The

Evolutionary Significance of the Burgess Shale and its Taphonomy

PhD Preliminary Examination

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The Burgess Shale is a significant paleontological site from a variety of viewpoints. Perhaps the most outstanding of its attributes is the preservation of animals that only consisted of soft tissue. Fossilized organisms with hard shells, body parts, or exoskeletons made of chitin, are plentiful. Fossilized soft tissue, however, had not been available in any meaningful amounts until the discovery of the Burgess Shale Deposits. These deposits provided a more accurate picture of the diversity of the early Paleozoic and gave paleontologists a better feel for the complexity of the Cambrian explosion.

The Burgess Shale has a very romantic history for paleontologists. It begins in the 1870’s when a survey was being done to determine the route of the trans-Canada Railway through the Canadian Rockies at British Columbia. One of the survey team, Otto Klotz, reported finding large numbers of “stone bugs” in the mountain areas around Mt. Stephens. An American scientist, Charles Walcott, a paleontologist from the Smithsonian Institute, was doing some work north of that area at the time and heard about this description. He made it a point to go through there and take a look around on the way back from his research area in 1909. The story goes that he had to take one of the small trails in the mountain by horseback with his wife accompanying him. In one area on Mt. Wapta, Walcott’s wife’s horse slid off the trail and kicked a stone that split open, revealing a Marrella. Whether or not this story is accurate is questioned. In any case, he immediately began to invest a great deal of time and effort into studying the Burgess Shale and amassing an enormous collection for the Smithsonian. He brought back about 80,000 specimens, most of which remain uncatalogued and still reside in crates within that institution (Gould, 1989). During the ten years that he worked at the Burgess Shale
site, he named or described most of the organisms preserved in that area. Although a
great deal of controversy has remained about his designations, he clearly had a most
profound influence on dealing with that collection of specimens. Other major
contributors to the exploration of the Burgess Shale site were: Percy Raymond in 1930,
who was also a curator at the Pittsburgh Museum but at Harvard at this time; Harry
Whittington, later replaced at Harvard by Stephen Jay Gould, working at Cambridge
since the 1960’s; Simon Conway Morris and Derek Briggs, of Cambridge, who started in
the 1970’s; Des Collins from the Royal Ontario Museum, working in 1975 (Gould, 1989;
Gadd, 1946). All of their names will be prominent in any research of the Burgess Shale.

Location

The Burgess Shale is located on Mt. Wapta in the Canadian Rocky Mountains on
the eastern border of British Columbia just west of Calgary, Alberta. It is preserved in
Yoho National Park and designated as an Internationally Protected Site. Mt. Wapta is to
the north. Across the river and to the south, above the town of Field is Mt. Stephens,
another Internationally Protected Site and Burgess Shale-type preservation.

What is meant by Burgess Shale and BST designation
The term Burgess Shale has taken on a much more significant meaning than simply a place designation or geologic formation. Anyone familiar with paleontology who hears the term immediately thinks of the special attributes that go along with that site. It is also used as a descriptive term in referring to similar preservation sites all over the world as Burgess Shale-Type (BST). Another term frequently associated with this designation is lagerstätten. This was originally a German term meaning any geologic deposit of economic value. It follows, then, that a fossil lagerstätte is a deposit of fossils of value (Martin, 1999). That designation can be further broken down into two divisions: one being a conservation lagerstätte which includes unusual organisms; or a concentration lagerstätte that includes a large number of organisms (Gaines, 2005b, Martin, 1999, Caron, 2004). The Burgess Shale obviously fits both categories.

**Time**

The time period that defines the Burgess Shale preservation site is 530 million years ago. It is generally associated with the leveling off in increasing diversity of the Cambrian explosion which lasted from 540 to 525 million years ago (Conway Morris, 1986). Other similar sites are of a similar time frame. It is estimated that the Chengjiang site in China dated to about 10 million years earlier (Hagadorn, 2002). The Wheeler Formation in Utah is also considered mid-Cambrian (Gaines, Kennedy, Droser, 2005b).

The variety of organisms appears to be extraordinary. It has been estimated that 100 genera are represented in the middle Cambrian Phyllopod Bed (Conway Morris, 1986), which is the unit originally explored by Walcott (Whittington, 1985). A more
recent estimate is that 158 genera were in that setting (Caron, 2006). The more
significant aspect of these organisms is that 70 percent or more were soft-body
organisms. Another source states 86% were soft-bodied (Briggs, Erwin, Collier, 1994).
The preservation of those organisms without hard parts, such as bony skeletons, shells or
chitinous parts, is very rare. The conditions that must exist to effect such preservation
are extraordinary. In general, most fossils found do contain those hard parts, as these are
more readily fossilized. The result is a skewed fossil record of hard- versus soft-bodied
organisms, giving a false picture of the past (Conway Morris, 1986). The Burgess Shale
and similar sites give paleontologists the opportunity to observe the extensive diversity
that existed at these unusual sites, and thus obtain a better picture of the time. It is
estimated that the Burgess Shale site alone contains 15 to 20 phyla of the possible 32
known to date (which may be a loose estimate) (Gould, 1989). On the other hand,
several phyla appeared that do not fit into any modern group (Martin, 2004, Ausich,
1999). The significance of this finding is the previously unrecognized possibility that the
diversity of life today, at least at the phylum level, has been on the earth since the
Cambrian explosion.

Environment

The environment of the Burgess Shale fauna was marine and described as “a
single benthic community” (Conway Morris, 1986). Conway Morris designated it to be a
“Marella-Ottoia community” because of the large numbers of those two species of
epifaunal arthropods and infaunal priapulid worms. He also designated the Amiskwia-
Odontogriphus community as another. This group was a pelagic community that was
buried “infrequently by turbidity currents.” In a higher formation, the Raymond Quarry, a different “benthic assemblage from the Marella-Ottoia community of the Phyllopod Bed was identified.” (Conway Morris, 1986) This assemblage was the more typical group found in the surrounding areas at Mount Field and Mount Stephens. Conway Morris made the point that most of the taxa were found in all areas, but the proportions varied from site to site.

Briggs, et al, describes the varying habitats, occupying the different niches (tiering) of nektonic, epifaunal and infaunal distribution. He states that “most of the Burgess Shale animals lived on the surface of the sediment.” The priapulids Ottoia and Louisella, worm-like animals, were infaunal along with the polychaete Burgesschaeta, another worm-like organism. The Eldonia, or holothurian, (jellyfish-like organism) was Pelagic. The sponges Vauria, Choia, and Pirauia, along with the remaining 30% of organisms classified as filter feeders, fed at levels above 10 millimeters. Deposit feeders, which made up about 60% of the organisms, were confined to the sediment. Predators, including Anomalocaris, Yohoia, Santacaris and Marrella, along with scavengers, made up the remaining 10%. Briggs, et al, calculates the biomass of each of the three categories as being “nearly equal” (Briggs, et al, 1994).

It is noted in reviewing the characteristics of many of the individual species that the same strategy of tiering is obvious in the Burgess Shale. What was previously thought to be a crinoid, Echmatocrinus, represented a different feeding strategy, i.e., at a different height (8 cm) above the sediment. Echmatocrinus is now thought to be an unclassified species (Simms, 1999). Gogia, a cystoid, although somewhat similar in feeding habit, was at a lower level of about 2 cm above the floor.
Predators play a role as well. For example, *Sidneyia* is an organism, and incidentally the only one, that showed definite evidence of ingesting hard-shelled organisms. Some prey were well armored such as *Habelia*. Many were adapted as sediment feeders with dorsal shells of varying designs and shapes to guard against predators. Of course, each species had adaptations for feeding as well as adaptations for defense (if prey) or for attack (if predator). The list is too long to totally describe here, but a great deal is known about many of these organisms and a fairly detailed description of the total inter-related picture is now possible.

**Sedimentary Environment**

Given the extraordinary preservation event at the Burgess Shale site and at other areas of similar character, some attention must be given to the geologic circumstances that facilitated this occurrence. During the Cambrian, the continents were in much different positions than today. Although paleomagnetic dating has been very helpful in reconfiguring the continents during the Mesozoic and Cenozoic, it is not so accurate during the Paleozoic and especially the Precambrian time period (Kearey et al, 1996) (Palmer, 1974). Even with that uncertainty, estimates have been made as to the positioning of the continents involved. A great deal of the global land mass was aggregated into Gondwanaland. Another smaller continental unit, Laurentia (which was comprised of modern-day North America, Greenland and other North Atlantic land masses), was located in a more isolated position. All of the land masses lay along the equatorial belt. Today’s position of Hudson Bay, in relationship to that land mass, would
have been at about the center of Laurentia. Most of Laurentia was submerged in shallow seas, resulting in the deposition of the sedimentary structure we see in the Burgess Shale area. Regressions and transgressions created the interdigitation of limestone, dolomite, sandstone and shale that we see there today (Whittington, 1985). Although this work will refer to this area known as the Burgess Shale, this reference is to the much broader expanse which includes the entire studied area around Field, Canada.

The Burgess Shale stratigraphy is dominated by a 250-meter carbonate escarpment with these bedded dolomites. This is called the Cathedral Limestone formation. At the base of that escarpment is a carbonate debris formation called the Takkakaw Tongue. Layered up from that tongue on the escarpment face are several layers of shale, all considered to be the Burgess Shale formation. Each one of these layers has various surface exposures today which contain fossil combinations that are unique to each particular area. Each are named, such as the Walcott Quarry Shale member, the Raymond Quarry Shale member, the Emerald Lake Oncolite (an ooid formed by non-calcifying microbes coating the grain surfaces and collecting sediments in successive layers) member, etc. This entire formation, called the Burgess Shale, is about 350 meters thick including the Marpole Limestone member, which caps the entire structure, as well as the Cathedral Escarpment. An additional cap above that which extends over the entire area is designated the Eldow Limestone formation. The Stephens Formation is more to the east of the Cathedral Limestone but still lies beneath the Marpole Limestone (Hagadorn, 2002).
The climate of the Burgess Shale appears to have been tropical due to the location about 15 degrees north of the equator, allowing for its distribution of fauna, according to Conway Morris. These conditions must have been the same for the entire continent, thus providing widespread potential for similar deposits. Indeed more deposits are being discovered which seem to confirm that (Conway Morris, 1986). Other examples that
have been studied include the Wheeler formation in Utah, the Pioche formation in Nevada (Liberman, 2002) and the Conasauga formation in Georgia (Schwimmer, 2002). In addition, the particular characteristics of the Cathedral Escarpment may have been of particular value the potential for preservation that it provided. This combination of features, a high escarpment with a deep drop, may have been widespread especially around the continent of North America. There appears to be a consistent boundary between carbonate and other detrital sediments around that land mass (Palmer, 1974). Today those areas are covered with the Sauk Sequences that accumulated during the latest Precambrian to Ordovician time periods (Sloss, 1963, Aitken, 1993, Bailey, 1989).

The environment for deposition and preservation is somewhat debated. It appears that the Cathedral Escarpment was a reef structure, as described by the Canadian Geological Survey (Whittington, 1985). There had been some debate that it was a fault structure, but that was rejected on the basis that the Eldon Formation above it was not disturbed (Whittington, 1985). The area in front of it is filled with fine sediment and varying-sized fragments of limestone from the face of the escarpment. The organisms involved are thought to have lived on that debris field of fine sediment.
Conway Morris (1986, 1990) describes a three-phase depositional sequence for burial that he labeled the “pre-slide environment, the transport of fauna and the post-slide environment.” In the pre-slide environment, some further question exists as to whether the organisms found there were completely indigenous to that sediment at the base of the escarpment or whether some might have originated from the top of the escarpment. Subsequent studies have shown that the trilobites found on the upper surface of the Cathedral escarpment were the same age as those found in the Stephens formation (Whittington, 1985). The environment of the sloping sediments was within the photic zone of about 100 meters. Again controversy has arisen about the necessity of well-oxygenated environments for the growth of the organisms involved. Contrary to some
suggestions, organisms can do well in lower oxygen environments (Conway Morris, 1986). In any case, as slumping occurred down the slope, an anoxic environment would have been the eventual circumstance.

Figure 4. Conway Morris’s concept of a three-phase depositional environment. (Conway Morris, 1986)

Slumping down the slope is the theory of burial as described by both Whittington and Conway Morris. Whittington describes previous slumping that was so dramatic that transatlantic cables were destroyed by its force. Slumping events might have been triggered by earth tremors or even by debris falling from the face of the escarpment (Whittington, 1985). The number and frequency is not known, but according to Conway
Morris (1986) “if each graded bed of the Phyllopod Bed represents a separate slump, the estimated total of fifty presumably corresponds to the number of events.”

The transport of organisms is presumed to have been a low energy event. Fragmentation, although present, was not dramatic. Positioning of the organisms was somewhat randomized, with some exceptions. Elongated organisms, shaped in a way to establish flow resistance, appeared to be lined up with the flow. Flat organisms such as trilobites showed a tendency to stay flat and upright. Some of the predominately elongated soft tissue organisms were “folded” and “contorted” according to Conway Morris. Whittington (1985) goes through a good bit of effort to show that the sediment must have been very fine and could flow between the extremities and into the gut, as evidenced by the preservation of small delicate parts such as gills and legs and antennae. According to Martin (1999) organisms can avoid disarticulation for many hours between death and movement. The degree of fragmentation depends on the degree of decay of the animal. In contrast, hard tissue can survive up to 30 days before diagenesis (Briggs, 1993).

The post-slide environment was that of burial by the sediments and of anoxic conditions. There was no bioturbation or scavenging, and some pyrite-filled structures were found, thus indicating a lack of oxygen. Rapid burial was the other major factor. Two factors are involved with the rapidity of burial: one is the amount of sediment needed to immobilize the organism. Larger amounts resulted in more pressure upon and flattening of the organisms (Whittington, 1985). Specimens of Marrella often show a dark
stain projecting posteriorly which has been analyzed and found to contain amino acids and other body fluid chemistry. This is presumed to be extruded body fluids because of compression (Whittington, 1985). The other is the stunning effect of the burial. Some feel that the slumping event was dramatic enough that the organisms were either stunned or killed as a result. No evidence of escape structures or of the coiling which accompanies the death of many organisms such as trilobites, would seem to confirm that rapid burial. Conway Morris also suggested two other factors to be considered: osmotic shock (salinity differences) and thermal shock (sudden temperature change) (Allison, 1993, Allison, 1995, Aronson, 1992).

Preservation of the organism in the environment requires a somewhat complex set of circumstances. The common term of obrution, “catastrophic burial and smothering” (Martin, 1999), appears to be an oversimplification of the process. The anoxic environment would have precluded the presence of any aerobic bacteria. However, anaerobic bacteria would not be affected by oxygen deprivation. Decay of organisms occurs with anaerobic bacteria. According to Butterfield (1990, 1995, 1996, 2002), “Powerful anti-enzymatic and/or stabilizing effects of clay minerals on organic molecules…account for Burgess Shale-type preservation.” According to Hagadorn (2002), “replacement [of soft tissue] by clay minerals is not well constrained, replacement may have been catalyzed by bacteria, by variations in the composition of decaying tissues, and/or by variations in pore water chemistry” (Orr, et al, 1998, 2003). As is the case with much of the Burgess Shale-type phenomena, contradicting theories exist regarding this, as well. Powell, et.al., suggests that oxygen was actually present in
the bottom waters during the fossilization process of the Burgess Shale and must be taken into consideration in explaining the preservation (Powell, 2003). Hagadorn (2002) goes on to explain that geologic features of the area may have aided the preservation process; i.e., the escarpment itself may have provided a shielding effect to protect the area from tectonic or metamorphic influences. Particular damage done by shifting the preservation site around was thus avoided.

It must be emphasized that the exact process of some of the preservation is still unknown (Gould, 1989; Lin, 2006). A considerable amount is known, however, about preservation in this type of environment. The three processes of permineralization, petrifaction and replacement are often cited as the methods of fossilization. Permineralization is the filling of the cavities, to provide internal molds; petrification is the addition of minerals to the hard parts; and replacement is the final step of the preservation (Martin, 1999). It is noted by Martin (1999) that the term petrifaction and permineralization are used “synonymously.”

Pyritization is commonly associated with permineralization. This typically occurs early in the process of diagenesis. At depths with increasing organic materials and decreased oxygen, bacteria have anaerobic respiration. Sulfate is reduced: $2\text{CH}_2\text{O} + \text{SO}_4^{2-} \rightarrow \text{H}_2\text{S} + 2\text{HCO}_3^-$. $\text{H}_2\text{S}$ combines with iron to produce $\text{FeS}$. Martin (1999) states that rapid burial decreases the effect of sulfate production that normally oxidizes about “50% of organic matter in the near shore sediment.” As the burial sites get deeper with larger amounts of sediment the organisms are exposed less to oxygen environments.
Again the lack of bioturbation does not allow for the further exposure of oxygen to the buried structures.

With the slowing down of decay of soft tissue, pyrite is deposited. It can infill cavities of the organism; it can replace other detrital grains that are already in those cavities; and it can also encrust onto the surface of the organisms (overpyrite). The formation of pyrite depends on the concentration of inorganic carbon, dissolved sulfate and iron minerals. In marine environments, \( H_2S \) is plentiful from the anaerobic sulfate production. Iron may be the limiting factor (Allison, 1990). The process of pyritization occurs early and relatively quickly (80 days in some conditions). This provides a protective film over the organism and within its cavities, thus playing a major role in preservation (Zhu, 2005).

A question comes up regarding the sequence of steps in the process. After pyritization, occlusion of porosity, thus permeability, may occur by calcite cementation that is facilitated by microbes. The pyrite confirms the alkalinity that is necessary for carbonate cementation is present. Delta C\(^{13}\) values, however, indicate detrital sources for the carbonate and not organic matter. From that it could be assumed that there are multiple stages of carbonate cementation. The initial, microbial facilitated cementation, and a later, later stage of cementation from other sources. This would require that porosity must have been, at least, somewhat preserved until these later stages (Vorhies, 2005, Orr, 2003). This would be in line with the thinking that soft parts decay would not produce the amount of calcium necessary for fossilization which is in contrast with those
organisms with hard parts (shells, skeletons, etc.) that provide a much more adequate level of calcium (Martin, 1999).

Iron carbonate has also been shown to play a role in preservation of soft tissue. In some of the Chengjiang fossils the iron oxides on the surfaces of fossils may have been preceded by iron carbonates. This usually takes place in fresh water, however. It is proposed that sporadic inflows of fresh water might have provided those conditions. It has also been found that siderite (iron carbonate) has been found in marine clay, so that may have been a potential source (Zhu, 2005).

Phosphatization can also play a role in diagenesis of soft tissue. Although it is usually associated with skeletal material preservation, soft tissue “may be diagenetically altered to phosphate if there is enough organic matter available” (Prevot, 1990). This is also discussed by Zhu (2005). The release of CO$_2$ and H$_2$S during the beginning of dysaerobic organic decay caused a decrease in pH around the organism. This led to precipitation of francolite (carbonate-fluorapatite). Precipitation of apatite is controlled by the concentration of phosphorus. Phosphorus is normally lacking in this kind of environment but may be provided by the decaying organism. The apatite replaces and preserves the shape of carbonate structures such as shells. It can also “preserve morphological details that are easily lost within hours of the onset of decay” (Zhu, 2005) in soft tissue (Prevot, 1990).

Of all the types of preservation, silicification is probably the most difficult to explain in this environment. This process is more common in the fossilization of plants,
but seems to play a role in the Burgess Shale-type sites. Those fossils such as trilobites and brachiopods with shells have replacement of those structures with muscovite and chlorite, both of which contain silica. The difficulty comes in explaining how silification occurs in soft tissue. Indeed, Lin, et al., (2006) and Gould (1989) both state that process is unknown. According to Papanoeclous (2004 a&b), the soft tissue fossils contain also contain muscovite and chlorite, both sheet silicates. His study shows that the same silicate composition was present in the matrix. His conclusion was “that sheet silicate replacement of fossil diagenesis and metamorphism must have been bulk rock chemistry rather than pore-water composition” (Papanoeclous, 2004 a&b). The source of the silica is likely to be volcanic, which was prevalent in the west during the Precambrian (Martin, 1999). The silica could also come from evaporate. Hydrothermal vents along with geothermal gradients could have provided silica, if not provided with evaporates. Martin (1999) describes the association of pyritization and silification as found in aerobic conditions in later periods, and suggests that these findings may offer some insight into the dilemma of silification in the Burgess Shale-type sites.

Carbonization is a very prevalent method of preservation in the Burgess Shale. These are non-mineralized fossils that are left behind as carbon films. They are not replaced nor preserved as molds (Gaines et al, 2005a) (Gaines et al, 2005b). According to Gould (1989), “The soft parts are not preserved as carbon. By a chemical process not yet understood, the original carbon was replaced by silicates of alumina and calcium, forming a dark reflective layer.” In fact, Whittington spends a great deal of time
dissecting down through the various layers of different organisms (especially Marrella) to discern further details of underlying anatomy (Whittington, 1985).

**Conclusion:**

The outstanding characteristic of the Burgess Shale-type preservation that attracts so much attention is the preservation of soft tissue. Most preservation processes involved hard parts such as exoskeletons, shells, bones, and teeth. That process is comparatively more common since it is easier to effect. Those hard materials are more resistant to destruction after the death of the organism and are more likely to be buried under less extraordinary circumstances than the Burgess Shale-type sites. Once buried, they are less prone to decay, at least rapidly, so are likely to persist longer. This allows for deeper burial into conditions that allow for preservation. They also provide a more resistant matrix for permineralization or replacement.

Soft tissue preservation is much more difficult, resulting in much more rare preservation. This skews the paleontological record toward the organisms with hard parts which can only leave the biological history to speculation. The Burgess Shale-type sites provide an opportunity to see those spectrums of organisms that existed at least at those sites. This provides a look at the diversity of the age which allows more accuracy for the biology of that period (Whittington, 1985). Conway Morris voiced concern that the Burgess Shale preservation may be overrated. He explains that the process itself may filter out certain groups of animals and not really preserve a true cross section of
organisms. It could be a selective process that should be considered in using this information in “paleoecological analysis” (Conway Morris, 1986).

The special condition of rapid burial in anoxic environments that is often stated as THE method is probably over-simplified. Much of the controversy that exists about this special preservation indicates much more is to be learned. It is also likely that different sites may have variations on the known types of preservation. Different circumstances may promote different methods of soft tissue preservation.

As has been stated by many authors (Gould, 1989; Briggs et al, 1994; Whittington, 1985), it is likely that many such sites lay undiscovered, as is being confirmed by the increasing numbers of such sites around the world. Certainly the impact of the newer sites will not be the same. The Burgess Shale gave the paleontological community its first indication of the substantial diversity in the Precambrian era. This created an entirely new direction in perspective which does not happen often.
Bibliography


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