Extraordinary Fossils

Occasionally circumstances conspire to put flesh on the bones of the skeletal fossil record, thus leaving a vivid snapshot of an ancient world

Derek E. G. Briggs

Etched in the fossil record is nature's chronicle, a history of life on earth. Some of these fossils tell of lives lived and extinguished hundreds of millions of years ago, long before the advent of humankind. But nature is a biased scribe, an unreliable reporter, and nature's chronicle tells only part of the evolutionary tale. The process of fossilization itself inevitably skews the information in the fossil record. Only a fraction of the myriad creatures that have lived on the earth have left behind traces of their existence, and only specific parts of those organisms have been preserved.

Nature relies on recycling. Soft tissues, the fleshy parts of animals' bodies, are a rich source of nutrients and are consumed by predators, scavengers or micro-organisms. The soft parts are thus least likely to be preserved as fossils. More likely to be fossilized are mineralized tissues such as shells, bones and teeth, as well as heavily tanned or sclerotized arthropod skeletons; among plant tissues wood and certain kinds of cuticle are the best candidates for fossilization. But a decay-resistant skeleton is no guarantee of preservation, as skeletons too are broken down by physical and biological agents. Occasionally, however, some unusual combination of circumstances brings an extraordinarily clear message from the geologic past: a fossil specimen in which we can see the form of soft tissues.

For years many paleontologists considered extraordinary preservations of soft body parts little more than curiosities. They provided exciting and striking images of fossils, certainly, but their study was somewhat on the fringe of mainstream paleontology. This attitude is changing, however, and extraordinary fossils are moving increasingly to center stage. Soft-bodied fossils are turning out to have just as important a story to tell as the more familiar shells and bones.

When fossils preserve soft tissues, an astonishing amount of additional information becomes available. Extraordinary fossils provide three kinds of data beyond what can be read in the shelly fossil record. They give us insight into the morphology and relationships of organisms otherwise known only from problematic hard parts. They illuminate the nature and distribution of soft-bodied organisms, and they show us the complete diversity of ancient communities. In addition, some extraordinary fossils are a source of preserved biomolecules from which we may be able to glean information on taxonomic relationships and rates of evolution, as well as clues to the environment in which an organism lived.

Quantity vs. Quality

Occurrences of exceptional fossils have been grouped into two main categories: concentration deposits and conservation deposits (Seilacher, Reif and Westphal 1985). Concentration deposits are remarkable for the sheer abundance of material preserved, if not for the type of this material. They represent accumulations of skeletal remains over long periods of time where the associated sediment is either winnowed away by currents or deposited in very small quantities in the first place. Examples include ammonite coquinas and oyster beds, as well as bone beds and fissure and cave deposits.

In conservation deposits it is the quality of the preservation of the specimens that is significant. At one end of the spectrum the preservation of a single complete skeleton may be exceptional enough to warrant inclusion in this category, as, for example, the preservation of a complete starfish or crinoid skeleton. The skeletons of these echinoderms consist of large numbers of unfused plates, or ossicles, that are readily scattered after only a few days because the soft tissues decay. Their preservation intact is rare; when it happens, it is often the result of rapid burial by storms. At the other end of the spectrum are conservation deposits that preserve the soft tissues of organisms, the "extraordinary" fossils that are the focus of this article.

Perhaps the best known example of an extraordinary conservation deposit is the Burgess Shale of British Columbia. The Burgess Shale preserves an astonishing range of marine organisms including algae, sponges, various worm-like creatures, arthropods, the earliest chordate, and a variety of peculiar animals with no obvious parallels in today's oceans. Its middle Cambrian age, over 530 million years old, means that it provides an important window on the results of the Cambrian explosion, during which most of the major groups of metazoans evolved. The 300-million-year-old Mazon Creek deposit from southwest of Chicago provides a

Derek E. G. Briggs is Reader in Palaeobiology at the University of Bristol in England. He received his bachelor's degree from Trinity College, Dublin University, and his Ph .D. from the University of Cambridge, where he worked on the Burgess Shale. He is a research associate of the Royal Ontario Museum in Toronto. His major research interest is in the taphonomy and evolutionary significance of exceptionally preserved fossil biotas. This involves a range of approaches, from experimental work on the factors controlling decay and fossilization, through studies of early diagenetic mineralization, to field work on a range of extraordinary fossil occurrences in North American and Europe. He has recently edited Palaeobiology—A Synthesis, *with Peter Crowther. Address: Department of Geology, University of Bristol, Wills Memorial Building, Queen's Road, Bristol BS8 1RJ, England.*

Figure 1. Extraordinary fossils—those in which soft tissues have been preserved—provide striking images of ancient organisms such as the frog *Messelobatrachus*, which lived during the Eocene epoch, some 40 to 50 million years ago. The outline of soft tissue can be seen in this *Messelobatrachus* specimen from the Messel deposits near Frankfurt, Germany. Once valued chiefly as curiosities, soft-bodied fossils have become the source of insights into the nature, distribution, morphology and taxonomy of soft-bodied organisms, the diversity of ancient communities, rates of evolution and the environments in which ancient organisms lived. This specimen has been isolated from a matrix of oil shale by a process that transferred it onto an artificial resin. (Except where noted, all photographs courtesy of the author.)

unique view of life in the late Paleozoic (Pennsylvanian). It includes more than 350 animal and about 100 plant species from a wide range of environments, terrestrial to near-shore marine, preserved in iron carbonate (siderite) nodules. A more recent example is provided by the Eocene Green River Formation, the deposit of large lakes that extended over a wide area of Wyoming, Utah and Colorado about 40 million years ago. These lakes were permanently stratified with cool bottom waters low in oxygen. The spectacularly preserved biota is dominated by fishes, insects and plants.

Making Fossils

The normal fossil record of shells, bones and teeth gives a very incomplete picture of life in the past, particularly in the case of land biotas, where the potential for burial and fossilization is very limited. Even in shallow marine settings, where sediment transport and deposition increase the chances of preservation, the original ancient community is usually represented only by those animals with a mineralized skeleton.

The completeness of shelly fossil assemblages has been assessed in a seminal study by the late Tom Schopf of the University of Chicago, who considered the potential for preservation of the living intertidal fauna (Schopf 1978). He studied macroscopic organisms from three habitats—rock, mud and sand—at Friday Harbor, Washington, and obtained similar results for all three. About 30 percent of the organisms had a robust mineralized shell or tube, which would be expected to yield many identifiable fossils. Another 40 percent had fragile, largely unmineralized skeletons or hard parts, and therefore had a low preservation potential. The remaining 30 percent lacked any mineralized tissue and would not be expected to fossilize at all under normal conditions. Schopf found that although a full 70 percent of the Friday Harbor genera have some mineralized tissue, only 40 percent are known as fossils. It is clear from such studies that having a skeleton by no means guarantees fossilization.

Relative completeness can also be assessed by comparing extraordinary fos-

eon	era (duration in millions of years)	period	subperiod	epoch	years ago (millions)	exceptional fossil occurrences referred to in the text
Phanerozoic	Cenozoic (65)	Quaternary (1.64)		Holocene	0.01	
				Pleistocene	1.64	
		Tertiary (64)		Pliocene	5.2	
				Miocene	23.5	
				Oligocene	35.5	
				Eocene	56.5	Messel, Germany Green River, Wyoming
				Paleocene	65	
	Mesozoic (180)	Cretaceous (81)			146	Santana, Brazil
		Jurassic (61)			208	Solnhofen, Bavaria Christian Malford, England
		Triassic (37)			245	Grès à Voltzia, France
	Paleozoic (325)	Permian (45)			290	
		Carboniferous (73)	Pennsylvanian (33)		323	Mazon Creek, Illinois
			Mississippian (40)		363	Granton, Edinburgh, Scotland
		Devonian (46)			409	Gilboa, New York Hunsrück, Germany
		Silurian (31)			439	Waukesha, Wisconsin Lesmahagow, Scotland
		Ordovician (71)			510	Beecher's Bed, New York
		Cambrian (60)			570	House Range, Utah Burgess Shale, British Columbia Kangaroo Island, Australia Lancaster, Pennsylvania Peary Land, Greenland Yunnan Province, China
	Sinian (230)	Vendian (40)			610	Ediacara, Australia

Figure 2. Fossil assemblages that include soft-tissue preservations are more common than is generally realized. They provide evidence for the nature of some of the earliest metazoans in the Precambrian, and examples are known from every geologic period since. Listed here are the sites mentioned in the text. More than 60 major known sites around the world display significant preservation of soft parts.

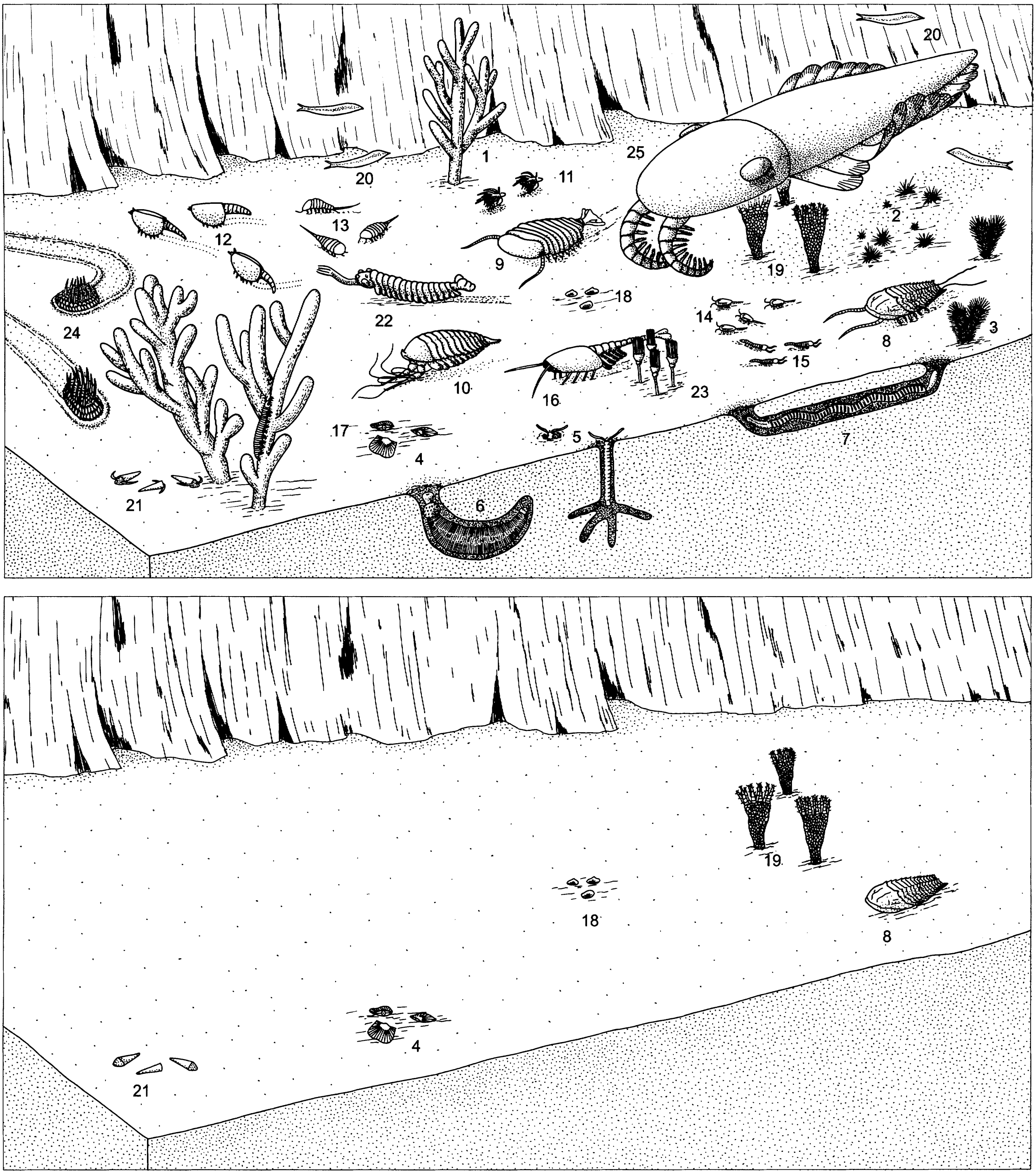

Figure 3. Soft-bodied fossils account for most of the species of the Burgess Shale of British Columbia, a large fossil assemblage that provides an extraordinary window on the results of the Cambrian explosion. No more than 20 percent of the Burgess Shale genera are preserved in shelly fossil assemblages from contemporaneous deposits in the same area. In this restoration can be seen some of the Burgess Shale species living on, above and in the muddy sediments being deposited at the foot of a submarine cliff. Of these species, only the five shown in the lower drawing had mineralized hard parts, and hence only they are preserved in contemporaneous localities where the preservation is not extraordinary. (After Conway Morris and Whittington 1985.)

sponges
1. *Vauxia*
2. *Choia*
3. *Pirania*

brachiopod
4. *Nisusia*

polychaete worm
5. *Burgessochaeta*

priapulid worms
6. *Ottoia*
7. *Louisella*

trilobite
8. *Olenoides*

non-trilobite arthropods
9. *Sidneyia*
10. *Leanchoilia*
11. *Marrella*
12. *Canadaspis*
13. *Molaria*
14. *Burgessia*
15. *Yohoia*
16. *Waptia*
17. *Aysheaia*

mollusc
18. *Scenella*

echinoderm
19. *Echmatocrinus*

chordate
20. *Pikaia*

miscellaneous
21. *Hyolithes*
22. *Opabinia*
23. *Dinomischus*
24. *Wiwaxia*
25. *Anomalocaris*

sil biotas with normal assemblages. One of the best known extraordinary deposits, the Burgess Shale biota, can be regarded as reasonably representative of a moderately deep marine community on the west side of the North American Craton during the middle Cambrian (Conway Morris 1986). It provides as complete a census of a diverse Paleozoic community as is ever likely to be achieved. However, no more than 20 percent of the genera are preserved in shelly fossil assemblages from contemporaneous deposits in the same area.

The likelihood that soft tissues will be fossilized depends on a number of factors, including the sedimentary environment, the sediment chemistry, the nature of individual organisms and the resistance of their tissues to decay.

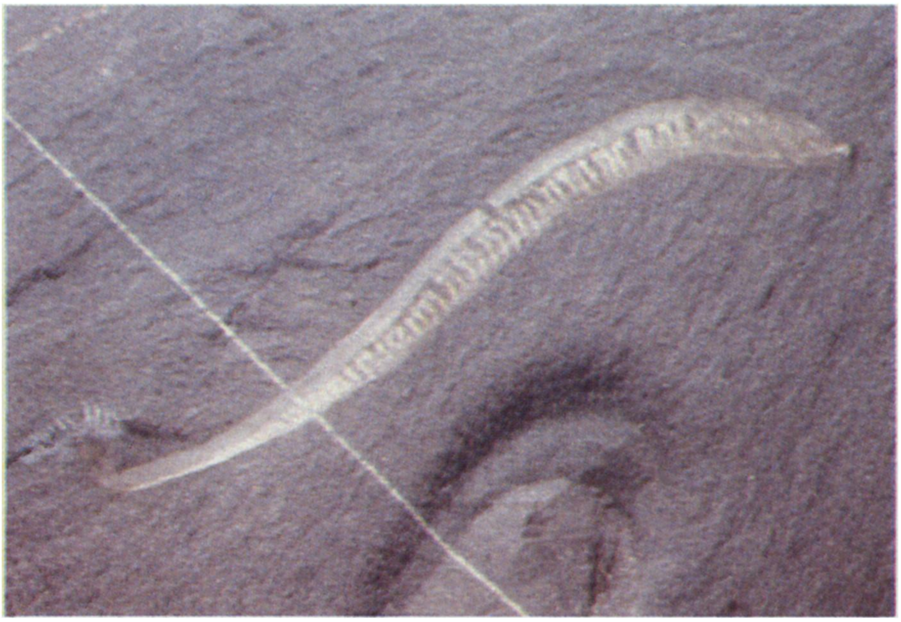

Figure 4. The soft-bodied *Pikaia* from the Burgess Shale is significant as the earliest known chordate, revealing the ancient ancestry of the group that includes ourselves. This specimen gives an impression of *Pikaia*'s elongate swimming form, muscle blocks in the trunk and axial structures.

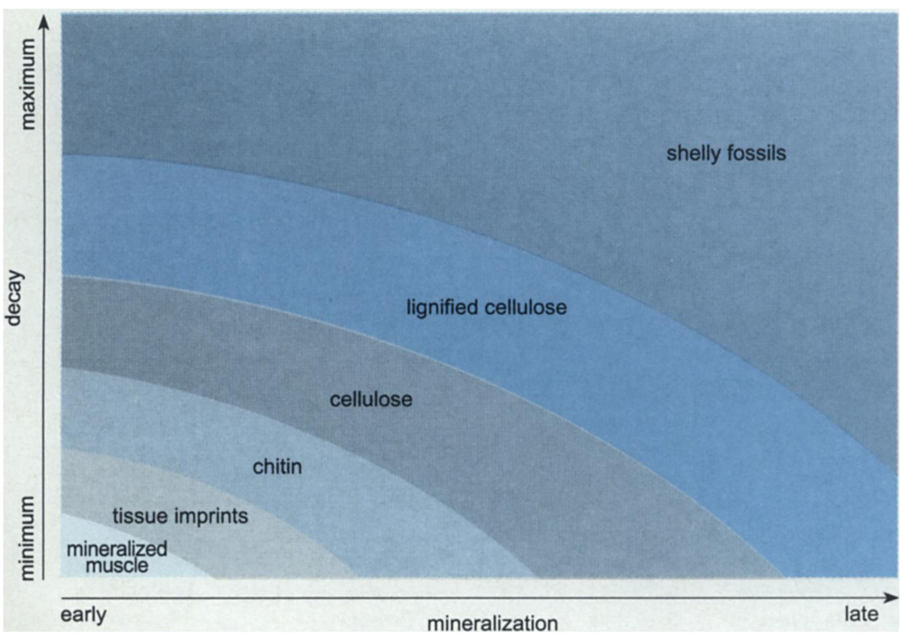

Figure 5. Relative rates of decay and mineralization determine the extent to which many soft tissues are preserved. This conceptual diagram shows the relationship between decay and mineralization in preserving various elements of a biota. Muscle and other volatile soft tissues survive only when decay is inhibited and mineralization is very rapid; this takes place, for example, when carcasses are buried rapidly in a sedimentary environment that promotes rapid diagenetic mineralization. At the other extreme, when the decay of soft tissues continues to completion, only shelly fossils will be preserved. (From Allison 1988b.)

Soft-bodied organisms must be protected from the attention of scavengers; this usually comes about through a lack of oxygen or by rapid burial. Although anaerobic conditions may eliminate scavengers, they do not prevent decay. Indeed, anaerobic decay is the norm, and can consume soft tissues in a few weeks (Allison 1988a). Even sclerotized arthropod cuticle can disappear within months. Ironically, when soft tissues are preserved, it is often through the agency of the decay bacteria, which under certain circumstances promote the formation of early diagenetic minerals that replicate the soft tissues. The bacteria themselves may even become mineralized, forming an image of the soft tissues (Wuttke 1983, Martill 1988).

The majority of extraordinary fossils are preserved as a result of the precipitation of one of three main mineral groups: pyrite, phosphate or carbonate (Allison 1988b). Silica is more rarely associated with soft-bodied fossils, and its formation in this context is poorly understood. Both silica and calcium carbonate, however, are important in preserving the fine anatomical details (even cells) of plants by the process of permineralization.

Pyrite forms as a result of the activity of sulfate-reducing bacteria, usually in fine-grained marine sediments, but pyritization of soft tissues is rare. It requires the rapid burial of carcasses to form isolated concentrations of organic matter. The two most important examples, Beecher's Bed in rocks of late Ordovician age in New York State, and the Hunsrück Slate of early Devonian age from Germany, both preserve the limbs of trilobites. Only the dorsal skeleton of a trilobite is strengthened by calcium carbonate. Hence we rely on extraordinary preservations for our knowledge of the whole anatomy of the animal. Without the few known examples of preserved limbs, we would have little idea of how trilobites moved about, fed and respired.

Soft-part preservation is most frequently associated with carbonate mineralization, in both marine and fresh-water environments. The Jurassic Lithographic Limestones at Solnhofen in Bavaria, which yielded *Archaeopteryx*, the first bird, are a classic example: The feather impressions are preserved in thinly bedded lime-

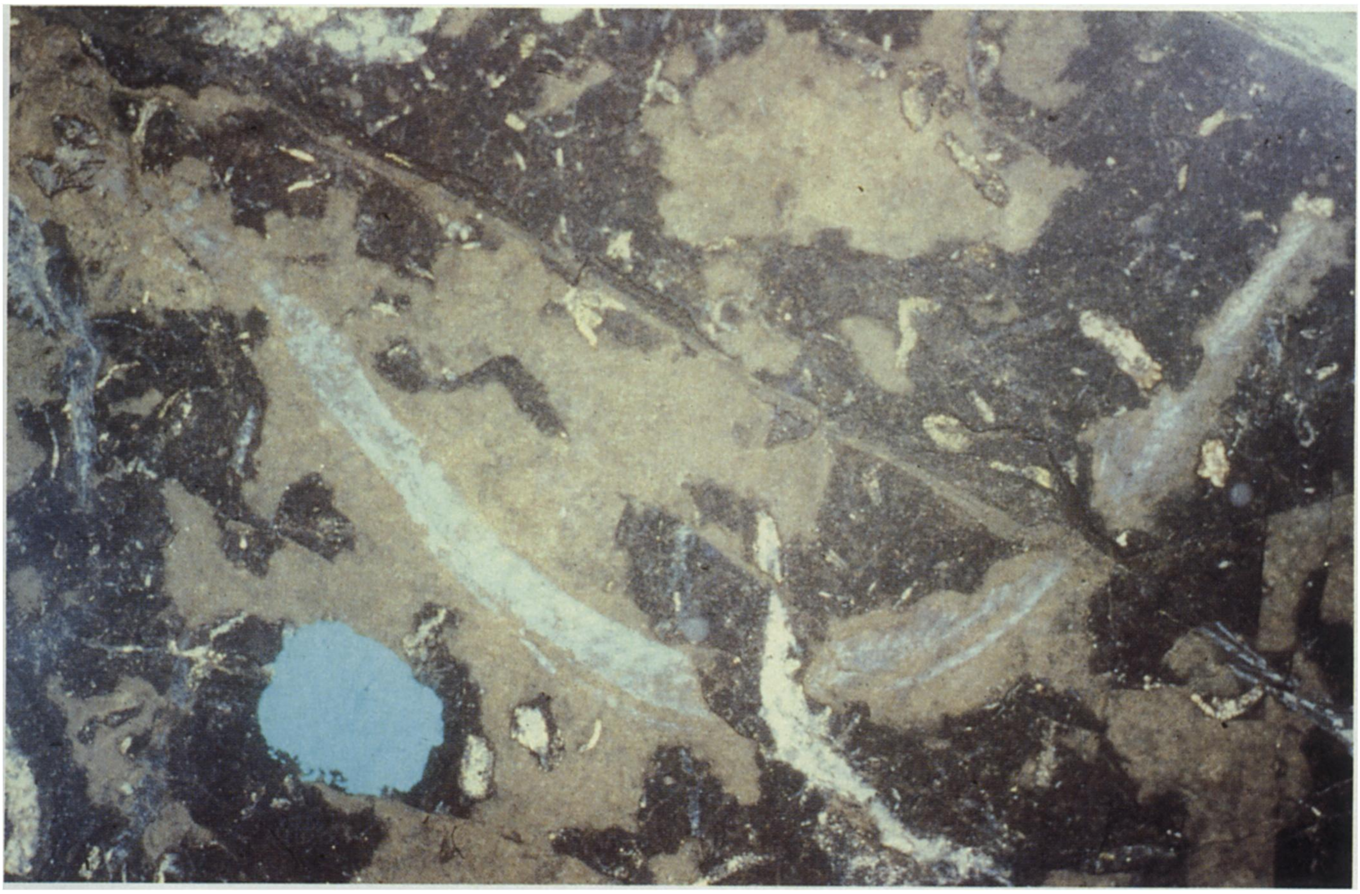

Figure 6. Conodont elements, tiny tooth-like microfossils that can be extracted from sedimentary rocks, are an example of hard parts that, by themselves, provide little information about the animals from which they came. The soft-bodied fossil shown above, found in the Granton Shrimp Bed in Edinburgh, provided the first evidence of the nature of the soft tissues of the conodont animal. The animal turned out to be a primitive chordate from the early Carboniferous period almost 400 million years ago. Some 40 millimeters long and 2 millimeters wide, it had an eel-like trunk, V-shaped muscle blocks and fins, and two lobes flanking the mouth. (Photograph courtesy of J. K. Ingham.)

stones. Rapid burial of large amounts of organic matter may lead to the formation of iron carbonate (siderite) concretions such as those that preserve the remarkably diverse Mazon Creek biota of Illinois.

Some of the most spectacular extraordinary fossils are those preserved in phosphate. These include muscles of squid from the Jurassic of Britain, and some three-dimensional fish with muscle, gills and gut contents from the Cretaceous of Brazil (Allison 1988c, Martill 1988). The decomposition of organisms is the most likely source of the phosphate. The phosphate concentration must exceed the concentration of bicarbonate in order to prevent the precipitation of calcium carbonate. This requires high organic input and very slow sedimentation.

In certain circumstances the organic tissues themselves can survive for geologically significant periods of time (Butterfield 1990). Refractory plant cuticles have the highest preservation potential, but heavily tanned arthropod cuticles also resist decay. For example, there is a diverse assemblage of early terrestrial arthropods from mudstones near Gilboa, New York, which date from the middle Devonian (Shear et al. 1984). The cuticles of trigonotarbids, centipedes, mites, spiders and possible insects are semi-translucent and appear unaltered.

Enigmatic Hard Parts

A number of extinct organisms are represented in the fossil record by hard parts that, in the absence of living examples, provide little clue to the nature of the animals from which they came. For example, among the most useful groups for identifying and dating geologic strata are the tiny tooth-like microfossils known as conodont elements (Sweet 1988). They are acid-resistant and can be extracted readily from most sedimentary rocks. In spite of their quantity, they and their origins have been at the center of controversy since 1856, when they were first discovered in Germany (Aldridge 1987).

Conodont elements come in a variety of shapes, ranging from simple cones to denticulate bars, flattened blades and broad, robust platforms. The discovery in the 1930s that different types of conodont element worked together to form a single apparatus, now considered to have functioned in feeding, yielded no insight into the identity of the soft-bodied organism from which these conodont elements came. As a consequence of this uncertainty, conodont elements have been variously interpreted as parts of plants, assorted worms, arrow worms, molluscs, arthropods and several groups of chordates.

The issue was resolved only as recently as 1983, when my colleagues and I discovered in the Granton Shrimp Bed in Edinburgh, Scotland, soft-bodied fossils from an animal with conodont elements in place (Briggs, Clarkson and Aldridge 1983). The animal, which had an eel-like trunk, was approximately 40 millimeters long and 2 millimeters wide and had V-shaped muscle blocks and fins, and two lobes flanking the mouth.

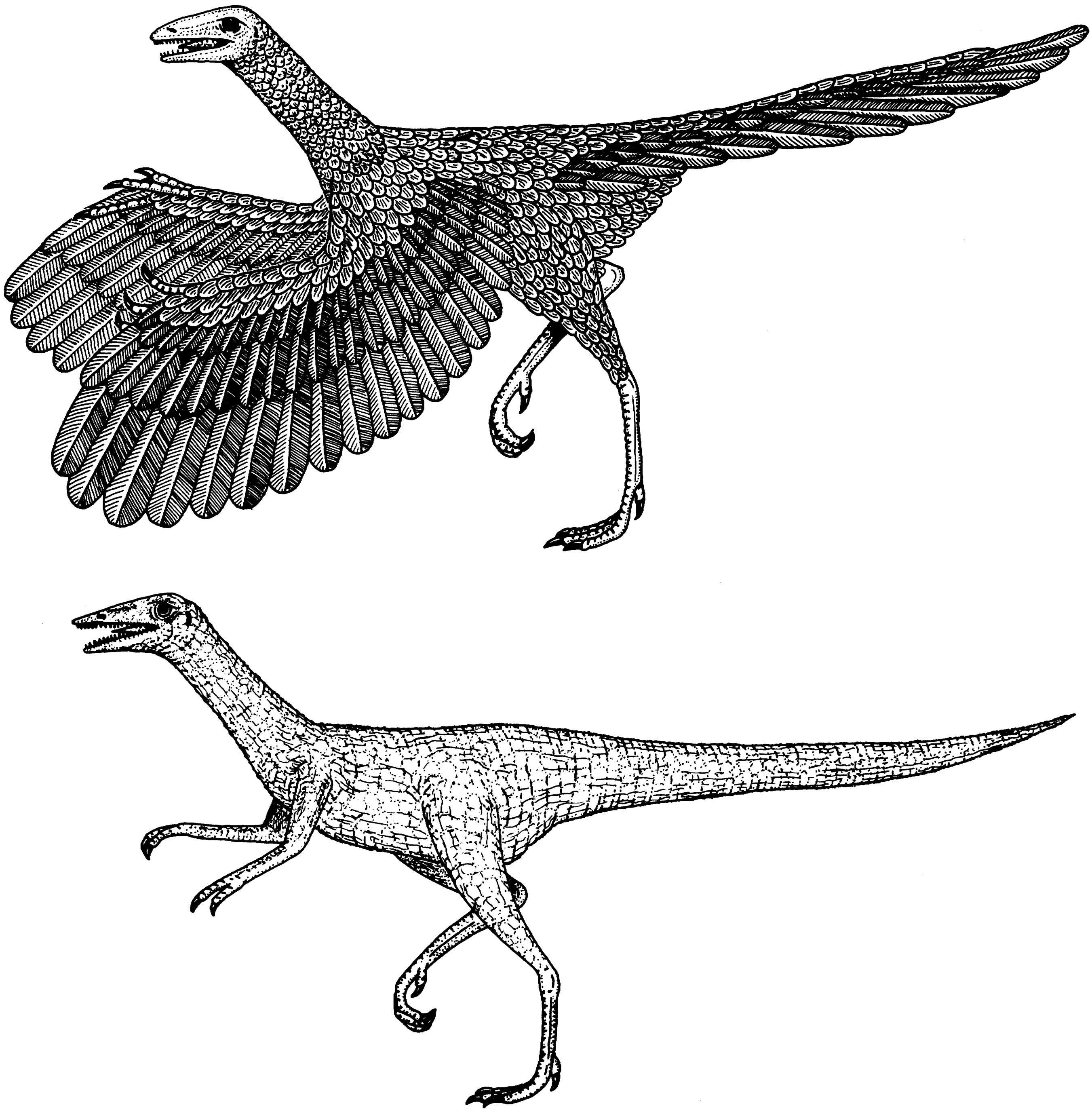

Figure 7. ***Archaeopteryx lithographica (top)*****, the world's oldest known bird, could be mistaken for a small dinosaur on the basis of skeletal fossils taken alone; one of the six known skeletons was, in fact, initially confused with the small dinosaur** ***Compsognathus (bottom)*** **until feather impressions were recognized.** ***Archaeopteryx,*** **which dates from the late Jurassic period, provides critical evidence in the investigation of bird origins; its morphology supports the hypothesis that the first flying vertebrates achieved flight by gliding rather than flapping.**

As it turns out, the animal from which these conodont elements came is now thought to be a primitive chordate that lived almost 400 million years ago, early in the Carboniferous period (Aldridge et al. 1986).

A second example of a fossil whose true nature was revealed by extraordinary preservation is *Archaeopteryx lithographica* from the late Jurassic. If identification were to rely solely on skeletal fossils, *Archaeopteryx* could easily be mistaken for a small dinosaur—and indeed it has been. One of the six known skeletons was initially misidentified as a dinosaur until the feather impressions were recognized. Upon reevaluation, the specimen was found to be *Archaeopteryx*. Feathers are not conclusive evidence of an ability to fly, but, in combination with other features, they show that *Archaeopteryx* was at the very least a glider (Rayner 1989). Indeed, *Archaeopteryx* is generally referred to as the first bird, and its fossils provide critical data on bird origins.

Discoveries

Mineralized skeletons are not ubiquitous in the animal kingdom. Two-thirds of existing phyla lack any mineralized hard parts. Many lower-ranking taxa fall into the same category, including most arthropods, because their exoskeletons are very lightly sclerotized. Extraordinary fossils are the only direct source of data on the evolutionary history of soft-bodied animals, including all animals more than about 600 million years old that predate the appearance, in the late Precambrian, of the first mineralized skeletons. Extraordinary fossil remains are important in estimating at least the minimum age of soft-bodied taxa and in assessing the time of their diversification.

The discovery in Waukesha, Wisconsin, of the first significant assemblage of soft-bodied animals from the Silurian period, 400 million years ago, extends the known time range of some taxa back several millions of years (Mikulic, Briggs and Kluessendorf 1985 a, b). For example, among the fossils discovered at Waukesha was a well-preserved centipede-like organism, the earliest known example by 20 million years of a uniramian, a member of the major group that includes the millipedes, centipedes and insects. A recent finding of the fossil remains of a related organism in Utah may push this date back another 100 million years (Robison 1990). The Waukesha occurrence shows that the ancestors of the modern uniramians were marine and at least as old as the early Silurian period.

Also discovered at Waukesha was a rare large annulate worm with what looks to be a circular structure reminiscent of a leech's sucker. If further material allows the specimen to be confidently identified, the range of the Hirudinea, the class of animal to which the leeches belong, will be extended back by some 280 million years. The earliest leech previously known was only 150 million years old.

The fossil record of the soft-bodied priapulid worms provides important insights into their changing role in marine communities through time. A priapulid worm is known from the Mazon Creek fauna of the Carboniferous period, about 300 million years old. A number of priapulids occur in the Burgess Shale-type faunas of British Columbia, Utah and China—200 million years earlier (Conway Morris 1977). What is particularly interesting is that in the Burgess Shale communities, priapulids are more abundant than are polychaete worms, and the fossil priapulids are more diverse morphologically than their living descendants. Modern priapulids constitute only a minor element of marine communities; they appear to have been displaced over time by the polychaetes.

Even more significant than fossils that reveal the age and origins of living soft-bodied taxa are extraordinary fossils that reveal the existence of unfamiliar animals—creatures that belong to groups without living representatives, which would otherwise be unknown.

The more bizarre of these forms are termed Problematica, implying that

Figure 8. Faint feather impressions, important in identifying *Archaeopteryx* as a bird, are not immediately evident on this specimen discovered in 1951 at Eichstätt, Germany, but can be detected by close examination.

they do not fall within the description of any known phylum. One of the most widely distributed examples is a creature called *Anomalocaris* (Whittington and Briggs 1985). The animal has been found in rocks of Cambrian age in British Columbia, Utah, California, Pennsylvania, Poland and China. Half a meter long, *Anomalocaris* was one of the largest beasts of its time, and its morphology suggests it must have been a formidable predator. A pair of segmented spiny appendages flanked the mouth, and the jaw comprised a circle of 32 radiating plates armed with inwardly facing spines. This jaw appears to have functioned in a unique way, unknown in any living animal. The plates seem to have swung downward and outward to increase the aperture; then they pulled up again to bite or break the prey. Fossils of the now-extinct trilobites have wounds that may have been inflicted by these jaws, suggesting that the trilobites may have been prey for *Anomalocaris*.

Figure 9. Well-preserved myriapod found at Waukesha, Wisconsin, predates by 20 million years other examples of uniramians, the major group that includes the millipedes, centipedes and insects. The organism was part of the first significant soft-bodied assemblage found from the Silurian period, 400 million years ago. Its occurrence shows that the ancestors of the modern uniramians were marine and appeared much earlier than had been thought.

Figure 10. Sucker-like structure seen in a large annulate worm specimen from the Waukesha assemblage of soft-bodied fossils may belong to the first leech. Leeches had been known to exist for only the past 150 million years; this discovery, however, may extend the range of the class Hirudinea back by some 280 million years.

Even in its movements, *Anomalocaris* appears to have developed a unique locomotive mechanism. The animal's trunk bore 11 pairs of closely spaced, overlapping lateral fins that moved in an undulatory fashion to create a propulsive wave. Some modern fish create a similar kind of motion using a single fin, but no creature other than *Anomalocaris* is known to have used an overlapping series of fins.

Other examples of Problematica revealed by extraordinary preservations include *Opabinia* and *Hallucigenia* from the Burgess Shale, *Ainiktozoon* from the Silurian of Lesmahagow in Scotland, and *Tullimonstrum* from the Carboniferous at Mazon Creek.

The head of *Opabinia* had five eyes and a long, flexible proboscis that terminated in opposing bundles of spines, which could presumably be used to grasp food. The 15 trunk divisions each bore a paired lobe. These were presumably used in swimming. On the surface of each lobe was a series of lamellae, probably forming a gill. A series of projections on the tail was used to stabilize the animal during swimming.

A new interpretation of *Hallucigenia* has turned current restorations literally upside down (Ramsköld and Hou in press). The head was poorly defined. It had seven pairs of flexible limbs, each terminating in a claw. It was protected dorsally by seven pairs of long spines. The trunk terminated posteriorly in an extended tube.

The most striking features of *Ainiktozoon* were an ovoid capsule and a segmented tail. The capsule was surrounded by a variety of enigmatic structures, including a compound eye. The organism has been tentatively interpreted as a swimming, filter-feeding protochordate.

Tullimonstrum was an elongate dorsoventrally flattened animal with a paired triangular tail fin. Anteriorly the head, which had a transverse bar-like structure terminating at each end in an eye, projected into a long proboscis-like extension ending in a toothed claw.

Evolutionary Patterns

Even though assemblages of extraordinary fossils provide the most complete chronicle of ancient communities available, until recently they have been largely ignored in considerations of evolutionary patterns, in favor of the much less complete shelly fossil record. This anomaly is the result of two central perceptions regarding extraordinary preservations. First, they are thought to be rare, and therefore they are believed to introduce distortions into analyses of diversity through time. Second, their very nature allows them to be perceived as atypical and consequently unrepresentative.

The fact is, extraordinary fossils *do* introduce distortions into global compilations of diversity through time, but that is because such compilations are necessarily based on the shelly fossil record. Exceptionally preserved fossils can provide a complementary data base that allows equally important questions to be addressed.

Burgess Shale–type preservations are now known from a range of localities, and it is clear that although some of the animals appear bizarre, the fauna is representative of their time and place. About 12 present-day phyla and about 20 genera of Problematica are represented (Briggs and Conway Morris 1986). Problematica are most numerous in the strata corresponding to the Cambrian period, with numbers declining throughout the remainder of the Paleozoic era.

What we learn from the Burgess Shale deposit, and others like it, is that the Cambrian was a period of explosive evolution. The initial radiation of major body plans probably took place largely unhindered by much competition or predation. As later extinctions left ecospace vacant, it was recolonized by new species from existing taxa; there was no potential for evolving new phyla. This suggests that the Cambrian radiation resulted in the rapid evolution of a much larger number of phyla than have survived to the present day (see Gould 1989), and that after the Cambrian the major feature of metazoan evolution was a decrease in the number of major body plans.

The questions before us now concern the number of phyla to have evolved during the Cambrian explosion. It also remains for us to assess the amount of disparity in the morphologies of Cambrian animals versus those of the present day.

Part of the apparent disparity is a reflection of taxonomic practice rather than of actual taxonomic differences. Phyla are defined by their uniqueness. When an organism does not seem to fit into any existing phylum, it is thought to be a part of a phylum of its own. During the hundreds of millions of years since the initial radiation of the metazoan phyla, intermediate forms have become extinct. Hence the morphological separation between the survivors has increased, so that the representatives of the living phyla are quite distinct. Thus when we try to insert Cambrian animals into a classification based on living fauna, it is hardly surprising that they cannot be accommodated. A more meaningful interpretation of the Cambrian radiation may be achieved by analyzing the relationships of the Cambrian organisms to each other, without reference to a modern classification.

Figure 11. Specimens of *Anomalocaris*, a formidable predator that was likely among the largest of Cambrian beasts, suggest that this Burgess Shale animal developed a unique mechanism for locomotion. The animal had 11 pairs of closely spaced, overlapping lateral fins that undulated to create a propulsive wave. *Anomalocaris*, whose jaw is preserved in the unusual fossil on the cover of this issue of *American Scientist*, is currently classified among the Problematica, indicating that its relationships to other animals are uncertain.

This approach has already overturned the established theory of evolutionary relationships among arthropods (Briggs and Fortey 1989, Briggs 1990). One possible explanation for the vast diversity of these creatures is that each major group originated independently. For example, a long-held view was that the trilobites were the first arthropods to evolve, and the crustaceans were believed to have arisen later, independently. Yet the analysis of complete arthropod fossils from extraordinary preservations has suggested that the opposite is true. Based on analyses of a large number of morphological characteristics, we now believe the crustaceans to be the most primitive of the arthropods, whereas the trilobites occupy a more derived position. And it is likely that the arthropods as a whole represent a single radiation, rather than a series of independent originations.

How generally representative are these extraordinary preservations? First, they are not as rare as originally thought. From the beginning of the Cambrian the number of known sites

Figure 12. *Tullimonstrum,* the Tully Monster, found in the 300-million-year-old Mazon Creek deposit in Illinois, is another oddball; although it has been interpreted as a bizarre gastropod, it is usually placed in its own phylum. *Tullimonstrum* was an elongate, flattened animal with a paired triangular tail fin (to the left above); its head projected anteriorly into a long proboscis-like extension, ending in a toothed claw.

Figure 13. *Hallucigenia,* from the Burgess Shale, had seven pairs of long, dorsal spines and an equal number of flexible limbs, each terminating in a claw. Like *Anomalocaris* and *Tullimonstrum,* its body plan does not fit readily into any living phylum.

displaying significant soft-part preservation exceeds 60, and for each of these major sites there are many minor ones. For example, major occurrences of extraordinary fossils of Burgess Shale type are found in Yunnan Province, China; Peary Land, Greenland; near Lancaster, Pennsylvania; Kangaroo Island, South Australia; and in the Wellsville Mountains and the House Range in Utah, as well as at the original locality in British Columbia; but at least another 27 sites also yield some Burgess Shale taxa (Conway Morris 1989).

It can be argued that extraordinary fossils are preserved in environments that differ from those represented by the normal shelly fossil record. Nevertheless, the environments that preserve soft-bodied fossils may be equally or even more significant in evolutionary terms. The relative stability of the Burgess Shale fauna over extremely long periods may indicate that life forms established in deeper water are more conservative evolutionarily than were forms living at shallower depths (Conway Morris 1989).

A large number of extraordinary fossil deposits occur in association with broad coastal delta plains in tropical latitudes. In coastal swamps, interdistributary bays, and lagoons, restricted water bodies receive large quantities of organic material and are subject to changes in salinity and rapid influxes of sediment. A comparison of Carboniferous biotas such as Mazon Creek, which are preserved in such transitional environments, with an example from the Triassic of France some 100 million years younger, shows a striking continuity in the types of animal present (Briggs and Gall 1990). This is in contrast to the major changes that affected marine shelly groups in the same interval as a result of the extinction at the end of the Permian, which wiped out 54 percent of marine families. The animals in the fluctuating environments of the coastal plains were much less severely affected by the extinction, probably because of their greater tolerance to habitat variations. They were likely much more resistant to selection pressures than their more narrowly adapted open-marine counterparts.

Understanding the factors contributing to the formation of extraordinary fossils, their ecology and evolutionary significance requires an interdisciplinary approach. Although I have concentrated here on evolutionary aspects, current research ranges from experiments in decay and mineralization, through microbiology, geochemistry, sedimentology, systematic paleontology, functional and paleoecological interpretation, to the compilation and analysis of taxonomic data bases. Extraordinary fossils are no longer perceived as paleontological curiosities preserved in ecological and evolutionary isolation. We now recognize that they are the key to untapped data on patterns in the history of life.

Bibliography

Aldridge, R. J. 1987. Conodont palaeobiology: a historical review. In *Palaeobiology of Conodonts*, ed. R. J. Aldridge, 11–34. Chichester: The British Micropalaeontological Society.

Aldridge, R. J., D. E. G. Briggs, E. N. K. Clarkson and M. P. Smith. 1986. The affinities of conodonts—new evidence from the Carboniferous of Edinburgh, Scotland. *Lethaia* 19:273-291.

Allison, P. A. 1988a. The role of anoxia in the decay and mineralization of proteinaceous macro-fossils. *Paleobiology* 14: 139–154.

Allison, P. A. 1988b. Konservat-Lagerstätten: cause and classification. *Paleobiology* 14:331–344.

Allison, P. A. 1988c. Phosphatized soft-bodied squids from the Jurassic Oxford Clay. *Lethaia* 21:403–410.

Briggs, D. E. G. 1990. Early arthropods: dampening the Cambrian explosion. In *Short Courses in Paleontology 3, pp. 24–43* Knoxville, Tennessee: Paleontological Society.

Briggs, D. E. G., E. N. K. Clarkson and R. L. Aldridge. 1983. The conodont animal. *Lethaia* 16:1–14.

Briggs, D. E. G., and S. Conway Morris. 1986. Burgess Shale Problematica. In *Problematic Fossil Taxa*, ed. A. Hoffman and M. H. Nitecki, 167–183. New York: Oxford University Press.

Briggs, D. E. G., and J.-C. Gall. 1990. The continuum in soft-bodied biotas from transitional environments: a quantitative comparison of Triassic and Carboniferous Konservat-Lagerstätten. *Paleobiology* 16:204–218.

Briggs, D. E. G., and R. A. Fortey. 1989. The early radiation and relationships of the major arthropod groups. *Science* 246:241–243.

Butterfield, N. J. 1990. Organic preservation of non-mineralizing organisms and the taphonomy of the Burgess Shale. *Paleobiology* 16:272–286.

Conway, Morris S. 1977. Fossil priapulid worms. *Special Papers in Palaeontology* 20.

Conway Morris S. 1986. The community structure of the Middle Cambrian phyllopod bed (Burgess Shale). *Palaeontology* 29:423–467.

Conway Morris S. 1989. The persistence of Burgess Shale–type faunas: implications for the evolution of deeper-water faunas. *Transactions of the Royal Society of Edinburgh: Earth Sciences* 80:271–283.

Conway Morris, S., and H. B. Whittington. 1985. Fossils of the Burgess Shale: A National Treasure in Yoho National Park, British Columbia. *Geological Survey of Canada, Miscellaneous Reports* 43:1-31.

Gould, S. J. 1989. *Wonderful Life—The Burgess Shale and the Nature of History.* New York: Norton.

Martill, D. M. 1988. Preservation of fish in the Cretaceous Santana formation of Brazil. *Palaeontology* 31:1–18.

Mikulic, D. G., D. E. G. Briggs and J. Kluessendorf. 1985a. A new exceptionally preserved biota from the lower Silurian of Wisconsin, U.S.A. *Philosophical Transactions of the Royal Society of London* B311:75–85.

Mikulic, D. G., D. E. G. Briggs and J. Kluessendorf. 1985b. A Silurian soft-bodied biota. *Science* 228:715–717.

Ramsköld, L., and Hou Xianguang. In press. New Early Cambrian animal and onychophoran affinities of enigmatic metazoans. *Nature.*

Rayner, J. M. V. 1989. Vertebrate flight and the origin of flying vertebrates. In *Evolution and the Fossil Record*, ed. K. C. Allen and D. E. G. Briggs, 188–217. London: Belhaven Press.

Robison, R. A. 1990. Earliest-known uniramous arthropod. *Nature* 343:163–164.

Schopf, R. J. M. 1978. Fossilization potential of an intertidal fauna: Friday Harbor, Washington. *Paleobiology* 4:261–270.

Seilacher, A., W.-E. Reif and F. Westphal. 1985. Sedimentological, ecological and temporal patterns of fossil Lagerstätten. *Philosophical Transactions of the Royal Society of London* B311:5–23.

Shear, W. A., P. M. Bonamo, J. D. Grierson, W. D. I. Rolfe, E. L. Smith and R. A. Norton. 1984. Early land animals in North America; evidence from Devonian age arthropods from Gilboa, New York. *Science* 224:492–494.

Sweet, W. C. 1988. *The Conodonta—Morphology, Taxonomy, Paleoecology, and Evolutionary History of a Long-Extinct Animal Phylum.* New York: Oxford University Press.

Whittington, H. B., and D. E. G. Briggs. 1985. The largest Cambrian animal, *Anomalocaris*, Burgess Shale, British Columbia. *Philosophical Transactions of the Royal Society of London* B309: 569–609.

Wuttke, M. 1983. "Weichteil-Erhaltung" durch lithifizierte Mikroorganismen bei mittel-eozänen Vertebraten aus den Ölschiefern der "Grube-Messel" bei Darmstadt. *Senckenbergiana lethaea* 64:509–527.