siliceous skeletal parts such as inarticulate brachiopods or sponge spicules may retain their original composition (Conway Morris 1985). Occurrences of mineralized skeletal elements range from thin, patchy, bedding-plane accumulations to centimeter-thick shell beds; although fragmentation and abrasion are minimal, most fossils are disarticulated and oriented convex up (Allison and Brett 1995).

PALEOBIOLOGY

One of the most notable features of the Burgess Shale fauna is the variety of morphologies and the diversity of taxonomic groups represented. The majority of work on this deposit has focused on describing and interpreting these biota, and it is recommended that readers consult the systematic literature as well as larger review-style atlases (Conway Morris et al. 1982; Whittington 1985; Briggs, Erwin, and Collier 1994) for detailed listings and photographic overviews. A crucial component in understanding the paleobiology and diversity of the faunas is reconciliation of their morphology, a task that has undergone an evolutionary shift. For example, initial work by Walcott and others placed all Burgess faunas within existing clades, whereas later studies suggested that many fossils were of indeterminate origin, leading others to propose that extreme morphologic disparity exists in the Burgess and hence reflects widespread developmental plasticity in the Cambrian (Gould 1989; for a strong opposing view, see Conway Morris 1998, and references therein). Recent work on other related Lagerstätten (Chapters 3 and 5), coupled with new preparation techniques and intensive re-collection of Mount Stephen localities, has caused this interpretive tide to ebb and allowed firmer placement of many of the more problematic faunas into conventional taxonomic groups. Thus, morphologic disparity of the Burgess fauna has been both understated and overstated in the past, with recent consensus that the range in morphologic diversity is comparable to that visible in modern communities (Briggs, Fortey, and Wills 1992). The following is a brief overview of some of the more notable Burgess Shale faunas, including forms that are clearly allied to modern groups and forms whose phylogenetic affinities are more enigmatic.

The most prominent fossils in the Burgess are likely the arthropods, as they encompass a wide variety of forms, including enigmatic taxa such as *Branchiocaris* and *Marella* (Figure 4.3), as well as more easily classified crustaceans. Arthropods also include chelicerates, trilobites, possible ostracods, possible cirripeds, and a number of arachnomorphs of indeterminate grade (Walcott 1908a, 1908b, 1911a, 1912a, 1916, 1918a, 1918b, 1931; Resser 1929, 1938, 1942; Rasetti 1951; Simonetta 1970; Whittington 1971b,

FIGURE 4.3 The arthropod *Marella.* Length of specimen is 2 cm. (From Whittington 1971b: pl. 16, fig. 2. Reproduced with the permission of the Minister of Public Works and Government Services Canada, 2201 and Courtesy of the Geological Survey of Canada)

1974, 1975b, 1980a, 1981b; Hughes 1975; Simonetta and Delle Cave 1975; Briggs 1976, 1977, 1978, 1981, 1992; Bruton 1981; Collins and Rudkin 1981; Conway Morris et al. 1982; Bruton and Whittington 1983; Briggs and Collins 1988). Although there are far too many arthropods to deal with systematically in this chapter, Briggs and Fortey (1989) review the Burgess arthropods' relationships to major arthropod groups, and Briggs, Erwin, and Collier (1994) provide an excellent photographic overview of the more spectacular forms.

Marella splendens (Figure 4.3) is by far the most abundant and well preserved organism in the Burgess Shale, and is preserved in a variety of attitudes relative to bedding planes (Walcott 1912a). This small (~1 to 2 cm long) arthropod has a wedge-shaped head with elongate tapered spines followed by a body with two pairs of jointed appendages and a series of chitinous leg and gill branches, which may have been used to swim or walk on the seafloor (Whittington 1971b; Briggs and Whittington 1985). Unlike many of the other arthropods in the fauna, *Marella* was likely blind—no eyes have been documented from known specimens.

Canadaspis perfecta is the second most common Burgess taxon, and is one of the earliest known crustaceans, perhaps together with various species of *Carnarvonia, Isoxys, Odaraia, Perspicaris, Plenocaris, Tuzoia,* and possibly *Waptia* (Walcott 1908a, 1912a, 1931; Resser 1929; Simonetta and Delle Cave 1975; Briggs 1977, 1978, 1981). *Canadaspis* was a benthic-feeding phyllocarid arthropod that often occurs with exquisitely preserved biramous limbs, abdomen, gut, spiny telson, gill branches, and sometimes antennae visible beyond or under its bivalved carapace (Briggs 1978, 1992). Another common arthropod is *Sidneyia inexpectans,* a large merostome-shaped organism often containing small trilobites, ostracods, and hyoliths in its gut—suggesting that it was also a predator (Bruton 1981). A similarly unusual arthropod is the crustacean-like *Odaraia,* a lobster-like form with large stalked eyes, a cylindrical carapace, and three fin-like projections on its tail (Briggs 1981).

The only described chelicerate from the Burgess is one of the most spectacular forms discovered under the aegis of Desmond Collins's (Collins, Briggs, and Conway Morris 1983) post-Whittington Burgess excavations. *Sanctacaris uncata* constitutes the earliest example of a chelicerate, and is characterized by six pairs of spiny appendages extending from its head (Figure 4.4). This form had a rather flattened telson and wide head shield, and is thought to have been a predator that lived on or near the seafloor (Briggs and Collins 1988). Several taxa with chelicerate affinities are known, and perhaps the most striking example is the blind form *Leanchoilia superlata* (Figure 4.5), which possesses unique whip-like attachments at the end of its frontal appendages and a triangular tail spine extending from its posterior (Bruton and Whittington 1983). Although

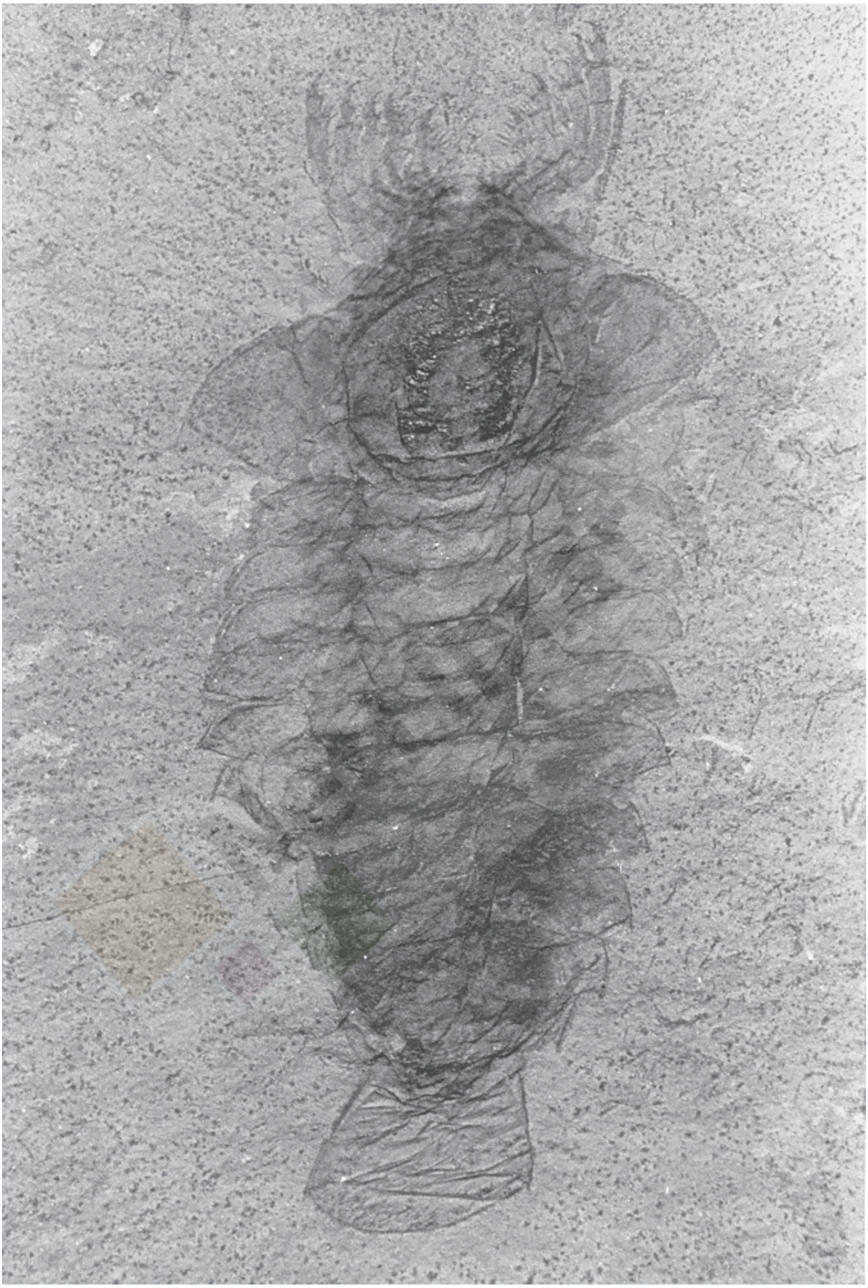

FIGURE 4.4 The chelicerate *Sanctacaris uncata.* Length of specimen is 7 cm. (Photo courtesy of D. Collins, Royal Ontario Museum, Toronto)

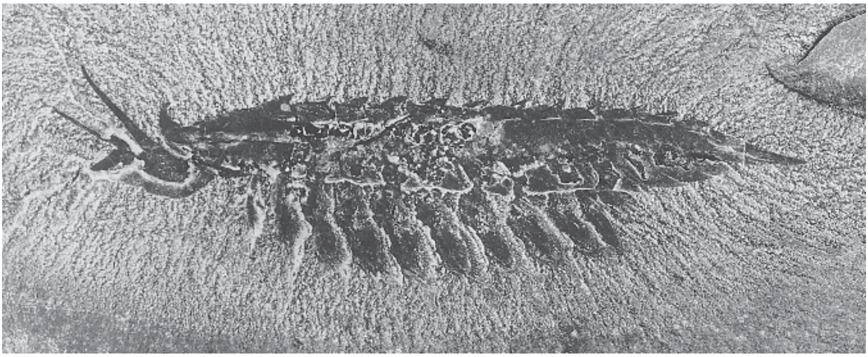

FIGURE 4.5 The arachnomorph *Leancholia superlata.* Length of specimen is 9.5 cm. (Photo courtesy of D. Collins, Royal Ontario Museum, Toronto)

its contents are not distinguishable as phosphatic skeletal debris, the gut trail of this form contains small concentrations of apatite.

Included in the more typical Cambrian arthropods in the Burgess are the 15 genera of trilobites or trilobite-like forms, including agnostids (Walcott 1908b, 1912a, 1916, 1918b, 1931; Resser 1938, 1942; Rasetti 1951; Simonetta and Delle Cave 1975). Among the trilobites, perhaps the most notable is the predatory form *Olenoides,* characterized by a broad cephalon, semicircular pygidium, elongate antennae, biramous head and thoracic limbs, filamentous gill branches, and spinose walking limbs (Whittington 1975b, 1980a). Another well-known trilobite-like arthropod is the burrowing form *Naraoia compacta* (Figure 4.6), an unusual bivalved trilobite that has similar limbs and antennae, but is characterized by a nonmineralized exoskeleton whose dorsal portion consists of two large shields (Whittington 1977). In some examples, traces of the inferred gut and diverticula are visible, although the contents are unknown.

Sponges compose the second most varied group of organisms within the deposit as well as one of the more morphologically ornate components of the fauna. As the dominant sessile epifaunal element of the fauna, this group includes both attached and unattached forms, which are documented in detail in monographs by Walcott (1920) and Rigby (1986). Although hexactinellid and calcareous sponges occur, the vast majority of forms are demosponges. The most common demosponge, *Vauxia gracilenta,* is also possibly one of the most unusual. With tube-like branches and a bush-like appearance, *Vauxia* is notable because its skeleton is composed of a tough organic fibrous network rather than discrete spicules. Other demosponges include forms with delicate radiating spines such as *Choia ridleyi,* the branching heavily spiculate *Pirania muricata,* the conical *Capospongia undulata,* the sac-like *Crumillospongia biporosa,* the elongate cone *Halichondrites elissa,* the double-walled tubular *Leptomitus lineatus,* the wrinkled *Wapkia gransis,* and a variety of forms of

FIGURE 4.6 The trilobite-like *Naraoia compacta.* Length of specimen is 3.6 cm. (Photo courtesy of D. Collins, Royal Ontario Museum, Toronto)

Hazelia and *Vauxia.* Calcareous sponges include forms such as the globe-like *Eiffelia globosa;* hexactinellid sponges include enigmatic forms such as *Protospongia* (thought to be an early lineage of this class) and the sac-like *Diagonialla hindei.*

A variety of polychaetes are also preserved in striking detail, with clear outlines of individual bristle setae, tentacles, trunk segments, appendages, gut, proboscises, and respiratory branchiae (Walcott 1911d; Conway Morris 1979a). *Burgessochaeta setigera* was the most abundant of these forms, a likely infaunal form characterized by long tentacles, biramous appendages, and at least 24 pairs of delicate setae. *Canadia spinosa,* characterized by dorsal and ventral lobes bearing many chitinous bristles, is perhaps one of the most beautiful of the polychaetes, and is also of evolutionary importance because its bristle microstructure is similar to that of *Wiwaxia* (Butterfield 1990b) (Figure 4.7).

Priapulids are relatively common within the Burgess Shale, and include forms like *Ancalagon minor, Fieldia lanceolata, Ottoia prolifica, Lecythioscopa simplex, Louisella pedunculata, Scolecofura rara,* and *Selkirkia columbia* (Walcott 1911d, 1912a; Conway Morris 1977d). Perhaps the best known is *Ottoia,* which may have been a predatory and possibly cannibalistic burrower, characterized by a pronounced proboscis and numerous small hooks around its oral aperture. Several specimens of *Ottoia* contain hyoliths and brachiopods in their guts, and almost all the priapulids exhibit exceptional anatomical details, including setae, gut, proboscis hooks, spines, and papillae.

Cnidarians are also known, including the elongate tubular anthozoan *Mackenzia costalis* and the frondose pennatulacean *Thaumaptilon walcotti*

FIGURE 4.7 The polychaete *Canadia spinosa.* Length of specimen is 3.2 cm. (Photo courtesy of D. Collins, Royal Ontario Museum, Toronto)

(Walcott 1911c; Briggs and Conway Morris 1986; Conway Morris 1993). *Thaumaptilon* is of importance because it may have close affinities to late Neoproterozoic Ediacaran fronds like *Charniodiscus,* and/or may reflect the first documented complex Ediacaran holdover taxon.

Although Middle Cambrian echinoderms are more frequently found articulated in other Burgess Shale–type deposits (Chapter 5), a possible early crinoid, *Echmatocrinus brachiatus,* occurs in the Burgess, as well as examples of more primitive groups of stalked echinoderms, such as the cystoid *Gogia radiata* (Sprinkle 1973; Sprinkle and Collins 1998; for alternative interpretations, see Conway Morris 1993, or Ausich and Babcock 1998). Both of these forms exhibit features thought to be ancestral to those of younger stalked echinoderms, including the presence of an attached holdfast, plated stalk and calyx, and arms radiating from the calyx. However, *Gogia* has rather unusual pores along its plate sutures, as well as brachioles along its ambulacra. All *Echmatocrinus* specimens are attached to hard objects such as the priapulid *Selkirkia* or to hyolithids, suggesting an immobile suspension-feeding life habit (Sprinkle and Collins 1998). Edriaoasteroids such as *Walcottidiscus magister* and *W. typicalis* are also known (Bassler 1935, 1936). *Eldonia ludwigi* is another form that may be allied with the echinoderms, as it possesses tube-feet, a discoidal center with a radial meshwork of fibers, a coiled gut, oral tentacles, and other features suggesting a holothurian affinity (Walcott 1911c; Durham 1974).

Although its affinity remains controversial (Butterfield 1990b), the lancelet-like *Pikaia gracilens* possesses features indicating the presence of a notochord and myotomic muscle tissue, which suggest that it may be one of the earliest known cephalochordates (Walcott 1911d; Conway Morris and Whittington 1979).

Ctenophores also occur, including forms such as the ornate globe-like *Ctenorhabdotus,* the bowl-shaped *Fasciculus vesanus,* and the stringy *Xanioascus canadensis,* all of which have typical features such as cilia, but atypical features such as the presence of many comb-rows and absence of tentacles (Simonetta and Delle Cave 1978; Conway Morris and Collins 1996). Another possible pelagic hydroid or cnidarian is *Scenella amii,* a chondrophorine preserved in dense aggregations of small, flattened cones on bedding planes (Matthew 1902; Babcock and Robison 1988).

In addition to the exceptionally preserved soft-bodied forms, the Burgess Shale contains a number of more traditional skeletonized faunas, including brachiopods, hyolithids, molluscs, and the trilobites mentioned previously. At least six brachiopod genera have been recognized, including relatively ordinary inarticulates such as *Lingulella waptaensis,* as well as more ornate forms like *Micromitra burgessensis,* which commonly exhibit exquisite preservation of elongate delicate setae extending beyond each shell's mantle fringe (Walcott 1912b, 1924; Resser 1938). Articulate brachiopods are also known, including the calcified forms *Diraphora bellicostata* and *Nisusia burgessensis* (Walcott 1924). *Haplophrentis carinatus* is one of the more famous, yet traditional, faunal elements in that it is one of the few examples of an articulated hyolith occurring with the helens, operculum, and conch all preserved and attached to one another (Matthew 1899; Babcock and Robison 1988).

Finally, in addition to metazoa, there are a number of trace fossils and algae in the deposit. Although little systematic work has been done on trace fossils within the more oxygenated layers of the deposit, bed-parallel forms such as *Cruziana* and *Planolites* and vertically inclined forms such as *Arenicolites* and *Monocraterian* occur (Allison and Brett 1995). At least 10 genera of elaborate frondose algae also occur, typically preserved as thin, isolated, shiny films (Walcott 1919, 1931; Walton 1923; Ruedemann 1931; Satterthwait 1976; Collins, Briggs, and Conway Morris 1983; Conway Morris and Robison 1988). Although the flora has not attracted the widespread attention that the fauna has generated, it may include approximately 10 percent of the fossils in the deposit (Conway Morris 1986). Algae include possible green algae, such as the kelp-like *Margaretia dorus* and the stipe-laden *Yuknessia simplex.* A variety of red algae also are found, ranging from simple forms such as the stick-like *Dalya nitens* and *Wahpia insolens,* to more elaborate forms such as the branching *Dalyia racemata,* the finely branching *Waputikia ramosa,* and the shrub-like *Bosworthia simulans.* Possible cyanobacteria such as the tuft-like *Marpolia aequalis,* the filamentous *Marpolia spissa,* and the perforated, sheet-like *Morania confluens* are also found.

Problematic Fauna

Some forms, such as the sponge-like *Chancelloria eros* and the graptolite-like *Chaunograptus scandens,* are of uncertain taxonomic affinity because their morphology is unlike that of modern or other fossil analogues (Walcott 1920; Ruedemann 1931). For example, although relatively large (up to 50 cm tall) specimens of the cone-like *Chancelloria* are known, the nature of their spicular construction is unlike that of modern sponges (Goryanskiy 1973; Bengtson and Missarzhevsky 1981; Bengtson, Collins, and Runnegar 1996; Butterfield and Nicholas 1996), and branching forms from other Burgess Shale–type deposits have not yet been formally described (K. Peterson, personal communication, 1999). Other forms are of enigmatic taxonomic affinity simply because they are known from only a single specimen, such as *Odontogriphus omalus* (Conway Morris 1976a), or because the few examples of these taxa are poorly preserved. Problematic members of the nekton include forms like *Nectocaris pteryx,* a probable chaetognath characterized by large eyes and a dart-shaped finned body (Conway Morris 1976b; Simonetta 1988).

Wiwaxia corrugata is another problematic form characterized by a double row of vertically extrusive and laterally spinose plates extending along its body and sides. The presence of broken and regenerated or replaced plates along the margins of *Wiwaxia* suggest that this organism was involved in predator–prey interactions and that it may have used its plates as defensive armor (Conway Morris 1985, 1992; Butterfield 1990b). Although the taxonomic affinity of *Wiwaxia* is unclear, the presence of shorter chitinous sclerites in interplate body surfaces suggests that *Wiwaxia* may be allied with halkieriids or polychaetes (Conway Morris 1985; Conway Morris and Peel 1995).

Opabinia regalis is one of the more striking problematic forms (Figure 4.8). This segmented organism had a flexible body and a nozzle-snouted proboscis at its anterior characterized by a claw-like apparatus on its end. Like *Anomalocaris, Opabinia* has lateral flaps along its trunk, a fan-shaped tail, and lobopodian-type legs, and is of uncertain taxonomic affinity (Whittington 1975a; Bergström 1986, 1987; Briggs and Whittington 1987). *Opabinia* may have swum about the bottom, collecting organic debris. Although the most striking physical aspect of this creature is its five eyes, the combination of the lobopod and arthropod morphologic characters is of greater importance, as they have led to the suggestion that this form reflects an early arthropod stem group (Budd 1996).

In an interesting history of early discovery, pieces of *Anomalocaris canadensis* and *A. nathorsti* were originally interpreted to be several indi-

FIGURE 4.8 The problematic *Opabinia regalis*. Length of specimen is 6.4 cm. (Photo courtesy of H. B. Whittington, University of Cambridge)

vidual organisms, including arthropods, crustaceans, and medusoids (Whiteaves 1892; Walcott 1911c, 1912a; Madsen 1957; Conway Morris 1978; Conway Morris and Whittington 1979). Subsequent to these reports, excavation of fossil appendages coupled with discovery of complete specimens revealed that *Anomalocaris* is one of the largest and most bizarre organisms of the Burgess Shale fauna, possessing a large lobed head, large eyes, two spiny shrimp-shaped feeding limbs, a lateral elongate series of flaps, lobopod-like legs, a fan-shaped tail, and a circular or square jaw surrounded by circlets of sharp plates or teeth. At present, *A. canadensis* and its close cousin *Laggania cambria* are among the largest organisms in the Burgess paleocommunity (up to 0.5 m) and are thought to belong to an extinct class of arthropods (Collins 1996a; Hou, Bergström, and Ahlberg 1995; Minicucci 1999). The combination of large lateral eyes, swimming lobes, and unique jaw structure suggests that these taxa may have been formidable mobile predators (Whittington and Briggs 1985).

Dinomischus isolatus, a cup-shaped organism characterized by a long thin stem, supported itself above the substrate by anchoring a bulbous holdfast into the seafloor. *Dinomischus* is also known from the Chengjiang Lagerstätte (Chapter 3), and had a stalk lined with cilia and plates. Although very small, this organism is thought to have been a passive suspension feeder and may represent a type of entoproct (Conway Morris 1977b; Chen and Erdtmann 1991).

Lobopodians are another group that is well constrained at the phylum level, but whose detailed systematic position is still poorly understood. The most well known of these mobile epifaunal organisms are *Asheaia pedunculata* and *Hallucigenia sparsa.* As with *Anomalocaris* and other problematica, the discovery of articulated specimens from other Burgess Shale–type deposits coupled with delicate extraction techniques have allowed us insight into their morphology and paleobiology (Robison 1985; Ramsköld and Hou 1991). *Asheaia* is commonly associated with sponges, and has soft legs with claws at their ends (Walcott 1911d; Whittington 1978; Monge-Najera 1995). *Hallucigenia* was an armored lobopod, originally thought to walk on seven pairs of spines, with seven tentacles on its top (Walcott 1911d; Conway Morris 1977a). Recent discovery of similar organisms in the Chengjiang Lagerstätte has revised this interpretation, indicating that the tentacles are actually walking legs and the spines are on top, possibly for defensive protection (Ramsköld and Hou 1991).

PALEOECOLOGY

Although a field-based paleoecologic study of the Burgess paleocommunity has yet to be published (but see Collins 1996b; Fletcher and Collins 1998), the combination of abundant fossiliferous material, concentration of such samples in a few institutions, widespread soft-tissue preservation, and systematic analysis of the fossils allows us remarkable insight into the distribution, diversity, and niches of the fauna and flora inhabiting the general vicinity of the soft seafloor at the base of the Cathedral Limestone Formation.

Like many modern communities, the Burgess Shale is dominated by arthropods (42 genera), but also contains a host of other organisms, including as many as 20 sponge genera, 18 problematic taxa, 10 algae, seven priapulids, six brachiopods, five polychaetes, four echinoderms, four cnidarians, three ctenophores, two hemichordates, two chordates, two onychophorans, one genus of hyolithid, and several types of trace fossils (syntheses in Conway Morris 1986; Briggs, Erwin, and Collier 1994; Allison and Brett 1995). Although the majority of this information was collected from the classic Walcott and Raymond quarries, rough diversity information compiled from more recent Royal Ontario Museum (ROM) sites in coeval strata exhibits a similar range in diversity, with at least 37 genera representing at least five major phyla (Collins, Briggs, and Conway Morris 1983). Like most fossiliferous deposits, strata in these deposits record burial of animals living at the time of transport, as well as a large number of dead individuals or discarded skeletal elements. Thus, discarded or dead skeletal elements in the Burgess Shale may significantly bias analyses of abundance and diversity in this deposit. Conway Morris (1986), however, was able to minimize these biases in his analyses by compensating for trilobite ecdysis, noting both the presence or absence of opercula and helens in hyolithids and the extended mantle setae in inarticulate brachiopods in his attempts to reconstruct the original relative composition of the Burgess Shale community. After accounting for dead or discarded skeletal elements, his analyses of species diversity yielded results similar to those from analysis of generic diversity—an important correlation because exclusion of dead individuals significantly decreases the relative contribution of shelly components to the total biodiversity.

Abundance estimates were made through systematic analysis of over 65,000 Burgess Shale museum specimens on over 30,000 slabs, with animals comprising up to 87.9 percent; algae, at least 11.3 percent; and indeterminate material, approximately 0.8 percent (Conway Morris 1986; Briggs, Erwin, and Collier 1994). Typical Cambrian shelly marine taxa (trilobites, brachiopods, monoplacophorans, hyolithids, echinoderms, sponges) account for approximately 20 percent of the genera and less than 2 percent of the individuals. In addition, whereas the Burgess is similar to other Cambrian deposits because arthropods dominate its taxonomic composition, it is different because trilobites compose only a small portion (<14 percent of "living" genera and <0.5 percent of "living" individuals) of these assemblages (Conway Morris 1986). Although only a small portion of the information compiled by Conway Morris (1986) is presented here, it reiterates that the vast majority of faunas inhabiting typical Cambrian marine settings would be unknown were it not for Lagerstätte such as the Burgess Shale.

PALEOECOLOGICAL RECONSTRUCTION

Although most of the soft-bodied forms have been transported, Conway Morris (1986) was able to classify Burgess taxa based on their inferred life habits, feeding type, trophic grouping, and position in a trophic web. In doing so, he noted that the Burgess fauna is dominated by infaunal and epifaunal benthic forms that likely lived on and in the muddy substrates adjacent to their locus of final deposition. Although this does not provide *in situ* information about tiering, commensalism, or related habits, much of this information has been gleaned from careful analysis of the paleobiology and taphonomy of individual specimens.

In general, the infauna appears to be dominated by priapulids, including a variety of mobile forms such as *Ottoia* and sessile forms such as *Louisella.* The epifauna is considerably more diverse, including a variety of attached forms such as the sponge *Vauxia* (Collins 1996b) and the enigmatic *Dinomischus* and *Chancelloria,* as well as a variety of mobile forms reflected by the myriad arthropods such as *Marella* and the problematic *Wiwaxia.* Pelagic additions to the fauna include agnostoid and eodiscoid trilobites (Robison 1972) and rare soft-bodied taxa such as the floating holothuroid *Eldonia* and the actively mobile chordate *Pikaia.*

In addition to these guilds, there is strong evidence for ecologic interactions between members of the Burgess fauna. The sponge *Pirania,* for example, has brachiopods growing on it (Whittington 1985), and the sponge *Choia* is often found in clusters (Walcott 1920), suggesting a gregarious habit. In some cases, postmortem links provide clues about the life habits of faunas, such as occurrences of the sponge *Eiffelia* attached to empty tubes of the priapulid *Selkirkia* (Conway Morris et al. 1982).

Feeding preference is also quite variable, with important benthic assemblages dominated by deposit-feeding arthropods, carnivores, or scavengers dominated by forms such as *Sidneyia,* and epifaunal suspension feeders dominated by sponges and brachiopods (Conway Morris 1986). Feeding habits are based largely on analogy with inferred habits of similar extant and fossil taxa, in addition to circumstantial morphologic evidence such as the predator-like mouth apparatus of *Anomalocaris* and *Laggania* (Whittington and Briggs 1985). Evidence for predation is also inferred by identifiable gut contents, including hyolithids and brachiopods in the gut of *Ottoia* (Walcott 1911d), and trilobites, brachiopods, and hyolithids in the gut of *Sidneyia* (Bruton 1981). Possible scavenging is also suggested from occurrences of the lobopod *Hallucigenia* on top of an undescribed worm (Conway Morris 1977a).

Correlation of the data on inferred life habit and feeding type with respect to numbers of individuals and biovolume suggests that epifaunal vagrant deposit feeders are the most dominant Burgess Shale organisms, with secondary importance of infaunal sessile suspension feeders, nektobenthic suspension feeders, epifaunal vagrant carnivores, epifaunal sessile (high-level) suspension feeders, and infaunal vagrant carnivores (Conway Morris 1986).

Analysis of the trophic nucleus suggests that the Burgess Shale community was quite similar to modern communities, in that it was dominated by relatively few species; 10 percent of the benthic species comprise 91 percent of the individuals and 82 percent of the biovolume of the entire community. A hypothetical generalized trophic web constructed by Conway Morris (1986) indicates that primary consumers are an important component of the Burgess community. Suspension feeders are thought to have consumed phytoplankton and suspended detritus, while deposit feeders may have exploited bacterial and microbial forms, benthic algae, and detritus. Carnivores may have played an important part in this trophic system, as they occupied a high level and account for a large amount of the biovolume of the fauna.

One of the most significant contrasts between the Burgess Shale fauna and other Cambrian assemblages is the significant role of predation, as evidenced by the large number of carnivores and "armored" organisms. Although predatorial borings and bite marks are occasional features of deposits from this interval (Conway Morris and Jenkins 1985; Conway Morris and Bengtson 1994), evidence of predation in other Cambrian deposits may be underrepresented due to lack of preservation of mobile predatory organisms. Because most of the carnivorous or scavenging animals from the Burgess Shale are soft-bodied, they would likely never have been preserved under normal taphonomic conditions characteristic of typical Cambrian deposits.

Niche partitioning and possible food selection by epifaunal vagrant deposit feeders may also be inferred from the Burgess fauna. Whereas data from Cambrian paleocommunities where only skeletonized organisms are preserved suggests that Cambrian communities were ecologically generalized, niche partitioning in the Burgess Shale indicates that they may have been relatively complex. For example, epifaunal tiering by sponges, rare eocrinoids, and pseudo-crinoids may have extended to levels as high as 20 cm above the substrate (Conway Morris 1979b).

CONCLUSIONS

The unusual paleoenvironmental and taphonomic regimes of the Burgess Shale allowed the preservation of a rich soft- and hard-bodied Middle Cambrian fauna. Although not unique, it is certainly one of the best-preserved sources of information on Cambrian life. Whereas this fauna currently has analogues in similar Middle and Lower Cambrian deposits, it is important both in a historical context, because it helped focus attention on the Cambrian radiation, and in a paleontological context, because study of the fauna has revealed myriad new and different taxa, including potential new phyla. More important, the Burgess Shale fundamentally changed the way paleontologists thought about the complexity and diversity of Cambrian paleocommunities because it helped redirect shelly fauna-based thinking about the biota and conditions of the Cambrian explosion (Conway Morris 1989; Aronson 1992).

Despite all the accomplishments that have been made through several generations of work on this deposit, it is striking that many of Walcott's original Burgess specimens have yet to be reexamined or described using modern methods of specimen preparation and dissection. Perhaps the discovery of better preserved specimens in the older Cambrian Lagerstätte in Chengjiang (Chapter 3) and additional Middle Cambrian Lagerstätten in sites such as northern Greenland (Chapter 5) has helped alleviate the need for such work. However, correlation of information from the Burgess Shale fauna with that from other Burgess Shale–type faunas is an obvious focus for future work, and may aid in identifying the signature of the metazoan radiation during the Cambrian, as well as evaluating the role of contingency in early animal evolution. Further insights into Burgess Shale paleoecology might also be made through field-based analysis of fossil distribution within the Burgess Shale, perhaps together with taphonomic information and x-radiographic ichnofabric analyses (*sensu* Gaines and Droser 1999).

ACKNOWLEDGMENTS

I would like to thank D. Collins and S. Conway Morris for their constructive comments, which helped improve this contribution.

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5

Burgess Shale–Type Localities: The Global Picture

James W. Hagadorn

INCREASED AWARENESS OF THE BURGESS SHALE BIOTA HAS led to systematic searching for and accidental discovery of a plethora of soft-bodied faunas throughout Lower and Middle Cambrian strata all across the globe. Many of these soft-bodied forms are known from the Burgess Shale or are closely allied with taxa from the Burgess Shale. Over the past 30 years, these Burgess Shale–type faunas have been documented throughout the Cambrian, as well as from Ordovician and Silurian strata. In some cases, such as Chengjiang (Chapter 3), these faunas have actually begun to approach or eclipse the paleontological impact of the original Burgess quarries.

Furthermore, as this awareness peaked, many obscure, previously undescribed, or isolated soft-bodied specimens from other deposits were recognized as Burgess Shale–type faunas and have been placed into a larger-scale paleobiologic context (e.g., Parker Slate and Kinzers Formation biotas) (Conway Morris 1993; Garcia-Bellido Capdevila and Conway Morris 1999). Although the faunal abundance and preservation in many of these deposits is less than that in the Burgess Shale, many of them have provided additional information about soft-bodied paleocommunities that inhabited a wide range of paleoenvironments during the Cambrian explosion.

Like those in the original locality, Burgess Shale–type faunas are usually preserved in shales, exhibit a range in preservation from exceptional articulated specimens to disarticulated fragments, and were formed by a combination of taphonomic scenarios (e.g., obrution and stagnation). In general, Burgess Shale–type deposits are dominated by nontrilobite arthropods, with a large contingent of priapulid worms, a diverse array of sponges, and a minor assortment of sclerite-bearing lobopodians. Based on these taxa, key observations about the distribution, temporal persistence, mode of life, and identity of soft-bodied faunas have been made, in addition to hypotheses about early animal evolution. Some of these observations are presented in this chapter, as well as a brief review of the key features of the major Burgess Shale–type localities (for a more thorough overview, see Conway Morris 1985, 1989b, and references therein).

GEOLOGICAL CONTEXT

This chapter utilizes a broad definition of a Burgess Shale–type locality, which includes deposits with articulated soft-bodied taxa that are also known from the Burgess Shale, as well as other Cambrian soft-bodied occurrences that may contain different nonmineralized taxa. For taphonomic studies, however, it is probably more prudent to delimit Burgess Shale–type deposits by their mode of preservation (Butterfield 1990b) than by the occurrence of a shared fauna or simply by the presence of soft-tissue preservation, which may have occurred through different taphonomic pathways (Butterfield 1994). Because a strict taphonomic definition eliminates many isolated occurrences of shared taxa, which extend the geographic and temporal range of Burgess Shale taxa, and because these occurrences are utilized in many of the phylogenetic and evolutionary studies focusing on Burgess Shale–type taxa (see "Paleoecology"), these shared taxa occurrences are included in this chapter.

Burgess Shale–type biotas have been documented from at least 40 Cambrian localities distributed across every continent except Antarctica and South America (Conway Morris 1989b, 1990; Allison and Briggs 1991, and references therein) (Figure 5.1). In the Cambrian, most faunas occur in strata ranging in age from the Atdabanian Stage of the Early Cambrian to the top of the Marjuman Stage of the Middle Cambrian (Conway Morris 1989a; Allison and Briggs 1991). A few Burgess Shale–type assemblages are also known from the Upper Cambrian, Ordovician, and Silurian, but most of these younger occurrences consist of isolated specimens (Dawson and Hinde 1889; Dawson 1896; Rigby 1986b; Barskov and Zhuravlev 1988).

Conway Morris (1989b) thoroughly reviewed the geographic distribution of Burgess Shale–type faunas and noted that the majority of these taxa come from a dozen or so well-exposed highly fossiliferous localities, which will be briefly discussed. Although not covered here, isolated occurrences of more common Burgess Shale–type taxa are known from exposures in England (Breadstone and Shineton Shales; Whittard 1953), Sardinia (Vasenapov Suite; Repina and Okuneva 1969), Spain (Murero

FIGURE 5.1 Distribution of most of the Burgess Shale–type localities (indicated by dots). (Modified from Conway Morris 1989a)

Shale; Conway Morris and Robison 1986), eastern Siberia (Chabdy Suite; Krishtofovich 1953; Barskov and Zhuravlev 1988), north-central Russia (Chopko, Lena, and Sinsk Formations; Voropinov 1957; Goryansky 1977; Rigby 1986a; Barskov and Zhuravlev 1988), Guizhou Province, China (Kaili Formation; Zhao 1994), and Quebec, Canada (Metis Shale; Dawson and Hinde 1889; Dawson 1896), as well as from deposits in California (Carrara Formation; M. Vendrasco, personal communication, 1999), Idaho (Gibson Jack Formation; Robison 1984) (Rennie Shale; Resser 1938), Nevada (unit B7; Stewart and Palmer 1967) (Pioche Shale; McCollum 1994) (Emigrant Formation; Hagadorn 1998), and Utah (Bloomington Formation; Briggs and Robison 1984) (Ute Formation; Briggs and Robison 1984). Many of these localities are relatively nonfossiliferous (e.g., Pioche and Latham Shales), and many are no longer available for paleontological inquiry, due to their subsurface nature (e.g., Zawiszyn Formation), infilling of quarries, or burial by housing developments (e.g., Kinzers Shale, Parker Slate of the eastern United States) (Campbell 1969).

PALEOENVIRONMENTAL SETTINGS

Many Burgess Shale–type localities were characterized by depositional environments broadly similar to those of the original Burgess Shale. Faunas tend to have been deposited in relatively deep settings at or below storm wave base (Rees 1984; Robison 1991), where periodically dysaerobic bottom-waters, anaerobic sediments, and clay–organic interactions coupled with rapid burial may have mediated exceptional soft-bodied preservation (Conway Morris 1989b; Butterfield 1990b; Briggs and Fortey 1992; Allison and Brett 1995). In Laurentia, for example, most localities occur on the seaward side of a large carbonate platform that extended along the Laurentian margin during much of the Cambrian, in settings broadly interpreted to reflect outer shelf environments (Palmer 1960; Robison 1960; overviews in Conway Morris 1986; Conway Morris 1989a, 1989b). Soft-bodied fossils are typically preserved within or at bed interfaces of graded mudstone and siltstone units deposited adjacent to these carbonate banks or in a deep subtidal outer shelf-type setting. Fossils occur in beds with sharp or erosive bases, both in uniformly oriented concentrations on bed surfaces and in quasi-randomly oriented positions within beds. In most cases, Burgess Shale–type deposits reflect deposition outboard of this bank. In a few instances, however, such as the upper Wheeler Formation in Utah and, perhaps, the Mount Cap Formation of northwestern Canada, fossils were deposited landward of the carbonate platform, in a relatively quiescent, muddy subtidal environment (Palmer 1960; Robison 1960, 1984, 1991; Brady and Koepnick 1979; Rees 1984, 1986; Rogers 1984; Butterfield and Nicholas 1996). The Latham Shale faunas of California also may have been deposited in a similar inner detrital belt setting (Briggs and Mount 1982).

Outside North America, there appears to be significantly more variety in paleoenvironments that preserve Burgess Shale–type faunas. An exception to the Laurentian-style deposition that characterizes many of the deeper subtidal Burgess Shale–type localities (e.g., Chengjiang) is the finely laminated siltstones and mudstones of the Soom Shale of South Africa. Because it conformably overlies glacial tillites, the Soom Shale was probably deposited under anoxic conditions in a glacioestuarine to shallow-marine environment, at the initial phase of a glacioeustatic rise in sea level, through turbiditic deposition of outwash silts and muds from retreating glaciers (Theron, Rickards, and Aldridge 1990).

The Venenäs Conglomerate fauna of southeastern Sweden may also represent a paleoenvironmental anomaly, as quasi-Burgess Shale–type faunas occur in sandstones, rather than in finely laminated shales (Pompeckj 1927; Jaeger and Martinsson 1967; Krumbiegel, Deichfuss, and Deichfuss 1980). Unfortunately, soft-bodied fossils are known from only glacial erratics, so little is known about the paleoecology or paleobiology of soft-bodied faunas that may have been living in or adjacent to these coarser clastic Early Cambrian environments. At the one outcrop of this unit, only biomineralized fossils such as *Mobergella* are preserved and occur in calcite-cemented, medium-grained, well-rounded sandstones (Bengtson 1968). Fossils are preserved throughout the conglomerate,