

Chapter 10

MULTIDISCIPLINARY CASE STUDIES IN PALEONTOLOGY

10.1 PALEONTOLOGY AS AN INTEGRATIVE SCIENCE

While the procedures highlighted throughout this book will undoubtedly continue to evolve well into the future, many basic paleontological principles that have emerged in the past half-century will be with us for a long time. To cite but one example, consider the development of principles and methods for phylogenetic reconstruction. As noted earlier, paleontologists continue to investigate the relative merits of different procedures for phylogenetic analysis. At the same time, it is clear that the centrality of phylogenetic reconstruction has now been well established for a host of paleontological themes, including studies of classification [SEE SECTION 4.3], the tempo and mode of evolution [SECTION 7.3], and morphological diversification [SECTION 8.6].

Although these basic goals may be considered timeless, the problems to which they are applied are not. Paleontology has become an increasingly dynamic science, with a growing interdisciplinary focus on broadly based research questions, propelled by discoveries reported nearly every week in leading scientific journals. Although any attempt to review these themes will undoubtedly be somewhat outdated by the time this book is published, it is nevertheless useful to illustrate the application of paleontological principles and procedures to a diverse set of questions ranging from the

investigation of the most primitive forms of life on earth—and perhaps elsewhere—to the assessment of human-induced pressures that living organisms have been forced to confront in the present day.

10.2 THE CAMBRIAN EXPLOSION OF MARINE LIFE

Many periods of evolutionary radiation and extinction (see Chapter 8) can be seen as simple increases in the rate of turnover of species, genera, and families. By contrast, there are certain unique episodes in the history of life that were of fundamental importance in permanently reshaping the biosphere. For animals, the most important of these is the so-called **Cambrian Explosion**, a time of great morphological and functional diversification during which most of the basic animal body plans—the phyla—appeared within just a few tens of millions of years (Figure 10.1). This statement applies, of course, to the skeletonized phyla; the later appearance of a number of soft-bodied phyla almost certainly reflects a failure of preservation.

Here we consider a few of the principal questions that surround the Cambrian Explosion:

1. What evidence does the fossil record provide of the basic sequence of events?
2. How is this evidence interpreted from an evolutionary standpoint?

Proterozoic	Paleozoic						Mesozoic			Ceno
	Cm	O	S	D	C	P	Tr	Jr	K	
Cnidaria • Porifera • Mollusca • Brachiopoda • Ctenophora • Priapulida • Onychophora • Arthropoda • Phoronida • Annelida • Echinodermata • Chordata • Hemichordata • Tardigrada • Bryozoa •										
				Nematoda • Nemertina •					Entoprocta •	
										Rotifera • Nematomorpha •

FIGURE 10.1 First appearances of animal phyla in the fossil record. Most skeletonized phyla first appear in the Cambrian and Ordovician. Subsequent first appearances probably reflect sampling failure rather than later origins. (From Valentine *et al.*, 1999)

3. Why did the radiation of animal phyla occur when it did, and why has such a profound proliferation of animal body plans not occurred since?

The Fossil Record

Prokaryotes and algae were abundant and diverse through much of the Proterozoic Eon, but the oldest undoubted body fossils of animals are phosphatized embryos from the Neoproterozoic, around 570 million years old (Figure 1.15). Shortly after this, a diversity of biotic forms appears in the fossil record, many of which are of unknown phylogenetic affinities (Figure 10.2). These are informally referred to as the Ediacaran Fauna, after one of the classic collecting localities in Ediacara Hills, Australia. Many other problematic fossils have been described from other Proterozoic localities (for example, see Box 4.3). In addition, the oldest unambiguous trace fossils [SEE SECTION 1.2] come from the Neoproterozoic and are about 560 million years old. Possible traces and animal body fossils may be as old as 600 million years, but there is some uncertainty about these.

Figure 10.1 shows the approximate times at which the animal phyla first appear in the fossil record. Of the groups that first appear in the Cambrian, many—such as

priapulids, onychophorans, and chordates—are soft-bodied, and others—such as arthropods—include mostly unmineralized forms. We are fortunate to have a Cambrian record of these phyla thanks to several deposits with exceptional fossil preservation. The best known of these is the Middle Cambrian Burgess Shale of British Columbia. As we noted in Chapter 1, the great majority of Burgess Shale species are soft-bodied, and the mineralized taxa seem to be fairly typical of shelly Cambrian deposits. A number of Burgess Shale forms have clear affinities with living phyla, and arthropods are especially common.

There are numerous problematic taxa, however. Every paleontologist has a favorite example: *Opabinia*, with its segmented body, five eyes, and hose-like snout terminating in what appears to be a grasping organ, is the most charming of beasts (Figure 10.3). Other unusual Burgess Shale animals include *Odontogriphus*, a flattened, annulated animal whose mouth was surrounded by a ring of toothlike structures that may have supported feeding tentacles (Figure 10.4); and *Hallucigenia*, an elongate animal with two prominent rows of dorsal protective spines (Figure 10.5). When the animal was first described, the spines of *Hallucigenia* were thought to be legs, but more complete material of this and related

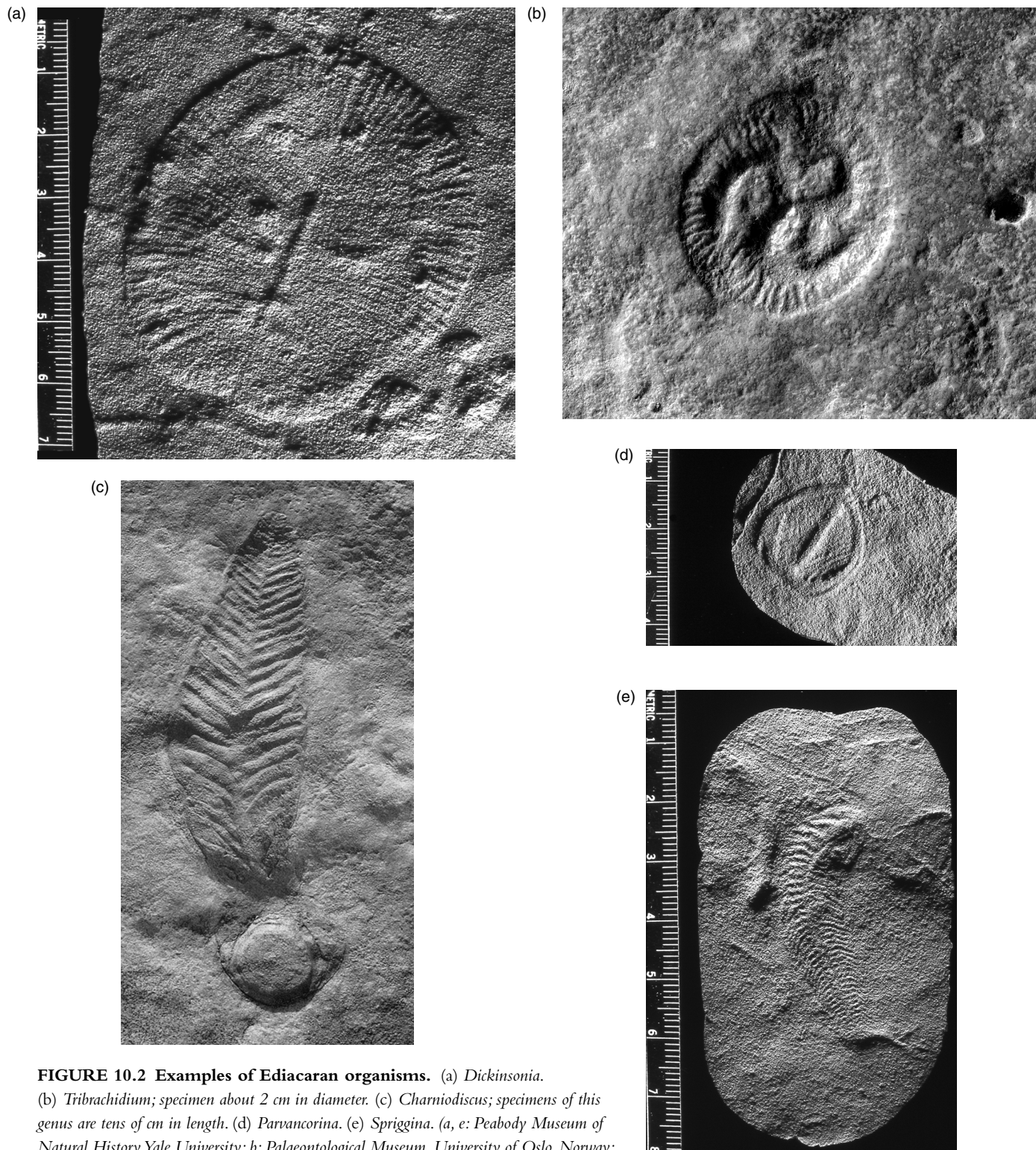


FIGURE 10.2 Examples of Ediacaran organisms. (a) *Dickinsonia*. (b) *Tribrachidium*; specimen about 2 cm in diameter. (c) *Charmiodiscus*; specimens of this genus are tens of cm in length. (d) *Parvancorina*. (e) *Spriggina*. (a, e: Peabody Museum of Natural History, Yale University; b: Palaeontological Museum, University of Oslo, Norway; c: South Australian Museum; d: W. K. Sacco/Peabody Museum of Natural History)

forms from elsewhere in the world now suggests that the spines are dorsal and that *Hallucigenia* is a member of a group of animals known as Lobopodia after their characteristic legs.

The animal *Anomalocaris* illustrates well the difficulty that has attended the interpretation of Burgess Shale fossils. In 1892, C. D. Walcott described the genus *Anomalocaris* on the basis of a segmented fossil that he

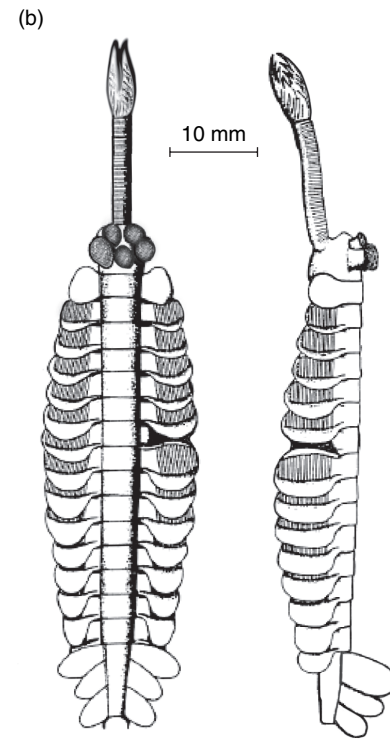


FIGURE 10.3 The Burgess Shale animal *Opabinia*. (a) Specimen in lateral view. (b) Reconstruction in dorsal and lateral views. (From Whittington, 1985, reproduced with permission of the Minister of Public Works, Canada)

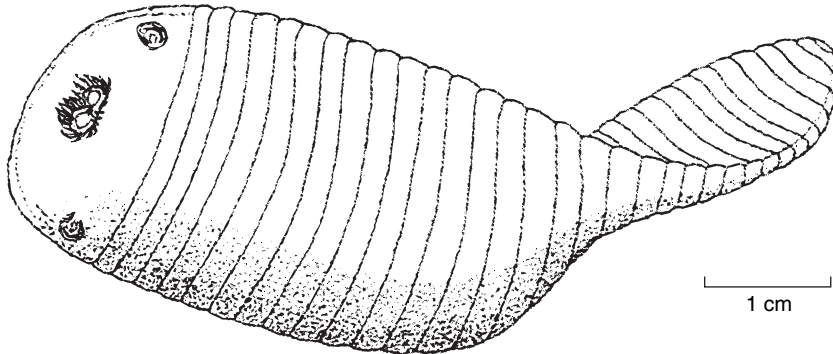


FIGURE 10.4 Reconstruction of the Burgess Shale animal *Odontogriphus*. (From Conway Morris, 1976)

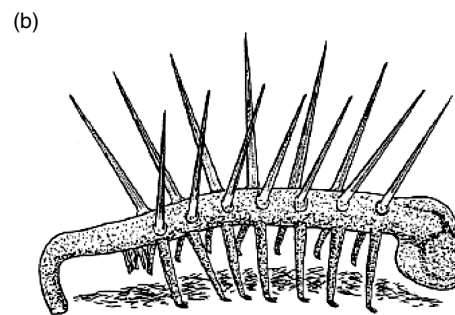
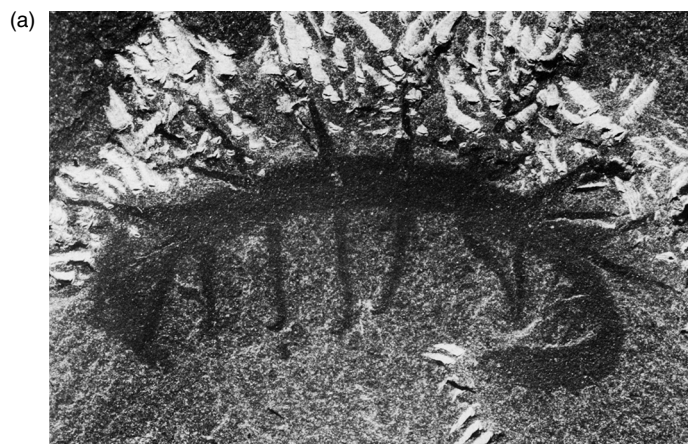


FIGURE 10.5 The Burgess shale animal *Hallucigenia*. (a) Specimen in lateral view. Field of view is about 1.4 cm wide. (b) Reconstruction. (From Conway Morris, 1998)

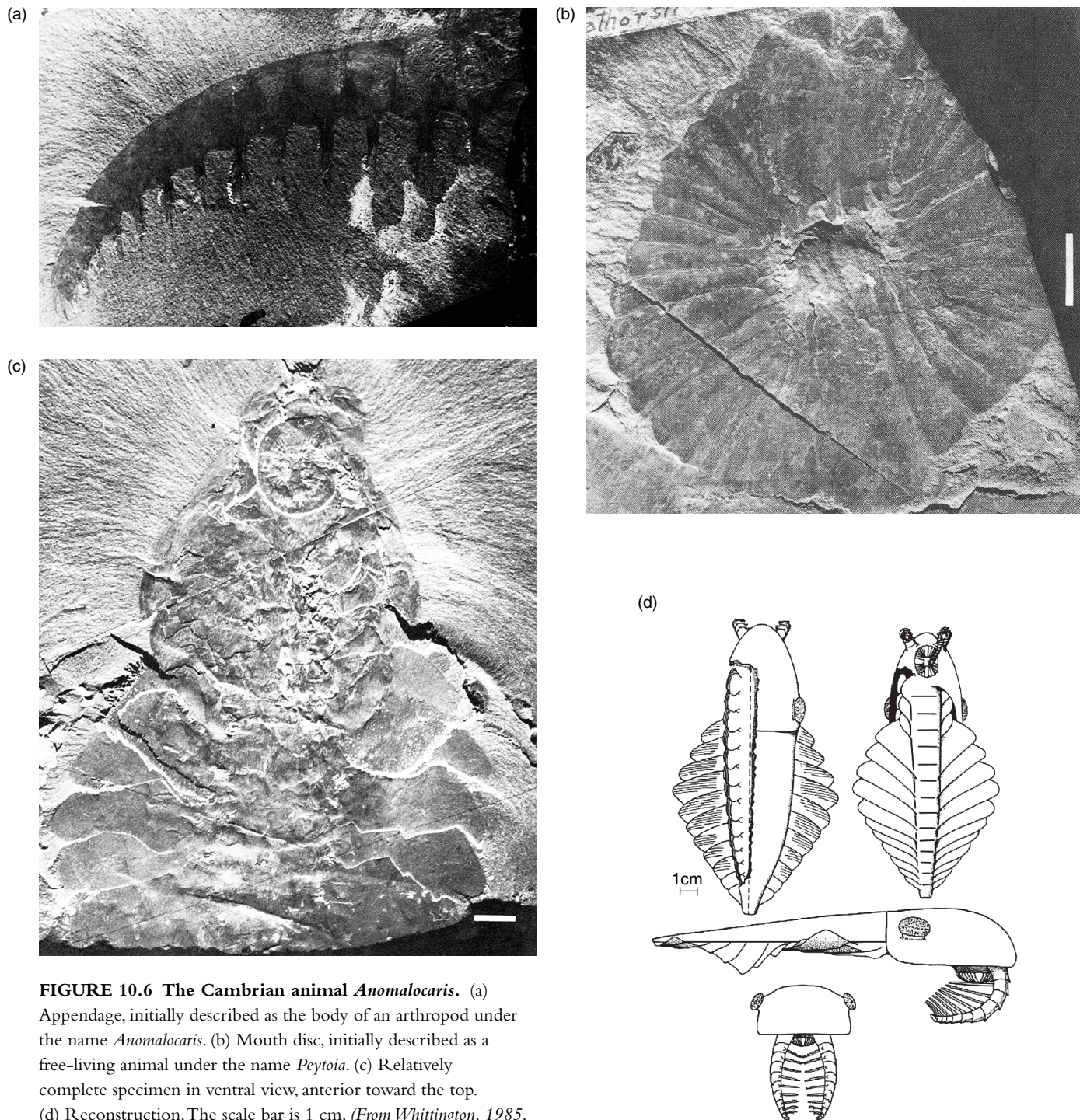


FIGURE 10.6 The Cambrian animal *Anomalocaris*. (a) Appendage, initially described as the body of an arthropod under the name *Anomalocaris*. (b) Mouth disc, initially described as a free-living animal under the name *Peytoia*. (c) Relatively complete specimen in ventral view, anterior toward the top. (d) Reconstruction. The scale bar is 1 cm. (From Whittington, 1985, reproduced with permission of the Minister of Public Works, Canada)

thought to be the body of an arthropod (Figure 10.6a). Later, in 1911, he reported a vaguely jellyfishlike fossil, a plated disk that he named *Peytoia* (Figure 10.6b). In the same year, he also described an incomplete, segmented body under the genus name *Laggania*. Only in the late 1970s was it revealed, through painstaking specimen preparation, that the *Anomalocaris* fossil is actual-

ly the limb of a much larger animal, of which *Laggania* is part of the body and *Peytoia* the mouth (Figure 10.6c). By the rule of priority [SEE SECTION 4.1], the entire animal is given the name *Anomalocaris*. Shown reconstructed in Figure 10.6d, this animal, with its grasping limb, plated mouth, and streamlined body, was evidently a predator.

Since the initial discovery of the Burgess Shale, other instances of exceptional preservation in the Cambrian have been found. Most notable are the Chengjiang Fauna in Yunnan, China, and the Sirius Passet Fauna of Greenland. Although these Early Cambrian deposits are older than the Burgess Shale, they reveal a similar array of organisms, and some genera have proven to have long stratigraphic ranges. *Anomalocaris*, for example, is found through much of the Lower and Middle Cambrian.

The fossils of the Burgess Shale are preserved as carbonized films and clay sheets and are thought to have been deposited under low-oxygen conditions. Internal organs are often found preserved by early diagenetic mineralization. Motivated in part by questions of Burgess Shale preservation, experimental taphonomic investigations [SEE SECTION 1.2] have been conducted on shrimps and other organisms with proteinaceous exoskeletons. These have helped demonstrate that reduced oxygen levels promote the fossilization of soft parts and lightly skeletonized hard parts, and have also pinpointed the reasons why this is the case. Under controlled laboratory conditions, reduced oxygen levels do not appreciably inhibit the decay of soft parts. Rather, they promote mineralization, including the early formation of pyrite within the interstices of soft parts [SEE SECTION 1.2]. Therefore, it is this process of early mineralization, rather than the preservation of soft parts per se, that is largely responsible for the exquisite fossils of the Burgess Shale.

Evolutionary Interpretation of Cambrian Events

The fossil record suggests a brief early history of animals followed by a rapid radiation of the phyla. Although Proterozoic animals were unknown in Darwin's time, the sudden appearance of phyla had already been documented. Darwin and many after him have attributed this to a long gap in the stratigraphic record, during which the phyla as we know them evolved but were not preserved. This simple view can no longer be supported. For one thing, the trace fossils that are present in the Proterozoic are generally small and horizontal, indicating simple behavior, and they increase in size and complexity in the Cambrian. The kinds of animals that made complex traces in the Cambrian left no such traces in the Proterozoic. Moreover, Proterozoic rocks have been extensively studied, and they have yielded many body fossils (Figure 10.2). But there is no sign of brachiopods, trilobites, echinoderms, and so on. Because the condi-

tions needed to preserve body fossils were present in the Proterozoic, these groups should have been preserved if they had existed in abundance. Thus, the unpreserved history of the animal phyla that appear in the Cambrian cannot extend very far into the Proterozoic.

This conclusion depends partly on what we mean by a *phylum*, however. Familiar characteristics that we generally use to distinguish the members of a phylum or other taxonomic group need not have been present at the initial time of lineage splitting that led to that group. Take the earliest bird, *Archaeopteryx* [SEE SECTION 4.2]. It has feathers but largely resembles nonavian theropod dinosaurs rather than modern birds in its skeletal features. It does not have a well-developed breastbone that would indicate strong wing muscles, its bones are much denser than those of modern birds, and it is fully toothed. Similarly, it is possible that many of the animal phyla—in the phylogenetic sense of the lineages that led up to brachiopods, echinoderms, molluscs, and so on—were present in the Proterozoic, but that they evolved their distinctive features only in the Cambrian. In other words, there may have been a significant delay between the evolution of stem and crown groups [SEE SECTION 4.3]. Which particular features the members of the stem lineages might have had is rather speculative. Arthropod ancestors without a cuticle or jointed limbs may have resembled segmented worms, and molluscan ancestors may have resembled flatworms in general aspect. At the same time, if one imagines a brachiopod without its lophophore, shell, and musculature that opens and closes the shell, there is very little left to imagine.

One line of evidence in support of the delay between phylum origin and the evolution of diagnostic anatomical features comes from molecular biology. When a lineage splits, the two branches evolve independently and therefore accumulate genetic differences. On average, the longer the time since their divergence, the greater will be the genetic difference between the lineages. If we knew the rate of divergence, then the amount of genetic difference between two living lineages would reveal the amount of time the lineages have been evolving separately. Because divergence rates vary among genes, among lineages, and over time, there is great uncertainty in calibrating these so-called **molecular clocks**. Thus, estimated divergence dates among the living phyla vary widely, from just under 600 million to well over 1 billion years ago. Nonetheless, even the youngest estimated divergence dates are in the Proterozoic and suggest an unpreserved history of some tens of millions of years.

It therefore seems plausible that the first appearance of animal phyla in the Cambrian was not mainly a divergence of lineages but rather a series of evolutionary events in which the skeletal and other anatomical traits that characterize the phyla were acquired over a period of just 10 to 20 million years. This suggests rapid rates of morphological evolution, which can be assessed by comparing the range of anatomical diversity or disparity [SEE SECTION 8.10] that evolved during the Cambrian with that which accumulated during the rest of the Phanerozoic.

The arthropods are one of several animal groups that rapidly increased in disparity during the Cambrian. Figure 10.7 portrays Cambrian and Recent arthropods ordinated along three axes that summarize multivariate morphological data in much the same way as principal components do [SEE SECTION 3.2]. The plot depicts 24 Cambrian taxa that are sufficiently well preserved for the morphological features to be observed, and 24 Recent taxa that were chosen to represent the living classes and subclasses. The Cambrian and Recent taxa are indicated in oblique and plain type, respectively. The most striking

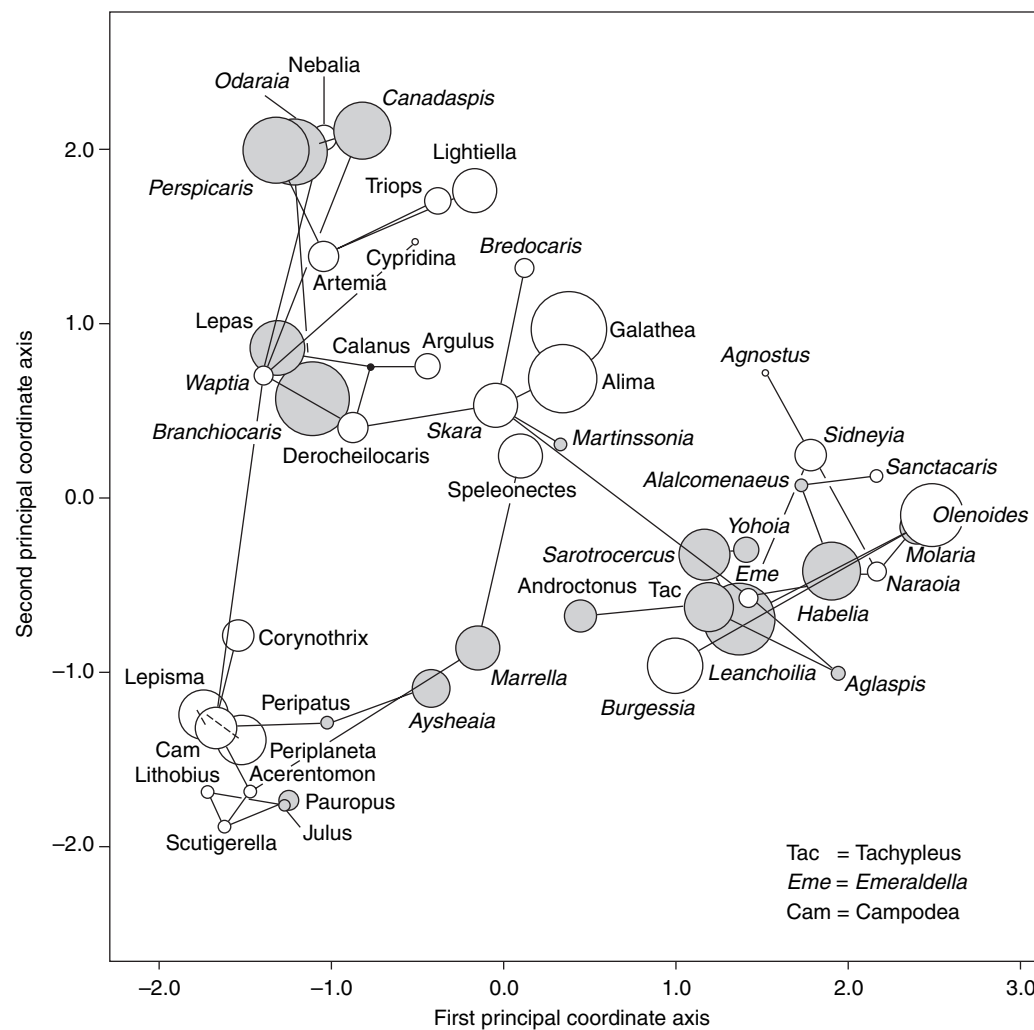


FIGURE 10.7 Ordination of Cambrian and Recent arthropods based on multivariate morphological data and using a method similar to principal-component analysis [SEE SECTION 3.2]. Cambrian taxa are indicated in oblique type, Recent taxa in plain type. The original data from which these axes were formed consist of about 120 morphological characters having two or more character states. The third dimension in this plot is represented by the size and shading of the circles; dark circles are positive values while open circles are negative, and larger circles represent larger positive or negative values. In addition, lines are drawn between taxa that are most similar to each other on the basis of the entire set of characters that were studied. This plot shows that Cambrian marine arthropods were as diverse in morphology as are living forms. (From Wills *et al.*, 1994)

feature of Figure 10.7 is that Cambrian and Recent taxa are about equally dispersed. When the morphological distances between taxa are measured [SEE SECTION 8.10], the disparity of Cambrian arthropods is indistinguishable from that of Recent forms. Cambrian arthropods evolved a range of anatomical form that was not exceeded subsequently in over 500 million years. This same conclusion has been drawn from similar studies of priapulid worms and a few other groups.

The work on arthropod morphology suggests that rates of morphological evolution were much greater in the Cambrian than afterwards, and that morphological diversity has not increased substantially since the Cambrian Explosion. In fact, this question is not quite settled. There are at least three reasons for continued debate. First, Cambrian and post-Cambrian disparity have been compared for relatively few animal phyla. Although selected classes have been studied, we still do not have phylum-level analogs of Figure 10.7 for molluscs, echinoderms, brachiopods, sponges, cnidarians, and so on.

Second, some studies of morphological diversity have simply compared the Cambrian and the Recent, with little attention paid to the intervening time. It is conceivable that arthropod disparity increased substantially over the past half billion years and then declined to a level comparable to that of the Cambrian. This would imply that post-Cambrian evolution was not as limited as suggested by Figure 10.7.

Third, the traits studied represent a limited part of the overall anatomy of the organisms in question, and they have comparatively little discriminatory power. For example, a shrimp and a lobster are essentially identical with respect to the kinds of traits that have been used to compare disparity in Cambrian and Recent arthropods. This coarse resolution, which is nearly inevitable when studying such a wide range of organisms [SEE SECTIONS 2.2 AND 5.3], has left a number of workers skeptical as to whether the true history of disparity has been adequately documented. In what follows, we accept for the sake of discussion that evolutionary innovation was unusually pronounced in the Cambrian, but it is important to bear in mind that there is still debate about this point.

Reasons for the Cambrian Explosion

In explaining the Cambrian Explosion, just as in documenting the basic sequence of events, it is impor-

tant to distinguish between the splitting of lineages and the evolution of novel body forms. With respect to lineages, why is it that phylum and class originations are concentrated early in animal history, as shown in Figures 8.29 and 10.1?

A simple possibility, suggested by paleontologist David Raup, comes from mathematical modeling of the shape of evolutionary trees. Consider the partial evolutionary tree of Figure 10.8a, simulated with a computer program that holds the per-capita rate of origination and extinction constant over time [SEE SECTION 7.2]. Of the many species produced by this simulation, 28 are still extant at the “present day.” Each pair of species can be traced backward in time to the point at which the lineages leading up to the two species first diverged. For example, the two species farthest to the left within group A diverged just a single time increment before present. By similar reasoning, any pair consisting of one species from group A and one from group B can be traced back to a divergence at 21 time units before present. Likewise, any species from group A or B has a divergence time of 47 relative to any species from C or D, and so on.

With 28 living species, there are $28 \times 27 \div 2$, or 378 possible species pairs. [In general, if a group has N species, then there are $N \times (N - 1) \div 2$ species pairs within the group. For two groups with N_1 and N_2 species, there are $N_1 \times N_2$ between-group pairs.] If we tally the frequency distribution of divergence times, as in Figure 10.8b, we find that the majority of them—greater than two-thirds—are at either 41 or 47 time units before present.

The expected distribution of divergence times can be calculated exactly for any given rate of origination and extinction. As it turns out, the tree in Figure 10.8a represents a case of unrealistically high rates [SEE SECTION 7.2]. Trees produced with empirically reasonable rates—with species durations on the order of 1 to 10 million years (m.y.)—yield living species whose divergences can be extended much farther back in time than those of Figure 10.8a. In fact, for a wide range of origination and extinction rates, more than 90 percent of all possible pairs of living species are expected to share divergence times greater than 500 m.y. ago. The distribution of divergence times is dictated by the geometry of evolutionary trees, with many extinct species and with just a few living ones that can trace their common ancestry to divergence events deep in the past.

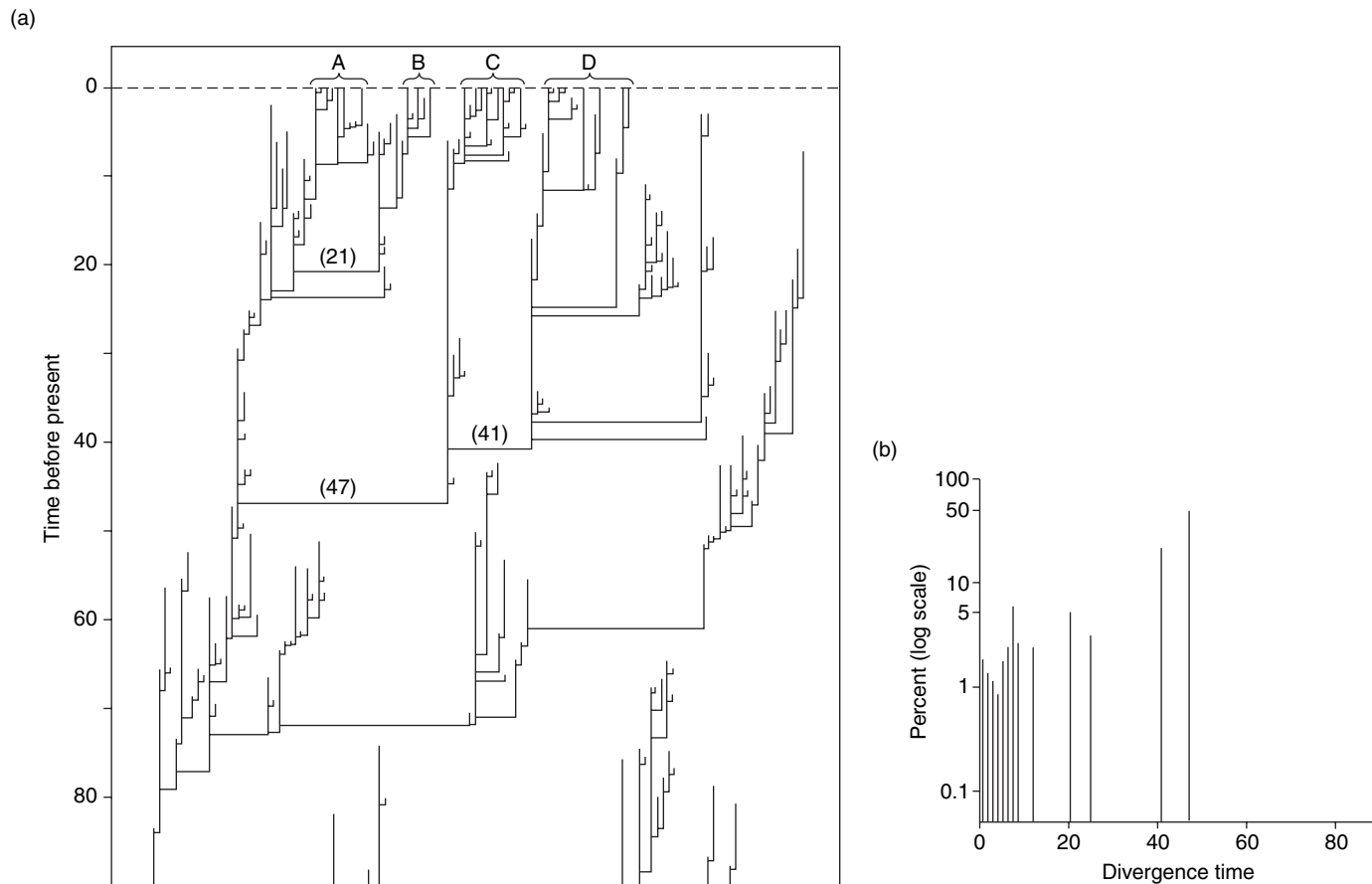


FIGURE 10.8 Mathematical modeling of the expected divergence times of living species, assuming that origination and extinction rates are constant over time. (a) A hypothetical evolutionary tree, with living species divided into four groups. Any species in group A and any species in group B share a latest common ancestor at 21 time units before present; this is the divergence time of the pair of species. Similar reasoning holds for other species pairs. (b) The frequency distribution of divergence times, showing that about two-thirds of all pairs of living species have divergence times of either 41 or 47 time units before present. (From Raup, 1983)

This result of the mathematical model is best appreciated by comparison with actual divergence times of living species. Although not known in detail, they can readily be sorted into those that involve pairs of species within the same phylum versus pairs of species in different phyla. Between-phylum pairs must have diverged at or before the time of divergence of their respective phyla, while within-phylum pairs must have diverged afterward. If we focus on the paleontologically important phyla that are still alive today, all except the Bryozoa had originated by the end of the Cambrian, about 500 m.y. ago, with the Bryozoa appearing in the Early

Ordovician, by 480 m.y. ago. If most species pairs today are between-phylum pairs, then most species divergences are older than 480 m.y. It would then stand to reason that the early origin of the phyla could in principle be explained by the geometry of evolutionary trees.

Species diversity and numbers of species pairs are given in Table 10.1 for the living representatives of the main fossil groups. There are more than 180,000 living species in these groups, and nearly 17 billion species pairs. Of these pairs, nearly 80 percent are between-phylum pairs and therefore represent divergences older

TABLE 10.1

Number of Living Species in Paleontologically Important Groups and Number of Species Pairs that Represent Divergences within the Same Phylum and between Different Phyla

Phylum	Number of Species	Within-Phylum Pairs
Annelida	11,600	6.72×10^8
Arthropoda	50,000	1.25×10^9
Brachiopoda	325	5.26×10^4
Bryozoa	5000	1.25×10^7
Chordata	45,000	1.01×10^9
Cnidaria	9000	4.05×10^7
Echinodermata	6000	1.80×10^7
Mollusca	50,000	1.25×10^9
Porifera	5000	1.25×10^7
Total species:	181,925	
Total species pairs:	1.65×10^{10}	
Total within-phylum pairs:	3.66×10^9	
Total between-phylum pairs:	1.29×10^{10}	
Percent of pairs within phyla:	22%	
Percent of pairs between phyla:	78%	

SOURCE: Valentine (2004); Barnes, Calow, & Olive (1993). Species count for arthropods excludes terrestrial arachnids and insects.

than 480 m.y. We therefore see that the actual distribution of divergence times is roughly in accord with the expectations of the simple mathematical model. This suggests that branching geometry may largely explain the early origins of phylum-level groups. Similar reasoning can be applied to the early origins of classes as depicted in Figure 8.29.

Turning now to the morphological aspect of evolution, why was the Cambrian a time of profound anatomical innovation? Many animal phyla share fundamental genetic pathways for body patterning and other important aspects of anatomy. One class of genes involved are the *Hox* genes, which were discussed in Chapter 4 [SECTION 4.2]. Figure 10.9 shows the phylogenetic relationships among some of the animal phyla, based on genetic sequences that do not include these *Hox* genes. Superimposed on this phylogeny is the number of *Hox* genes present in the living representatives of each phylum. Cladistic parsimony [SEE SECTION 4.2] allows one to estimate the character states present in the common ancestor to two sister taxa. Among BILATERIAN phyla—namely, all animals except sponges, cnidarians,

ctenophores, and some obscure groups—the smallest number of *Hox* genes is four. When evidence for secondary reduction in the nematode lineage is taken into

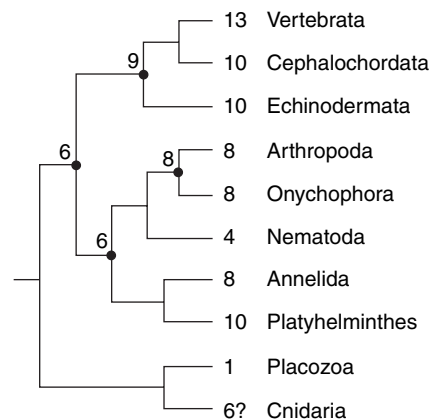


FIGURE 10.9 One estimate of cladistic relationships among selected animal phyla and subphyla, with the number of *Hox* genes to the left of the group name.

The numbers at nodes indicate the minimal number of *Hox* genes in the common ancestor to the sister taxa connected by the node. (From Valentine et al., 1999)

account, it seems probable that the common ancestor to the bilaterians had at least six *Hox* genes. If the phyla that share the corresponding genetic pathways today diverged from one another in the Proterozoic, this would suggest that *Hox* genes and other major genetic pathways were already in place well before the Cambrian Explosion, implying that it is something other than the acquisition of these pathways that led to the Cambrian Explosion.

Two main proposals have been offered to explain the burst of evolutionary innovation in the Cambrian. The first is that there was some trigger, or the release of a constraint, in the physical environment. The second is that innovations in some lineages changed the ecological world in a way that promoted evolutionary responses in other lineages. These explanations are not mutually exclusive, and in both cases there is still considerable uncertainty about the exact details.

With respect to external environment, lower oxygen levels prior to the Neoproterozoic may have limited gas exchange, thereby placing an upper bound on the size that animals could attain [SEE SECTION 2.3]. There is geochemical evidence for an increase in oxygen through much of the Proterozoic Eon. A Neoproterozoic surge, which may be implicated in animal evolution, is suggested by the record of carbon isotopes in marine sediments. Carbon has two stable isotopes, ^{12}C and ^{13}C . Lighter ^{12}C is preferentially incorporated into organic tissue during photosynthesis. Isotopically light organic carbon produced in the shallow oceans is transferred to deeper waters and to the sediment when it sinks (often as part of fecal pellets). If this organic carbon is buried, the oceans by default are enriched in ^{13}C because of the removal of ^{12}C . Organic carbon and the carbon in precipitated carbonate minerals will then show the signal of heavier carbon. Observed increases in ^{13}C in the geologic record may therefore indicate increased burial of organic carbon. This in turn means that less oxygen would be consumed in the oxidation of carbon. Thus, an increase in ^{13}C could indicate an increase in available oxygen. Exactly such changes in the record of carbon isotopes are observed toward the end of the Proterozoic.

With respect to ecology, there is no firm evidence of predation in the Proterozoic, while bite marks, gut contents, and morphological features that make sense only as predatory adaptations show that predation was well established by the Middle Cambrian (Figure 10.6). The armored skeletons that characterize a number of Cambrian forms may have evolved in response to predation. Com-

plex ecological relationships were clearly in place during the Cambrian, and such interactions between organisms would have provided a new suite of selective pressures that may have led to anatomical innovations.

As to why nothing as profound as the Cambrian Explosion has happened since, two principal explanations have been proposed. First is the idea that ecological opportunities as great as those present in the “empty” Cambrian world were never seen again (see Figure 8.29). Second is the concept that genetic and developmental systems of animals eventually became specialized or channeled in such ways that major innovations—of the kind that would lead to new phyla—were not possible after the Cambrian.

Because these two explanations make many similar predictions—for example, that evolutionary transitions in morphology should become smaller over time—the relative importance of the two has not yet been fully assessed. Testing these two possibilities against each other remains one of the most challenging and intriguing tasks as paleontologists continue to make sense of the Cambrian Explosion.

10.3 THE LATE PERMIAN EXTINCTION

Just as the Cambrian Explosion forever changed the course of animal evolution, one extinction event stands out because of the extent to which it profoundly altered life on earth. In the later part of the Permian Period, over 40 percent of the marine animal families and over 60 percent of the genera became extinct [SEE SECTION 8.6]. Numerous classes and orders also vanished, including trilobites, rugose and tabulate corals, blastoid echinoderms, rostroconch molluscs, and cystoporate bryozoans. Many of the clades that did survive were reduced to just a few lineages. Terrestrial vertebrates, insects, and some plant groups were also affected. These significant changes in biotic composition mark the end of the Paleozoic Era. Study of the Late Permian extinction has focused on three central questions:

1. Over how much time were the extinctions spread, and were they synchronous globally?
2. Can anything be learned from investigating the geographic locations of taxa that became extinct?
3. What caused the extinctions?

Timing of Extinctions

Because species have limited geographic and environmental ranges, biostratigraphic correlation is always difficult on a global scale. It is even harder than usual in the Late Permian and Early Triassic because of a sparse distribution of outcrops. There are nonetheless a number of regions around the globe where the Permian–Triassic transition is preserved. These include the Armenian–Iranian border region, Kashmir, and southern China. In these and other areas, striking faunal changes are seen in the Late Permian, but does this imply that the extinctions were synchronous everywhere? Biostratigraphic correlation always requires the assumption of synchronicity to some extent [SEE SECTION 6.1], but it would obviously be circular to start with the assumption that a particular set of extinctions occurred simultaneously around the world, then use the assumption to correlate local stages with each other, and then to use the correlation to infer synchronous extinction.

Ideally, one would assess synchronicity with high-resolution numerical dating, but the requisite conditions are not met everywhere. The standard approach to this problem is therefore to develop a correlation scheme

with one set of fossils, preferably those that have the desirable properties of index fossils [SEE SECTION 6.1], and to use the resulting correlation to study evolution and extinction in other groups of organisms. In the case of the Late Permian and Early Triassic, a global zonation has been constructed using the pelagic conodonts. This allows us to determine that, for data collected at the global scale, extinctions of marine genera were elevated in the Guadalupian Epoch and in the later part of the final stage of the Permian, the Changhsingian. Available data suggest that extinctions of terrestrial vertebrates may also have been concentrated in the Changhsingian.

While global analysis of marine genera indicates elevated extinction during the Changhsingian, the global data are not sufficiently well resolved to determine over precisely how much of the stage the extinctions were spread. To study the timing at a finer level of resolution, it is necessary to turn to local and regional data. Among the most thoroughly documented Late Permian through Early Triassic sections are those in southern China. Figure 10.10 shows the stratigraphic ranges of over 300 marine species in a series of sections at Meishan. A composite section was constructed by tracing distinctive clay beds among the individual

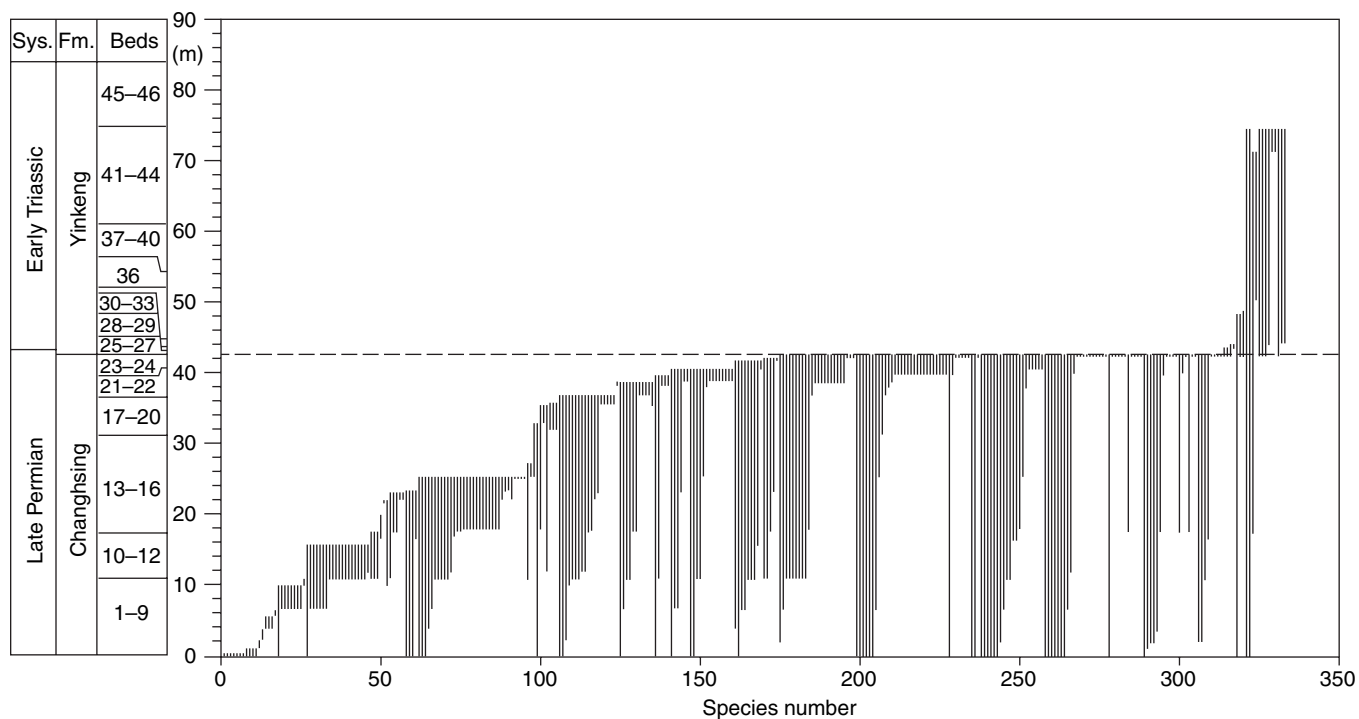


FIGURE 10.10 Stratigraphic ranges of marine species at Meishan, southern China, shown relative to a composite of several sections. The greatest concentration of last appearances is at the base of bed 25. (From Jin *et al.*, 2000)

sections, and the ranges are given relative to this composite. This reveals that the last appearances of species are not evenly spread throughout the last stage of the Permian. Rather, they are most strongly concentrated near the bottom of bed 25.

Over how much time are the last appearances spread in the sections at Meishan? Fortunately, the Meishan beds are interbedded with volcanic ashes that can be radiometrically dated [SEE SECTION 6.1]. An ash below bed 21 has a radiometric date of 252.3 million years old, and one within bed 25 has a date of 251.4 million years old (Bowring et al., 1998). Therefore, most of the last appearances occurred within about a million years or less. If the rate of accumulation of beds 21–24 was even approximately uniform, the extinctions at the base of bed 25 must represent substantially less than 1 million years.

The outstanding question is whether extinctions were concentrated in an equally short time, and at the same stratigraphic level, throughout the globe. For the most part, biostratigraphic resolution is not fine enough to provide an answer. Hopefully, future radiometric dating at other boundary sections, similar to the work at Meishan, will enable this question to be addressed.

Environmental Change, Biogeography, and Extinction Mechanisms

As noted in Chapter 8, to understand the causes of major changes in global biodiversity, it is helpful to consider them in a geographic context. During the Paleozoic Era, many of the continents familiar to us today were located in rather different places than they are at present [SEE SECTION 9.6]. In fact, several major present-day regions, such as Europe and China, are actually agglomerations of several smaller, Paleozoic paleocontinents that subsequently collided with one another. In addition, epicontinental seas—very broad, shallow seas that covered large expanses of continental interiors—were quite common in the Paleozoic. One of the most striking aspects of the transition from the Paleozoic to the post-Paleozoic is the decline and near-loss of these settings [SEE SECTION 1.4].

During the late Paleozoic and culminating in the Permian, many of the world's paleocontinents coalesced to form the supercontinent known as Pangea (Figure 10.11). In association with the formation of Pangea, many shallow-water areas around the world became fully emergent. It was once the prevailing view of

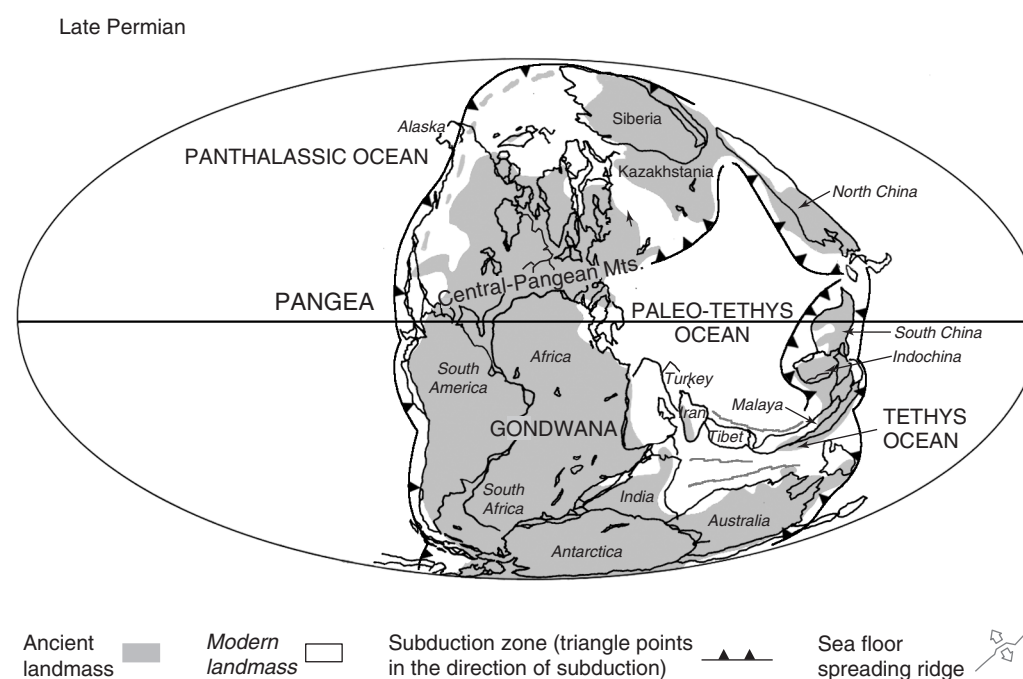


FIGURE 10.11 Global paleogeographic map, showing the positions of paleocontinents during the Permian period. There was a decline in the extent of epicontinental seas in the Permian, relative to much of the rest of the Paleozoic, in association with the formation of the supercontinent Pangea. (From the Web site of The Paleomap project, www.scotese.com/earth.htm)

paleontologists that this loss of shallow-water area caused the Late Permian extinction, at least among marine organisms. Indeed, it appears that entire marine faunal provinces dried up during the Late Permian (Figure 10.12), so it is difficult to dismiss the possibility that the loss of these marine settings played a significant role in the Guadalupian extinction interval.

Given the likelihood that the end-Changhsingian extinction occurred very rapidly (Figure 10.10), however, the emerging view is that it was caused by some mechanism(s) more catastrophic than that associated with the comparatively slow draining of shallow-water areas over a period of perhaps several million years. A clear consensus has yet to emerge about the primary cause of this end-Permian event, but there is growing evidence that the boundary between the Permian and Triassic periods was marked by events that were catastrophic in nature, including a massive volcanic eruption in Siberia, widespread anoxia in marine settings, and, possibly, the impact of one or more large comets or asteroids. There was also a series of dramatic shifts in carbon isotope ratios that appear to rival those exhibited during the Neoproterozoic, but the nature and causes of these shifts are still not entirely understood and remain under active investigation.

If continued scrutiny supports the idea that there were two phases of extinction (Guadalupian and Changhsingian), this will lend credence to a growing perception that several, if not all, of the major Phanerozoic mass extinctions were more complex temporally than once thought. In the end, we may discover that mass extinctions occurred at times when several things went wrong at around the same time, resulting in an overlapping set of biotic responses to two or more mechanisms.

10.4 THE PALEOCENE–EOCENE THERMAL MAXIMUM

Grounded in the collection and analysis of extensive sets of deep-sea cores (e.g., Figure 9.1b), a detailed picture is beginning to emerge of the intimate relationship between the earth's climate and major biotic transitions throughout the Cenozoic Era. Geochemical analyses of the skeletal compositions of foraminifera and other organisms preserved in these cores have permitted the detection of high-resolution, stratigraphic transitions in $\delta^{18}\text{O}$.

As noted in Chapter 9 [SECTION 9.5], assessments of $\delta^{18}\text{O}$ transitions in deep-sea cores are based on strati-

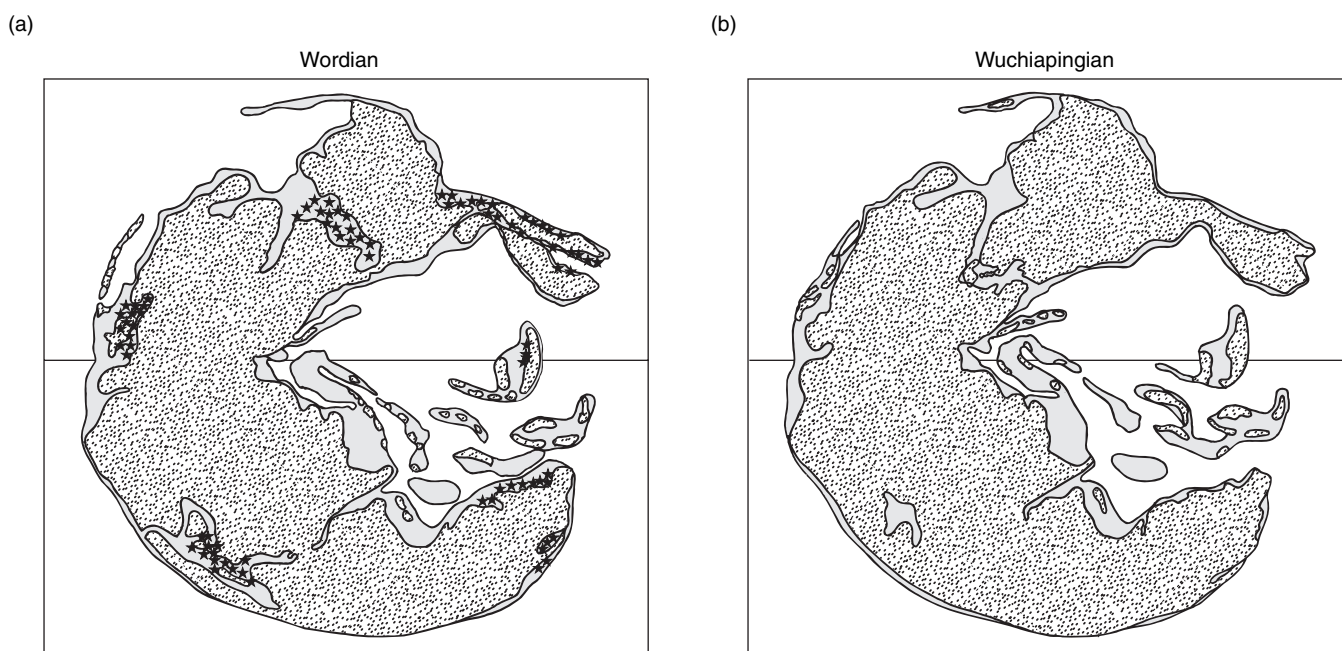


FIGURE 10.12 Paleogeographic maps illustrating the loss of major brachiopod faunas [indicated with stars in part (a)] through the Late Permian. Land areas are stippled, shallow-water areas are represented in grey, deeper water in white. In most cases, the loss of brachiopod faunas can be attributed to the loss of shallow-water areas that harbored them. Note that most of the starred regions in part (a) coincide with shallow-water areas that become emergent in part (b). (From Shen & Shi, 2002)

graphic variations in the average compositions of the skeletons of microorganisms. Because taxa differ in their propensities to fractionate oxygen, it is standard practice in these analyses to assess patterns separately for several species. If all or most of the species exhibit similar stratigraphic variations in $\delta^{18}\text{O}$, this demonstrates that the changes transcend the peculiarities of particular taxa.

In many cases, long- and short-term transitions in $\delta^{18}\text{O}$ can be recognized in correlated horizons around the world, indicating that they are diagnostic of global climatic shifts, which, in turn, have been linked to major transitions in marine and terrestrial biotas recognized throughout the Cenozoic. James Zachos and colleagues (2001) have compiled a global record of deep-sea $\delta^{18}\text{O}$ for the Late Cretaceous through the Cenozoic. This provides evidence of major episodes of warming and cooling during the first half of the Cenozoic, as indicated by positive (cooling) and negative (warming) excursions in $\delta^{18}\text{O}$ [SEE SECTION 9.5]. Particularly pronounced among these episodes is a warming interval from the Paleocene into the Early Eocene, followed by a protracted interval of cooling through the rest of the Eocene.

Superimposed on the long-term $\delta^{18}\text{O}$ trend are a series of short-term spikes, the most prominent of which is a sharp, negative excursion near the Paleocene–Eocene Boundary, some 55 million years ago (Figure 10.13a). This excursion has now been recognized globally, in the tropics as well as at high latitudes, and has been documented for many species of foraminifera. Based on the size of the $\delta^{18}\text{O}$ excursion, Zachos and colleagues have estimated that the size of the sea-surface temperature increase was 8° to 10°C at high latitudes and 5° to 8°C in the tropics, although other studies have suggested that the difference in warming between low and high latitudes may not have been so great. Furthermore, the shape of the $\delta^{18}\text{O}$ excursion indicates that this remarkable increase, which is known as the *Paleocene–Eocene Thermal Maximum* (PETM), occurred in fewer than 10,000 years. The subsequent “recovery” from the PETM was somewhat more protracted, taking place over about 200,000 years, although the entire Early Eocene was apparently characterized by the warmest temperatures of the Cenozoic.

Causes of the PETM

There is evidence suggesting that the PETM was associated with a catastrophic release of methane (CH_4) that had been sequestered previously in CH_4 hydrates, crystalline solids that effectively trap CH_4 in ice. In the

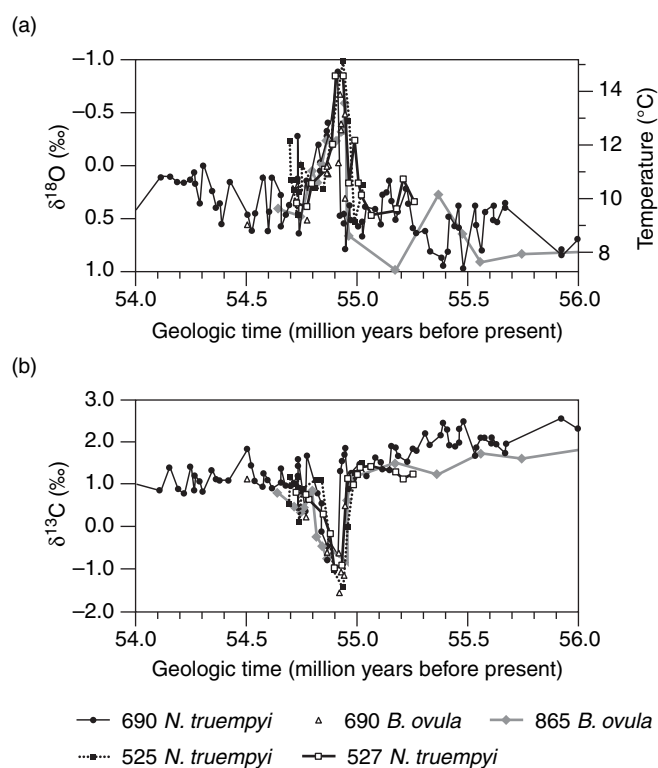


FIGURE 10.13 Significant excursions in $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ near the Paleocene–Eocene boundary, as recorded by multiple foraminiferal species preserved in a series of deep-sea cores collected from sites in the southern Atlantic (525, 527, and 690) and western Pacific (865) oceans.

(a) $\delta^{18}\text{O}$. The temperature scale on the right is based on the establishment of an empirical relationship between the size of a $\delta^{18}\text{O}$ excursion and the temperature excursion associated with it, under the assumption (appropriate in this case) that the oceans were ice-free at the time. (b) $\delta^{13}\text{C}$, showing substantial decline. (From Zachos et al., 2001)

present day, CH_4 hydrates are found in Arctic permafrost regions as well as in cold, marine settings, and the amount of CH_4 sequestered globally in this form is sufficiently extensive that it has even attracted the attention of researchers who view it as a major, new societal source of energy. Importantly, the CH_4 sequestered in CH_4 hydrates is known to be enriched in ^{12}C , which, as we noted earlier in this chapter, is indicative of a biogenic origin. This is relevant to our consideration of the PETM because, in addition to the negative $\delta^{18}\text{O}$ excursion, the PETM is also characterized by a major negative excursion in $\delta^{13}\text{C}$ —that is, an enrichment in ^{12}C (Figure 10.13b).

Of course, this does not *prove* that the release of CH_4 hydrates caused the $\delta^{13}\text{C}$ excursion or the PETM.

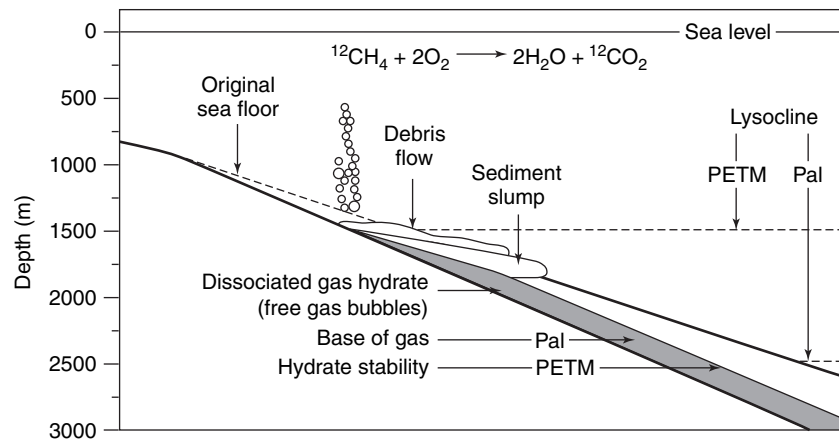


FIGURE 10.14 Schematic representation of a proposed model for the catastrophic release of methane (CH_4) as the cause of the Paleocene–Eocene Thermal Maximum (PETM). In the scenario illustrated, ongoing warming during the Late Paleocene (Pal) caused the release of methane gas bubbles that had previously been frozen. This induced major slumping that, in turn, caused a far more substantial release of methane. This is hypothesized to have caused a significant elevation of carbon dioxide (CO_2) levels in the atmosphere, inducing significant global warming and a shallowing of the lysocline. (From Katz *et al.*, 1999)

However, to date, CH_4 hydrates are among the only plausible sources known for the large amount of ^{12}C required to account for an excursion of the size observed. Moreover, a viable model has been proposed by Gerald Dickens and colleagues (1995) to account for this scenario and its relationship to the PETM (Figure 10.14).

The following sequence of events is envisioned: (1) Some CH_4 that was sequestered in hydrates on the continental slope was released as gas bubbles when subjected to the moderately increased temperatures associated with the long-term warming trend that preceded the PETM; (2) this release, in turn, caused a collapse in the pore space between sedimentary grains on the sea floor, inducing catastrophic sediment slumping and the associated release of a much larger quantity of CH_4 at water depths ranging from about 900 to 2000 m, the zone in which the estimated temperature increase would have promoted CH_4 release (i.e., the dissociation of the hydrates); (3) mediated by bacteria, the released CH_4 reacted with oxygen, which produced significant quantities of carbon dioxide (CO_2 ; see the equation for this reaction in Figure 10.14).

The major infusion of CO_2 into the global system should have affected marine and terrestrial settings alike. In marine settings, the addition of CO_2 likely promoted the dissolution of calcium carbonate, manifested in part as a shallowing of the lysocline (the depth in the oceans beneath which carbonate dissolution greatly increases).

This should have had a deleterious effect on calcium-carbonate-secreting organisms in these settings. Moreover, a major influx of CO_2 into the atmosphere would have induced an episode of global warming that significantly amplified the ongoing slow warming trend already underway. Given that CH_4 is, if anything, a more potent greenhouse gas than CO_2 , global warming would have ensued even if the CH_4 had not been converted to CO_2 . But under the hypothesized conditions, it seems likely that conversion to CO_2 indeed occurred.

Ideally, any test of this scenario should include physical and biological evidence of the postulated sequence of events. Such evidence was provided by Miriam Katz and colleagues (1999) based on data from a deep-sea site near the Bahamas, where a core was collected that includes the critical interval. Analysis of this core diagnosed a major decline in the number of benthic foraminiferal taxa from about 30 to fewer than 10, which coincides stratigraphically with negative excursions in $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$. This lends credence to the suggestion that a combination of warming and enhanced dissolution of calcium carbonate caused the loss of foraminiferal taxa observed at this site, as well as elsewhere around the world. Furthermore, a layer of mud clasts was observed immediately below the $\delta^{13}\text{C}$ excursion, indicating a major disturbance just prior to the onset of the excursion. This offers tantalizing evidence for a perturbation like that predicted by the catastrophic release of CH_4 .

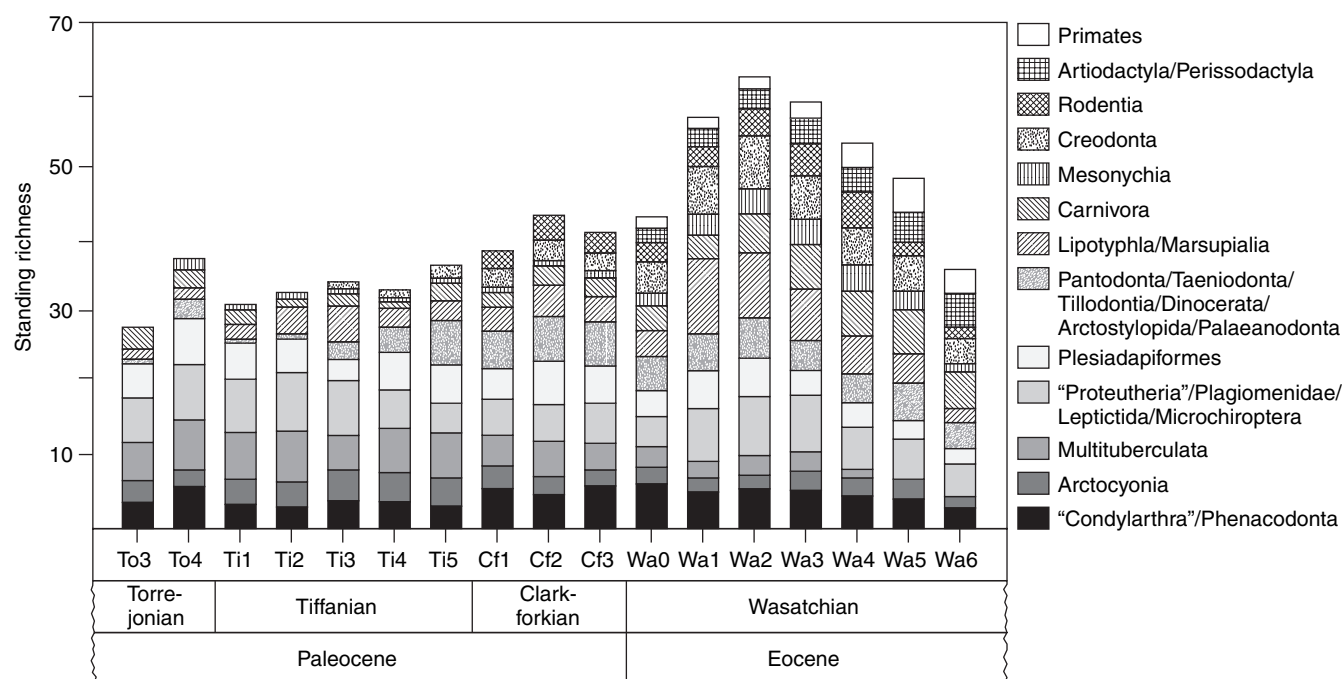


FIGURE 10.15 Transitions in the genus richness of major mammalian orders across the Paleocene–Eocene boundary in Wyoming and Montana, based on assessments in 17 separate faunal zones. Note that, as the boundary is crossed, primates, artiodactyls, and perissodactyls appear for the first time. (From Maas *et al.*, 1995)

Seismic profiles collected through the region also show chaotic reflections at the horizon in question, indicating a set of disturbed sedimentary layers. Finally, analyses of $\delta^{13}\text{C}$ in Late Paleocene–Early Eocene terrestrial samples, such as the tooth enamel of herbivorous mammals and carbonates contained in ancient soil-horizons (Koch *et al.*, 1992), demonstrate that geochemical changes associated with the PETM occurred in terrestrial and marine settings alike.

Biological Effects

As suggested by the foraminiferal decline in the deep-sea core from the Bahamas, the PETM was marked by a major extinction of foraminifera. The biotic effects of the PETM were not limited to marine settings, however. A growing number of studies of terrestrial vertebrate and plant biotas have yielded evidence of profound biogeographic and paleoecological transitions that mark the interval, some of which reverberate today.

Among terrestrial vertebrates, analyses of the fossil mammalian record in Wyoming and Montana by Mary Maas and colleagues (1995) illustrate well that the

PETM marks the first appearances of several modern mammalian orders (Figure 10.15) that would come to dominate terrestrial ecosystems thereafter, including primates and hoofed mammals (artiodactyls and perissodactyls). While the Wyoming and Montana occurrences likely reflect the first appearances of these taxa in North America, recent studies suggest that they originated elsewhere—quite possibly in Asia. Gabriel Bowen and colleagues (2002) analyzed carbon isotopic records from localities in Hunan Province, China, that also contain fossil primates, artiodactyls, and perissodactyls. They were able to recognize the negative $\delta^{13}\text{C}$ excursion that marks the PETM.

Strikingly, the first appearances of perissodactyls can be tied to strata that demonstrably precede the PETM, indicating that they occurred in Asia earlier than in North America. The first appearances in China of artiodactyls and primates appear to coincide with the PETM. This suggests that these taxa occurred at least as early in Asia as in North America, leaving open the possibility that, like perissodactyls, they originated in Asia and subsequently migrated to North America. In any case, it seems clear that the PETM had a lasting effect on the diversification and distribution of terrestrial mammals.

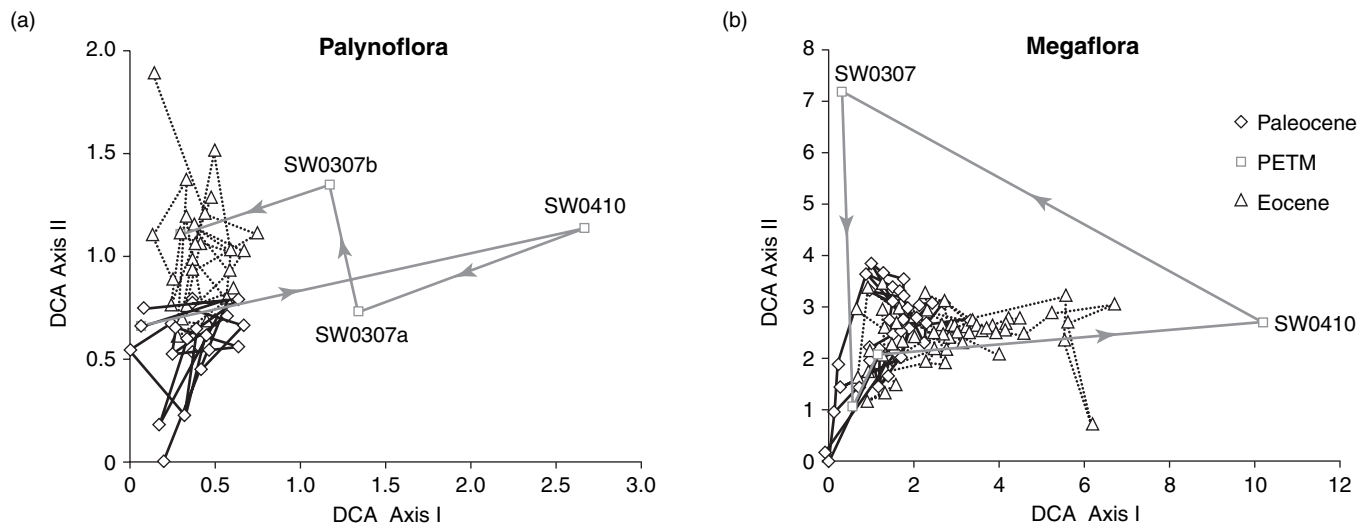


FIGURE 10.16 Paleobotanical transitions associated with the PETM in northern Wyoming. (a, b) Detrended correspondence analyses (DCA) of the palynoflora (e.g., pollen) and the megafloora (e.g., leaves and stems) contained in samples collected from below, within, and above the interval containing the PETM. Positions of samples with respect to DCA axes reflect differences in paleofloral composition. Labeled samples are for intervals contained within the PETM. Lines are drawn to connect samples in stratigraphic sequence, with arrows indicating the upward direction. Note that the compositions of samples within the PETM interval are decidedly different from those in intervals below and above the interval. (c) A map of the United States illustrating sites to the south and west of Wyoming containing Paleocene and Eocene floral elements that are restricted to the PETM interval at the two Wyoming localities labeled on the map. (From Wing et al., 2005)

That the PETM had a significant, but perhaps more ephemeral, impact on terrestrial plant biotas is suggested by an analysis of paleofloras that bracket the PETM in north-central Wyoming. The stratigraphic positions of samples collected throughout this interval were tied by Scott Wing and colleagues (2005) to strata located beneath, within, and above the PETM interval. Stratigraphic correlations were based on analyses of $\delta^{13}\text{C}$ (including the sharp negative excursion at the base of the PETM) and diagnostic elements of the mammalian fauna.

Wing and colleagues conducted separate analyses of the megafloora (macroscopic material, mainly leaves and stems) and palynoflora (microscopic material, mainly pollen). Detrended correspondence analyses [SEE SECTION 6.3] of samples collected throughout the interval revealed similar patterns for both sets of data (Figures 10.16a and 10.16b): Collections from within the PETM had compositions that were quite unusual when com-

pared with those from below and above the PETM. The compositional shift was caused by the inclusion in these samples of non-native taxa that were known to have occurred earlier in more southerly regions (Figure 10.16c) and therefore represent a migration that was almost certainly related to the warming event [SEE SECTION 9.6]. As the PETM came to a close, floras reverted back to compositions that were similar, but generally not identical, to their pre-PETM counterparts.

Wing and colleagues also conducted leaf margin analysis (LMA) and leaf area analysis (LAA) [SEE SECTION 9.5] of fossil leaf specimens collected throughout the interval, through which they diagnosed a temperature increase of about 5°C , as well as a 40 percent decline in mean annual precipitation with the onset of the PETM. Near the end of the PETM, precipitation levels rebounded to normal values. The temperature change diagnosed with LMA in this terrestrial setting is compa-

rable to that recognized for tropical sea-surface temperatures based on $\delta^{18}\text{O}$ measurements derived from foraminifera in deep-sea cores.

Furthermore, the PETM appears to have had a significant effect on ecological interactions among taxa, as demonstrated by an analysis of insect damage on fossil leaves [SEE SECTION 9.4] conducted by Peter Wilf and Conrad Labandeira (1999). In the present day, there is a marked increase in the rate of leaf predation toward the tropics, and Wilf and Labandeira hypothesized that, if this pattern relates to the warmer temperatures of the tropics (which is not a certainty), then we might expect to observe an increase in predation-related leaf damage during the PETM. To test this hypothesis, they compared the incidence of insect-produced leaf damage with fossil specimens from the Upper Eocene and Lower Paleocene collected from southwestern Wyoming.

The results demonstrate a significant increase in leaf predation by insects during the PETM (Figure 10.17). While the rate of predation increased substantially on leaves of Betulaceae (birch trees, a group whose leaves are known to be particularly palatable to insects in the present day), other plant groups were affected as well. In addition, Wilf and Labandeira observed an increase in the diversity of damage types exhibited by Eocene leaves.

Therefore, it is clear that the PETM profoundly affected terrestrial and marine life in ways that may be particularly instructive with respect to what we should expect in the face of present-day global warming. To be sure, there is still a long way to go in understanding the fabric of evolutionary transitions associated with the PETM (e.g., the development of a phylogenetic framework for the mammalian transition described earlier). Nonetheless, the range of ongoing investigations has already shown that a coupling of paleontological and geochemical data holds great promise for understanding the relationship between global climatic fluctuations and biotic transitions, and also for developing high-resolution correlations between marine transitions and their counterparts in the terrestrial realm.

10.5 PLEISTOCENE MEGAFANAL EXTINCTIONS

The case of Late Permian extinctions illustrates the importance of temporal resolution in documenting and understanding major evolutionary events. In that example, so remote in time, resolving a last appearance to the

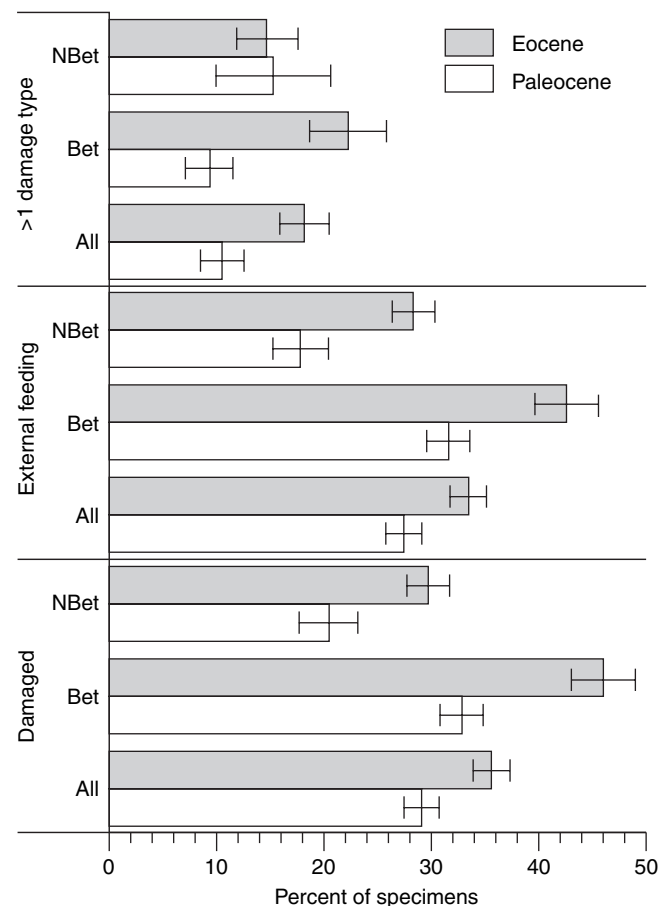


FIGURE 10.17 Changes across the Paleocene–Eocene boundary in the percentages of fossil leaf specimens containing damage by insects, as indicated by an analysis conducted in southwestern Wyoming. Bet and NBet are abbreviations for Betulaceae and non-Betulaceae. Predation is more pronounced in the Eocene, regardless of whether the analysis is restricted to the particularly ubiquitous and palatable Betulaceae (birches). The middle set of bars illustrates that much of the increase can be attributed to an increase in external feeding, as opposed to internal mining and other means of leaf damage. Moreover, the upper set of bars illustrates that there is an increase in the percentage of leaves exhibiting more than one kind of damage. (From Wilf & Labandeira, 1999)

nearest 100,000 years and determining that the extinctions were concentrated in an interval of less than 1 million years are significant accomplishments. With respect to the most recent extinction event in the fossil record, that of large terrestrial vertebrates in the Late Pleistocene, it has often been possible to resolve the geologic ages of individual specimens and the disappearances of species to within 1000 years. This extreme precision has been essential in inferring the causes of extinction.

The Nature of Late Pleistocene Extinctions

About 2.5 million years ago, the earth's climate entered its most recent glacial phase. We are now in an interglacial cycle but still overall in a glacial age. Toward the end of the last fully glacial interval—the end of the Pleistocene Epoch, about 10,000 years ago—a number of terrestrial mammals and other vertebrates became extinct in North America. What is most striking about these extinctions is that they are extremely selective. The so-called **megafauna**—conventionally said to be those animals with estimated body masses greater than about 40 kg—suffered significant extinction. In North America, for example, only about 14 of 50 megafaunal genera that were extant in the area north of Mexico during the Late Pleistocene survived into the Holocene (Figure 10.18). This translates to greater than 70 percent genus extinction—a level that would rival the most severe mass extinctions in the Phanerozoic, except that the Pleistocene event did not affect most groups of organisms.

Well-known victims of this extinction included mammoths, mastodons, ground sloths, giant beavers, and sabertooth cats. By contrast, small terrestrial mammals (Figure 10.18) and marine organisms were little affected

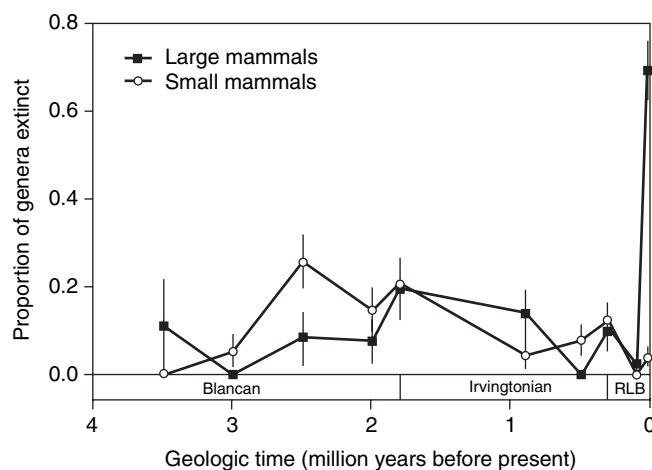


FIGURE 10.18 Proportional extinction of North American mammal genera. Stratigraphic intervals are North American land mammal ages; RLB denotes the Rancholabrean Age. The 4-million-year interval shown here is roughly equivalent to the post-Miocene. Error bars show 1 standard error on either side of extinction proportion (see Table 7.4). Solid curve, large mammals (44 kg or more); dashed curve, small mammals. Large mammals experienced much more extinction than small mammals at the end of the Rancholabrean, around 10,000 years ago. (Data from Martin & Steadman, 1999)

at this time. Moreover, a comparable extinction has been documented elsewhere, including South America, and there is a substantial record of extinction of mammals and birds on oceanic islands. In Australia, there was a megafaunal extinction some 46,000 years ago.

The Role of Humans in Megafaunal Extinction

The two leading candidates to explain these extinctions are climate change and human influence, especially through overhunting. Changes in climate accompanying deglaciation would have altered vegetation on which herbivorous mammals feed, and could therefore have had broad effects on food chains. Although there is abundant evidence for climate change—for example, an increase in seasonality—it still leaves two questions: Why were large terrestrial vertebrates the principal victims, and why did numerous other climatic changes during the glacial epoch not result in extinctions that were similar in severity and selectivity?

That humans played a role in the Late Pleistocene megafaunal extinctions now seems undeniable to many researchers. Here we summarize some of the major evidence for this conclusion. One of the challenges in weighing the climatic and hunting hypotheses has been to generate testable predictions that are consistent with one but not the other. Later we will discuss one such prediction and the evidence that bears on it, but it is important to keep in mind that climatic and human influences are not mutually exclusive.

There have been four principal lines of evidence for the so-called **overkill hypothesis**. First, variation in the timing of extinction among continents is such that the extinctions generally follow the presence of humans in significant numbers. This is consistent with the hunting scenario but does not rule out climate change as a mechanism. Humans would presumably migrate in response to climate change, and the timing could, in principle, be coincidental.

Second, it is clear that prehistoric humans in North America and elsewhere hunted game and processed the meat. Some of the most compelling evidence comes from a series of detailed taphonomic, morphologic, and geochemical studies of proboscideans, especially mastodons and mammoths, carried out by Daniel Fisher and his co-workers. Figure 10.19 illustrates a typical example of an in-place assemblage of mastodon bones, which was unearthed during the digging of a farm pond in southeastern Michigan. One of the most striking

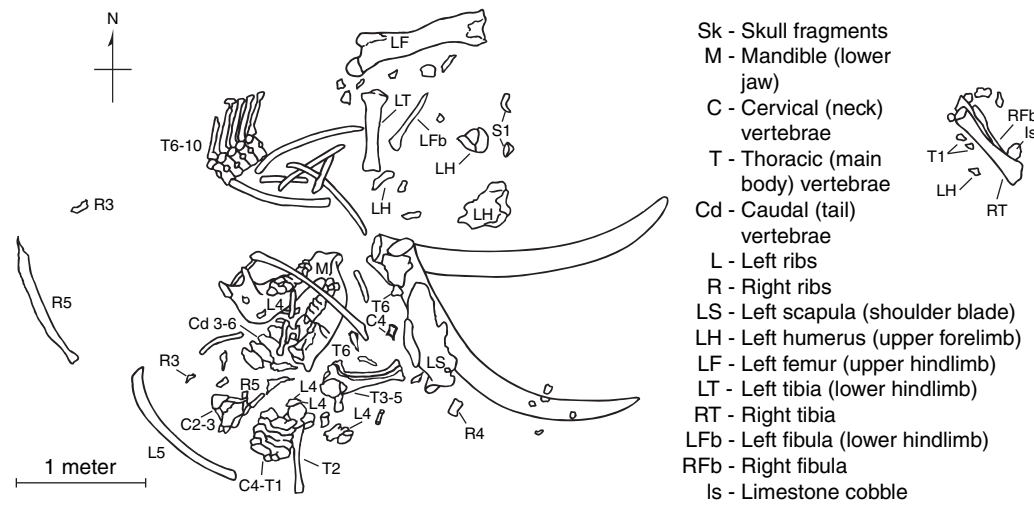


FIGURE 10.19 Assemblage of mastodon bones from southeastern Michigan. Groups of articulated bones are found together but are separate from other such groups, indicating butchery of the carcass. Letters denote different kinds of bones, and numbers indicate different elements in a series (such as ribs and vertebrae). The major elements represented here are shown in the key. The “Is” at far right denotes a limestone cobble. (From Fisher, 1984)

features of this assemblage is that groups of articulated bones that constitute whole sections of the mastodon are found together (e.g., the thoracic vertebrae T6–T10 in Figure 10.19) and that these large sections of the animal are separated by scattered bone fragments in no discernible order.

Based on observations of modern elephant carcasses, disarticulation of the joints tends to occur before tissues such as skin have broken down. For the bones of the mastodon to be displaced naturally would require the skin and other soft tissues to be degraded, but by the time this happened the bones would already have disarticulated from one another. In other words, under normal taphonomic conditions, it is not likely that groups of bones will remain articulated with one another and be displaced relative to other such groups. Thus, some other process is required. In this example, the presence of tool marks on facing surfaces of a number of joints indicates that certain joints were pried or wedged apart. This combination of observations makes sense only if the mastodon was butchered. Moreover, some bones show signs of burning—but only at limited points on the surface, indicating that most of the bone was still covered in flesh when it was exposed to fire. Thus, parts of the mastodon were also barbecued.

Many similar mastodon sites have been excavated, indicating that game processing was common. There is also taphonomic evidence that large sections of meat were deliberately submerged in ponds, sometimes with associated “clastic anchors” (sections of mastodon intestine

filled with sediment), in order to preserve them. Actualistic experiments show that meat from a large mammal can remain edible—as one of the authors of this book can attest first hand—even after being submerged for several months.

Clearly, mastodons were butchered, but were the animals actively hunted, or perhaps only scavenged? The argument for hunting in the case of mastodons relies partly on reconstructing the season of death of individual animals. Figure 10.20 schematically shows growth

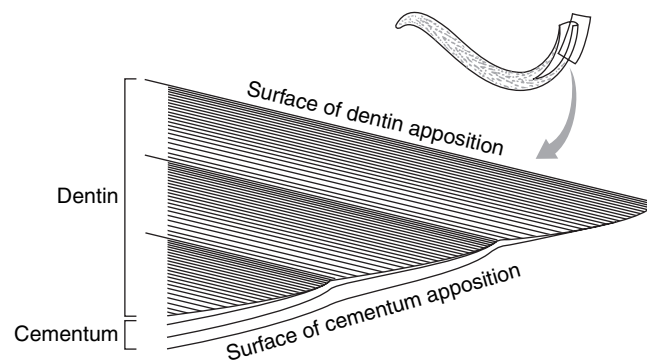


FIGURE 10.20 Pattern of tusk growth typical of elephants, mastodons, and mammoths. The upper drawing shows a longitudinally sectioned tusk. Material is accreted along the conical pulp cavity; thus, the older part of the tusk is at the tip (to the left). The lower drawing is an enlargement of a small part of the sectioned tusk. The numerous growth increments of dentin can be divided into three sets, interpreted to be annual. The finer-scale laminae are periodic, forming at roughly two-week intervals. (From Fisher, 1996)

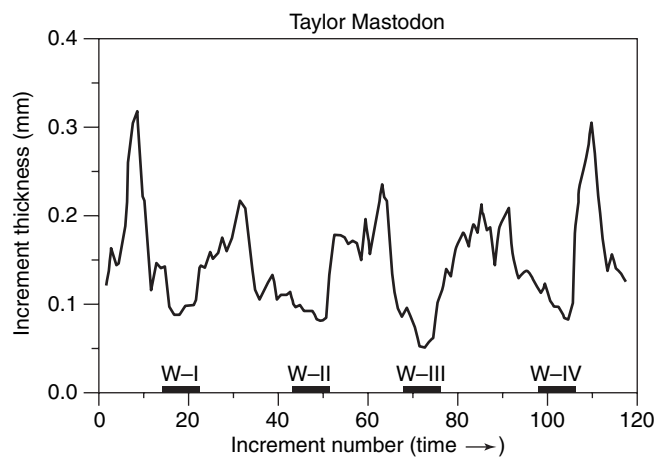


FIGURE 10.21 Increment thicknesses (see Figure 10.20) in the tusk of a mastodon. Thin layers marked W-I through W-IV correspond to winter growth. (From Koch et al., 1989)

bands in a mastodon tusk. By analogy with many living mammals, including elephants, thin, dark bands indicate the slow growth associated with winter. Therefore, the profile of increment thickness in Figure 10.21 is interpreted to show roughly four years' growth, with winters corresponding to thin layers. This inference can be tested with isotopic analysis of the growth increments [SEE SECTIONS 2.3 AND 9.5].

We have already seen that the ratio of ^{18}O to ^{16}O in skeletons of marine organisms is strongly affected by the ambient water temperature, with higher values (i.e., positive excursions in ^{18}O) in colder water. By contrast, the ratio of ^{18}O to ^{16}O deposited in the apatite of tusks as they grow depends largely on the oxygen isotope ratio of the water the animal ingests; according to the general trend of precipitation in continental regions, this ratio is lower, rather than higher, during colder seasons. Figure 10.22 shows the oxygen isotopic profile of the tusk from Figure 10.21. Negative excursions in $\delta^{18}\text{O}$ correspond with the thinnest growth increments, supporting the inference that thin increments were laid down in the winter.

Growth in the specimen detailed in Figures 10.21 and 10.22 ends between the summer peak and the winter trough in growth rate and in $\delta^{18}\text{O}$; it therefore appears to have died in autumn. This in itself says nothing about whether it was hunted or died a natural death, but season of death of a broader sample of animals may indicate whether the animals were hunted. The season

of death of butchered animals, such as that in Figure 10.19, can be compared with that of animals that show no sign of butchery (and therefore probably died of natural causes). If the distribution of season of death of butchered animals does not match that of animals that died natural deaths, then the butchered animals are unlikely to represent natural deaths. In other words, they are likely to have been hunted rather than scavenged. In one study, Daniel Fisher and Paul Koch (1989) determined the season of death of six butchered and seven nonbutchered mastodons. The nonbutchered individuals died in the late winter and early spring, whereas the butchered individuals all died in mid- to late autumn. Thus, the butchered mastodons were unlikely to have died by natural causes and so were most likely hunted.

Analysis of the season of death of North American mammoths, estimated with oxygen isotopes as for the mastodon in Figure 10.22, also shows a pattern consistent with hunting. Prior to significant human presence, around 12,500 years ago, most of the deaths were in late winter and early spring. After that time, once evidence for human activity is clear, about half the deaths were in mid- to late autumn.

Evidence for hunting of other species is also found in the form of stone tools, including Clovis projectile points, associated with fossil skeletons. At least one report

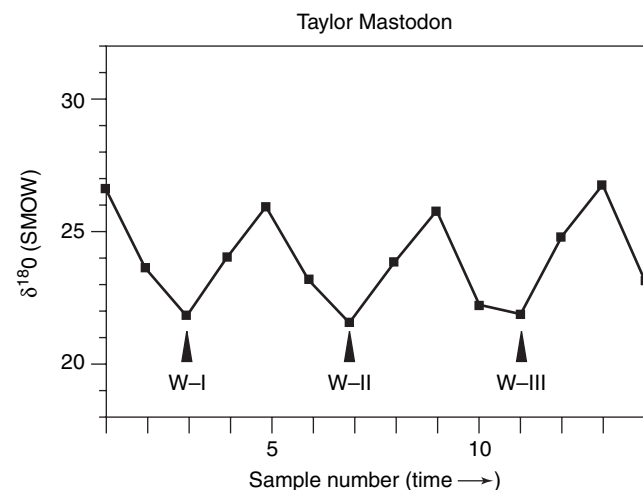


FIGURE 10.22 Oxygen isotope ratios in selected growth increments of the tusk depicted in Figure 10.21. Lighter oxygen corresponds to winter growth (W-I through W-III). Oxygen isotopes are compared with standard mean ocean water (SMOW). (From Koch et al., 1989)

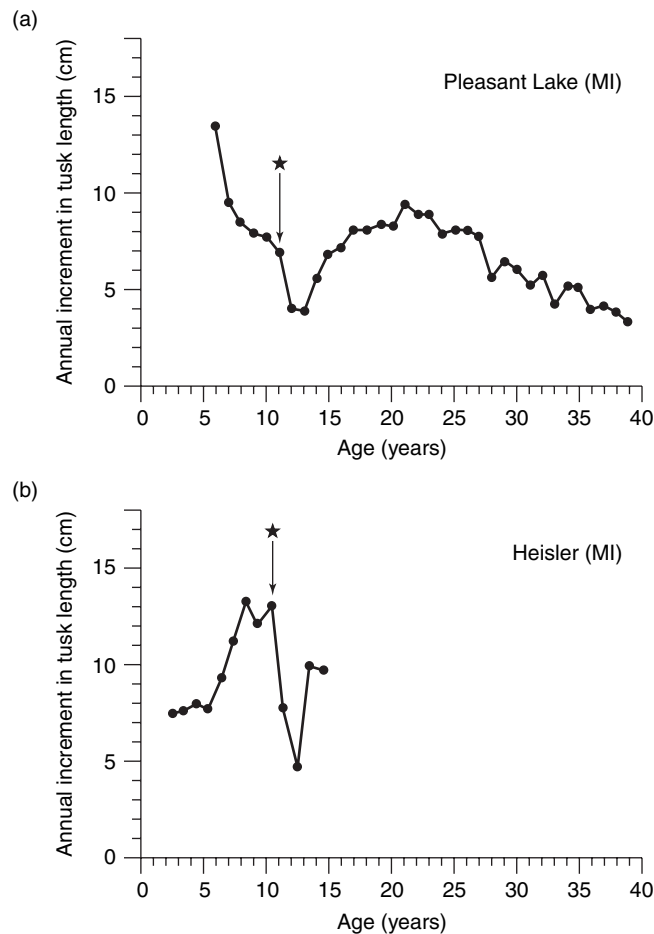


FIGURE 10.23 Thickness of annual growth increments in the tusks of two male mastodons from two localities in Michigan, (a) Pleasant Lake and (b) Heisler. By analogy with living elephants, sharp decline in growth rate, indicated by the asterisk, marks the onset of sexual maturity. (From Fisher, 1996)

indicates that a mammoth had points embedded in it but was not butchered and was not associated with other individuals that had been butchered. Evidently, then, this mammoth was attacked but subsequently escaped.

Thus, it is established that prehistoric humans hunted—but does this mean that hunting caused any of the megafaunal extinctions? The third, and most compelling, line of evidence that hunting was implicated in the extinctions comes in the form of a physiological response of prey species after the arrival of humans and before the time of the extinctions. Figure 10.23 shows the annual increments in tusk length for a number of male mastodons from North America. At a certain point, each individual shows a drop in the increment size—in

other words, a decline in growth rate—after which it takes a few years to return to the earlier growth rate. By analogy with living elephants, this is thought to mark the onset of sexual maturity in males, a time of great stress when they are evicted from the family group and must fend for themselves. Thus, the sharp drop in growth rate is used to determine the age of maturity of fossil males. Maturity in females is determined by the beginning of a 3-to-4-year cycle in growth rates that corresponds to the calving interval. In the two specimens of Figure 10.23, the decrease in growth rate occurs at an age of about 10 years.

The ability to determine growth rates and the age of sexual maturity enables a test of the hunting hypothesis against the climatic hypothesis, because the two hypotheses make different predictions about the probable effects on a stressed species and its response over time. The deleterious effects of climate change are supposed to be mediated through a change in vegetation consumed by many large mammals. If preferred food sources were less abundant, growth rates should have declined, and it is also likely that sexual maturation would have been delayed in response to poorer nutrition. If food sources had not deteriorated, but populations were instead stressed by hunting, then growth rates should not have declined. In fact, if populations were thinned by hunting, reduced competition within species may even have allowed faster growth.

It is also known from modern elephants that young males, whose maturation is inhibited by older males in musth (“rutting”), mature earlier if older males are removed from the population. Moreover, from an evolutionary standpoint, it would have been advantageous to mature at a younger age, to reproduce before being hunted. Figure 10.24 shows that mammoth growth rates just prior to the extinction were equal to or even a bit greater than the pre hunting values. Figure 10.25 shows that the age of sexual maturation in mastodons declined after the onset of hunting. These observations fit the predictions of the overkill hypothesis rather than the climate hypothesis.

Note that the geological ages of specimens in Figures 10.24 and 10.25 are given in “years before present.” Strictly speaking, these figures are referred to as *radiocarbon years* rather than *calendar years*. The relationship between radiocarbon years and calendar years is complicated, depending on such factors as the amount of radioactive ^{14}C in the atmosphere, which varies over time, and the ratio of ^{13}C to ^{12}C in the organism. The

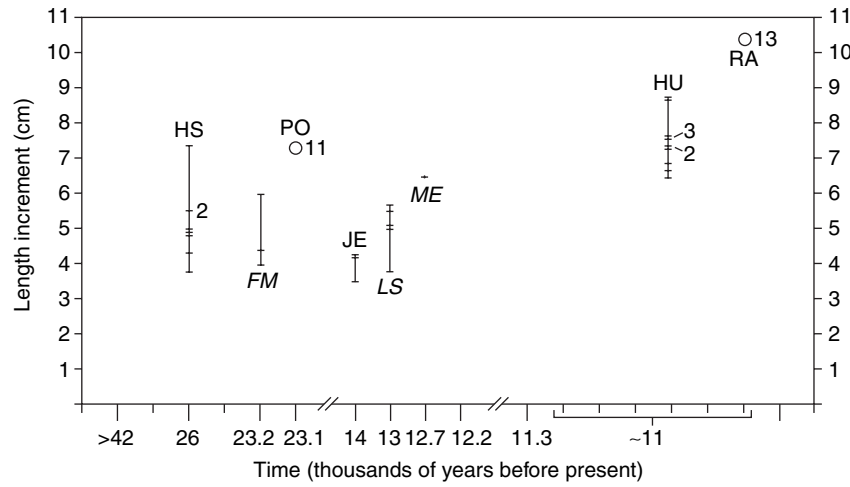


FIGURE 10.24 Growth rates (measured as annual increments in tusk length) in North American mammoth specimens compared with geologic age in thousands of years before present. Each tick mark shows the growth rate for a single year; the numbers next to certain tick marks indicate that multiple growth rates have the same value. Two-letter abbreviations are specimen codes; males are in plain font, females in oblique font. Circles show growth rates averaged over several years, with the number of years given to the right. Growth rates are somewhat higher just before extinction than they are prior to the onset of human hunting. (From Fisher, 2002)

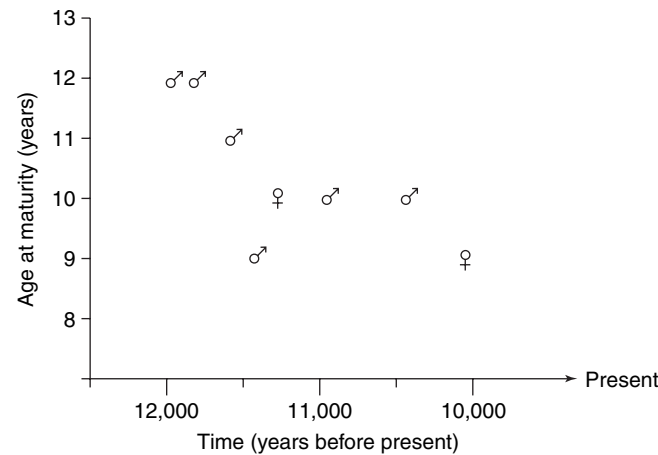


FIGURE 10.25 Inferred age of sexual maturation in mastodons compared with geological age in thousands of years before present. Maturity in males is inferred from a sharp decline in tusk growth rates (Figure 10.23). Maturity in females is inferred from the onset of a 3-to-4-year cycle in tusk growth rates that corresponds to the interval between successive offspring. Age of maturation declines after the onset of human hunting. (Courtesy of Daniel C. Fisher)

relative ordering of the geological ages in Figures 10.24 and 10.25 is approximately correct, however.

There is one last line of evidence in favor of the overkill hypothesis, which relates to the probable ecological response of various mammal species to human

hunting. What is known of the ecology of different kinds of mammals allows a reasonable prediction of which species would have been most susceptible to population decline in response to hunting. With this in mind, John Alroy (2001) constructed a computer model of human

hunting. This model has a few key elements: North America is seeded with a small number of humans of modest hunting ability; these humans harvest prey at random to satisfy their nutritional needs; and they gradually spread across the continent. Mammal species that serve as potential prey are characterized by factors such as geographic range and body mass, both of which can be estimated from fossil data. Body mass is especially important because it largely determines other factors that are incorporated into the model, such as birth and death rates and population density, and because the number of animals that must be killed to satisfy human nutritional needs depends on the amount of meat that can be obtained from an animal.

Simulations based on the ecological model break North America into 1°-by-1° cells. Within each cell in each year, the simulations determine the change in population size of each species (including humans) as the result of migration, birth, and death (including hunting). The computer model runs for 2500 virtual years, corresponding to the approximate time between the human colonization of North America in significant numbers and the time of the megafaunal extinctions. Over a wide range of model assumptions, the simulations predict with a fair degree of accuracy which species survive and which become extinct. In particular, they predict that large-bodied species will preferentially suffer extinction. *This happens even if humans do not hunt them selectively.* It is the small population size and low birth rate of large mammals that makes them most susceptible to extinction in response to hunting.

10.6 CONSERVATION PALEOBIOLOGY

Our discussion of the Pleistocene overkill hypothesis illustrates just one of the ways that humans may be affecting life on the earth. It has proven problematical to determine whether rates of human-induced extinction in the present day rival those observed in the fossil record for, say, the big five mass extinctions of the Phanerozoic [SEE SECTION 8.6]. In part, this is because taxa confined to limited areas in terrestrial settings, such as small islands, provide our most extensive data on the markedly elevated extinction rates of the present day. Terrestrial, endemic (localized) species would be more susceptible to extinction than, say, most marine species because, all else being equal, a marine species from an

open oceanic setting is likely to be more widespread geographically—a property that would be expected to reduce its susceptibility to extinction [SEE SECTION 8.6]. Given the inherent bias of the fossil record toward marine species [SEE SECTION 1.4] and toward widespread species, it therefore stands to reason that ancient Phanerozoic extinction rates derived from the marine record, such as those reported in Chapter 8, may not be indicative of ancient extinction rates exhibited by endemic terrestrial species, the very group whose extinction rates are best understood today.

Nevertheless, it is clear that *Homo sapiens* has caused the demise of untold numbers of species over the past several centuries. Just as significantly, human agriculture, industry, and commerce have dramatically impacted ecosystems around the world. In helping to analyze the long-term variability of ecosystems in particular regions before and during intervals that appear to exhibit substantial influence by *H. sapiens*, paleontologists are providing a unique perspective on the significance of present-day environmental and ecosystem deterioration and, in particular, on the prospect that ecosystems and the species that comprise them can survive the current crisis. Because the themes addressed by this research are of broad societal concern and, in some cases, of practical concern to the people living in regions where the work is conducted, it has been suggested that this constitutes a new branch of paleontological investigation, aptly termed **conservation paleobiology**.

Ecosystems that we might otherwise view as having been relatively unsullied prior to some obvious, recent episode of deterioration can be shown, with the help of a longer-term perspective, to have already experienced much longer periods of human-induced decline. Consider, for example, the case of tropical coral reefs in the western Atlantic, including the Caribbean Sea. During the early 1980s, because of the spread of a waterborne pathogen, the nature of which is still not entirely understood, there was a sudden, region-wide mass mortality of the long-spined sea urchin *Diadema antillarum*, an extremely prolific grazer that played a central role in preventing macroalgae from overgrowing the surfaces of living coral. At about that time, the major framework-building corals on western Atlantic reefs, *Acropora palmata* (elk horn coral) and *A. cervicornis* (stag horn coral) also went into a period of sharp decline from which they have yet to emerge, and most reefs throughout the western Atlantic are currently nearly bereft of living acroporids.

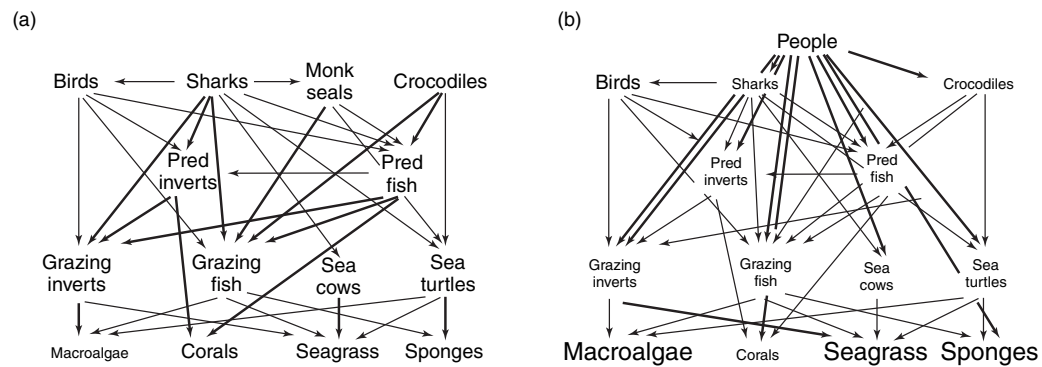


FIGURE 10.26 Illustrations of the effect of overhunting by humans on the food web for Caribbean coral reefs. (a) The food web prior to the onset of overhunting. (b) The food web after the onset of overhunting. Changes in abundances are indicated by change in font (larger fonts imply greater abundance). Note that monk seals were entirely eradicated. (From Jackson *et al.*, 2001)

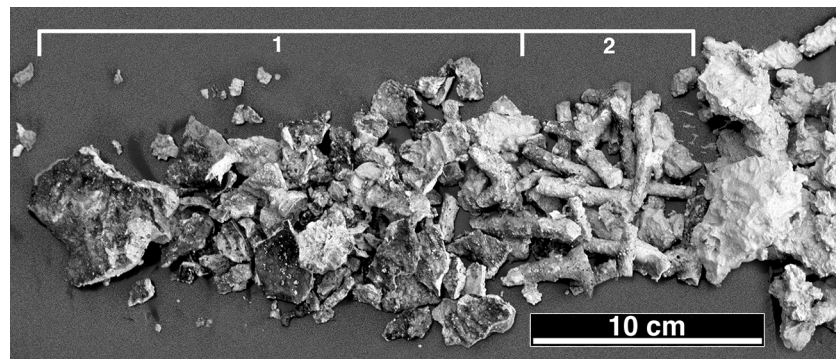
It is not clear that increased overgrowth by macroalgae and, in turn, the demise of *Diadema*, can be implicated as the primary cause of the decline of these corals; some researchers have argued for the importance of disease, perhaps associated with global warming, as an agent of coral decline (see below). But there can be no question that the loss of this major algal grazer has had a profound impact on reef ecosystems. What is not readily appreciated, however, is that, prior to the 1980s, these reefs had already suffered a significant loss that enhanced their vulnerability to algal overgrowth once *Diadema* declined. Historical records suggest that a host of large fish and other marine vertebrates, some of which were important grazers of macroalgae (Figure 10.26), had already been hunted to the point of near-disappearance long before the decline of *Diadema*. Thus, these reefs were already far removed from their natural states prior to the demise of *Diadema*.

In this case, the evidence for the demise of large marine vertebrates comes primarily from historical records rather than from paleontological data. Nevertheless,

paleontological research has been pivotal in offering a deeper temporal perspective on the nature of Late Cenozoic reefs throughout the western Atlantic and Caribbean. An important finding that has emerged from this work is that acroporids have dominated Caribbean reefs since the Late Pleistocene, and that their rapid decline over such a broad region is without precedent throughout at least the past several thousand years. Richard Aronson and colleagues (2002) have evaluated a transition that took place on the reefs of Belize in the late 1980s and early 1990s from *Acropora cervicornis* to *Agaricia tenuifolia*, a coral with a leafy appearance reflected by its common name, the “lettuce coral.”

The reign of *Agaricia tenuifolia* was itself temporary because this species experienced a major decline in Belize during 1998. Nevertheless, by collecting a series of cores from the sea floor (Figure 10.27) throughout a nearly 400-km² area off the coast of Belize, some of which penetrated records that were determined with radiometric techniques to be as old as 3000 years, Aronson and colleagues found that an extensive, regional transi-

FIGURE 10.27 The contents of a core sample collected in Belize, illustrating the transition (shown right to left) from *Acropora cervicornis* to *Agaricia tenuifolia* in the late 1980s and early 1990s. *Agaricia tenuifolia* is distinctively platelike in appearance and contrasts strongly with the sticklike appearance of *Acropora cervicornis*. (From Aronson *et al.*, 2002)



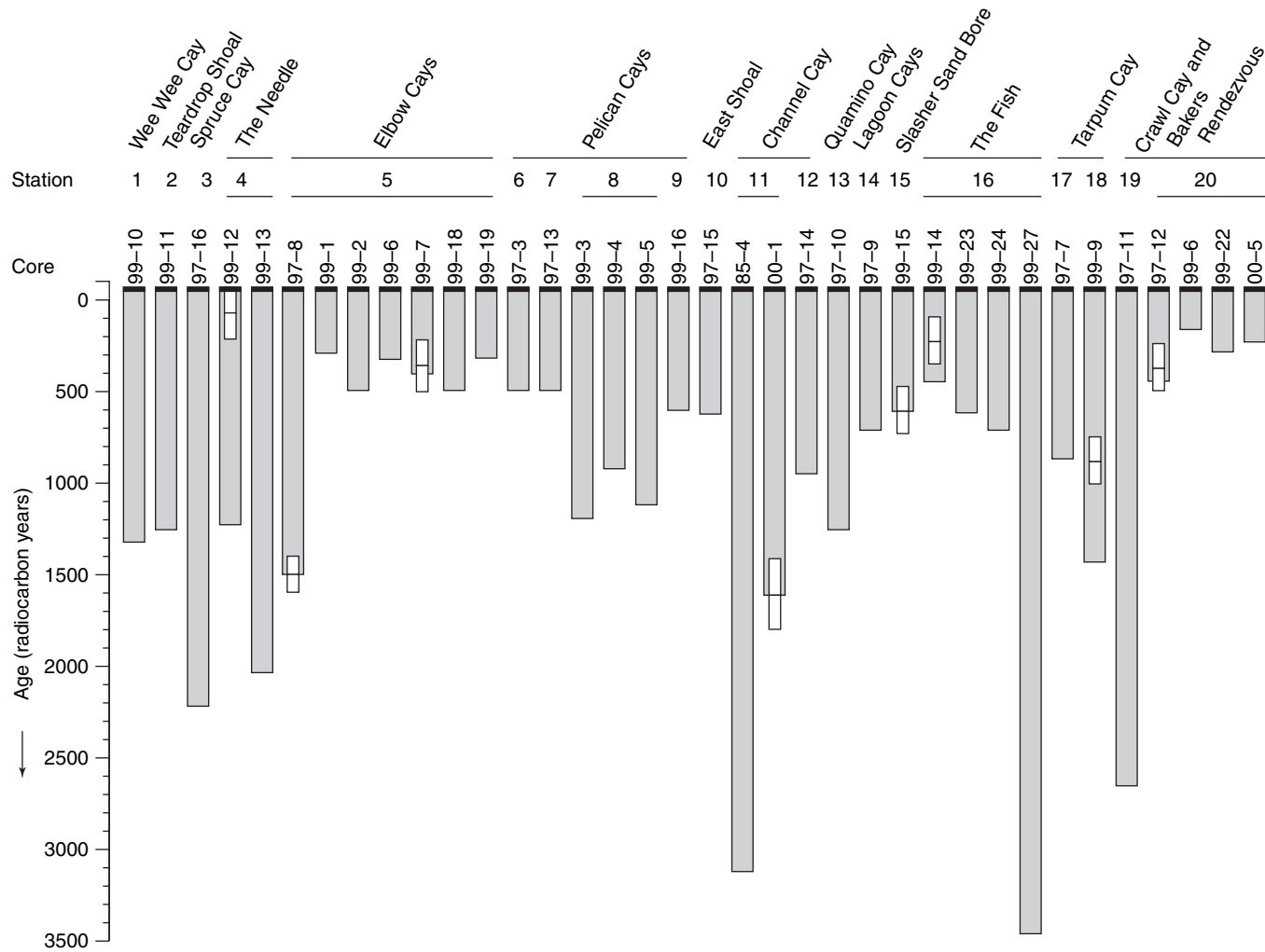


FIGURE 10.28 Representations of cores collected from reef localities in Belize. Gray fill represents dominance by *Acropora cervicornis*; black bars at the core tops and within the cores represent dominance by *Agaricia tenuifolia* (white rectangles surrounding the bars within cores are 95 percent confidence intervals on the dates of *Agaricia tenuifolia* “events” based on radiocarbon dating). Note the scarcity of *Agaricia tenuifolia* events prior to the area-wide transition at the top. (From Aronson et al., 2002)

tion from *Acropora cervicornis* to *Agaricia tenuifolia* was without precedent in the area (Figure 10.28). There were a few previous instances of temporary dominance by *Agaricia tenuifolia* indicated in some of the cores, but these were found to be far more patchy in space and time than the recent episode.

Processes implicated by some biologists in the decline of corals on present-day reefs, such as spontaneous events of bleaching (the expulsion by corals of their resident photosynthetic symbionts, known as *zooxanthellae*), may be associated with the current episode of global warming; this, in turn, has been linked to an atmospheric increase in the levels of greenhouse gases, notably CO₂ emitted from the burning of fossil fuels. For this reason,

there is growing concern that corals and other species will be adversely affected over the long term by global warming. After all, there are indications that, in other Cenozoic intervals, coral biotas have responded noticeably to episodes of warming and cooling [SEE SECTION 8.8]. Interestingly, however, recent analyses suggest that at least some species are capable of responding to global climatic changes through geographic range shifts into cooler waters. William Precht and Richard Aronson (2004) reviewed the present-day and historical distributions of acroporid corals along the coast of the state of Florida. They noted that in just the past few decades, there has been a northward, 50-km expansion in the geographic ranges of *Acropora* species. Fossil data available

for the same area demonstrate that some 6000 years ago, *Acropora* underwent a similar range expansion in association with a short-term increase in regional sea-surface temperatures. Taken together, these and similar analyses of the geographic distributions of corals suggest a degree of dynamism in geographic ranges reminiscent of that exhibited in response to climatic fluctuations throughout the Quaternary by terrestrial plants, insects, and other organisms [SEE SECTIONS 7.3 AND 9.6].

In a somewhat different vein, data garnered from the accumulated skeletal remains of bivalves have been instrumental in calibrating the loss of biological productivity on the Colorado River Delta in the Gulf of California, related to the establishment of a series of dams, beginning around 1930. There, the subfossil record of mollusc shells is being investigated to address an important question: How has the establishment of dams affected the population densities of living organisms and, therefore, the level of biological productivity? The damming of the river, and the associated cutoff of new sediment input to the delta, resulted in the exhumation by currents and waves of shells that were previously buried in intertidal muds. Subsequently, these shells became concentrated in a series of beach ridges, intertidal bars, and islands.

By assessing the total volume of these concentrations, coupled with an estimation of the number of shells contained within an average cubic meter of sediment in the study area, Michal Kowalewski and colleagues (2000) determined that at least 2×10^{12} dead individuals were present throughout the study area! Remarkably, when Kowalewski and colleagues determined the absolute ages of 125 shells collected for analysis, they found that none were produced by individuals that lived after the year 1950. When they sorted the data into 50-year time increments (Figure 10.29), they observed a steady falloff in the number of shells starting with those dating back to earlier than 1800 AD. This is what we might reasonably expect, given that older shells would have been exposed to taphonomic processes for longer periods of time. Thus, it is highly likely that the actual number of shells produced in the study area over the past millennium (the approximate interval represented by the shells contained in the sample; Figure 10.26) was substantially greater than the number found there today.

The vast majority (greater than 85 percent) of the shells in the vicinity of the Colorado Delta belong to a single species, *Mulinia coloradoensis*, the mean length of which is about 30 mm. Oxygen isotope profiles of shells

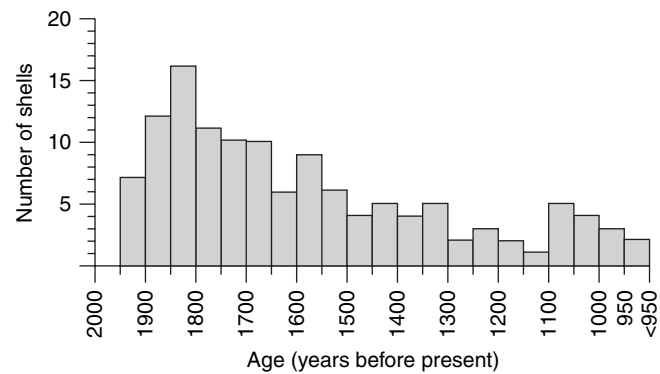


FIGURE 10.29 Age-frequency distribution of 125 shells of the species *Chione fluctifraga* collected from the vicinity of the Colorado River delta. (From Kowalewski et al., 2000)

of this species [SEE SECTION 9.5] permit the recognition of seasonal cycles of growth and demonstrate that a typical individual required at least three years to reach average size. Thus, over the past millennium, it can be estimated that about 333 generations of this species lived in the study area.

Armed with this information, Kowalewski and colleagues estimated that, at a minimum, some 6×10^9 members of this species ($2 \times 10^{12}/333$) were alive at any given time during the past millennium. Finally, given that *M. coloradoensis* is a brackish water species limited to environments that were affected by the influx of water from the river, and considering the area covered by the intertidal zone in the vicinity of the delta, the area in which these shells were produced measured some $1.2 \times 10^8 \text{ m}^2$ at most. Given the previous estimate of the standing population size, it can therefore be estimated that the average standing density of living individuals at any point in time over the past millennium prior to the damming of the Colorado River was about 50 individuals per square meter ($6 \times 10^9/1.2 \times 10^8$).

While these calculations are admittedly somewhat coarse, it should be understood that they err on the side of underestimating past abundance. In all likelihood, the pre-1950 density of living individuals, including smaller standing populations of other bivalves, was much greater than the number that Kowalewski and colleagues reported. More important, these estimates exceed current densities of living bivalves in the study area by at least an order of magnitude! Restoration of intermittent river flow over the past 20 years has had virtually no effect on these living densities, and the research by Kowalewski and colleagues has helped demonstrate the magnitude of

the reduction to biological productivity that resulted from the damming of the river.

Collectively, these examples illustrate an important new way in which paleontologists are influencing present-day discussions in the public policy arena. In the future, it is likely that this role will continue to expand, particularly in marine coastal regions worldwide, where human influence is particularly profound and, at the same time, the subfossil record is easily accessible. By mining the subfossil record, paleontologists are able to significantly extend the temporal reach of historical studies in threatened regions.

10.7 ASTROBIOLOGY

It seems fitting to conclude this book with a topic that is quite literally expanding the frontiers of paleontology, in this case off of the planet! In the search for evidence of life outside of the earth, which falls under the head-

ing of **astrobiology**, it might seem surprising that scientists would look to the fossil record for guidance, but there are good reasons why this has been the case. While it is reasonable, and certainly a lot of fun, to speculate on the nature of alien life forms, for the moment the only actual data that we have about the existence of life comes from the DNA- and **RNA**-based forms that we have on earth. And, in the direct search for evidence of life outside of the earth, we are limited for the present to our solar system.

At the moment that this chapter is being written, two rovers are still rolling around on the surface of Mars, far exceeding their expected life spans, sampling rocks and conducting geochemical analyses that have already provided compelling evidence of the previous existence of a considerable volume of standing water and the presence of evaporites (Figure 10.30). This lends strong support to the view that had been developing for some time that Mars was once significantly warmer and wetter than it is at present. Furthermore, satellite images of the

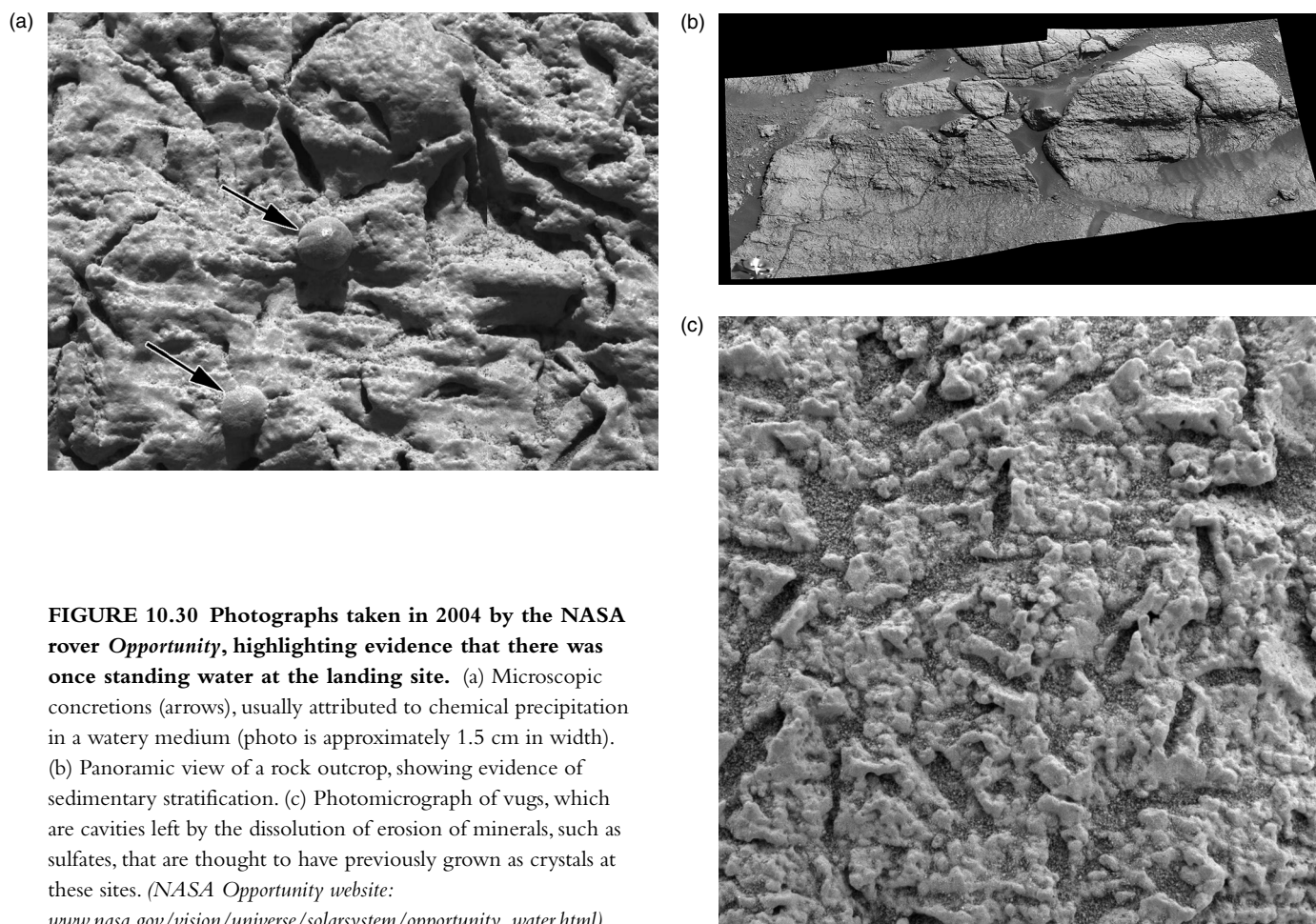


FIGURE 10.30 Photographs taken in 2004 by the NASA rover *Opportunity*, highlighting evidence that there was once standing water at the landing site. (a) Microscopic concretions (arrows), usually attributed to chemical precipitation in a watery medium (photo is approximately 1.5 cm in width). (b) Panoramic view of a rock outcrop, showing evidence of sedimentary stratification. (c) Photomicrograph of vugs, which are cavities left by the dissolution of erosion of minerals, such as sulfates, that are thought to have previously grown as crystals at these sites. (NASA *Opportunity* website: www.nasa.gov/vision/universe/solarsystem/opportunity_water.html)

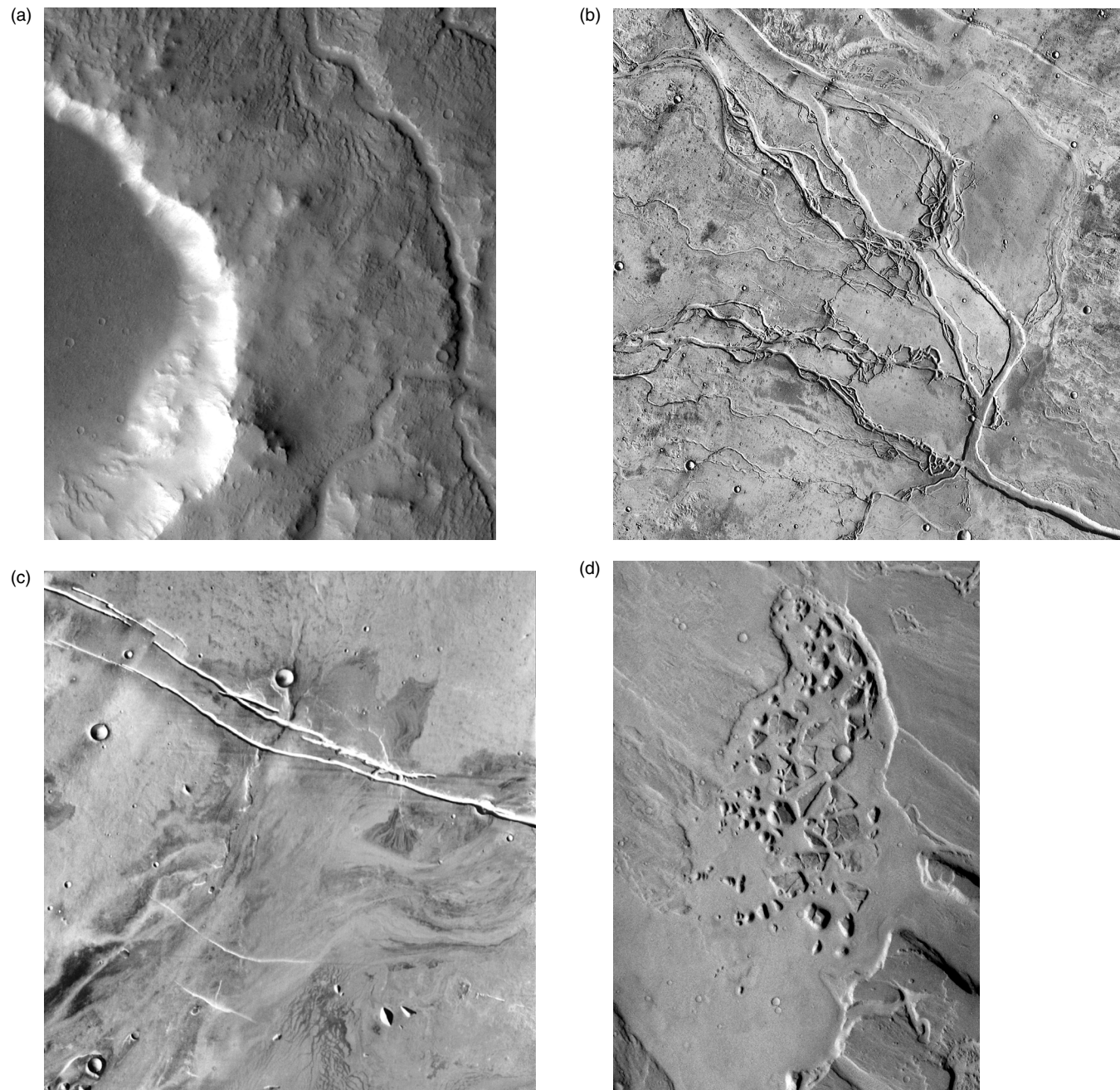


FIGURE 10.31 Images of the surface of Mars, showing cases in which there is evidence of hydrothermal activity, water movement associated with heating. (a) Water flow (right) linked to an impact (left). (b) A series of channels likely cut by water on the margin of Elysium Mons, the second-largest volcanic terrane on Mars. (c) Water flow in association with the opening of a fissure at Athabasca Valles. (d) Chaotic features and associated water flow at Mangala Valles; the chaotic features are thought to be related to a collapse produced by the melting of ice or removal of groundwater. [Images were captured by the Thermal Emission Imaging System (THEMIS) on NASA's Mars Odyssey Mission; From NASA/JPL/Arizona State University].

Martian surface reveal significant evidence not only of the past movement of water, but also of the existence of past hydrothermal activity (Figure 10.31).

Interestingly, sites of present-day hydrothermal activity on earth, such as areas associated with the activity of

geysers and hot springs, are hotbeds for some of the most primitive, microbial life forms known on the planet, including prokaryotic organisms classified as **EUBACTERIA**, as well as those belonging to another, less well-known, group called the **ARCHAEA**, which seem

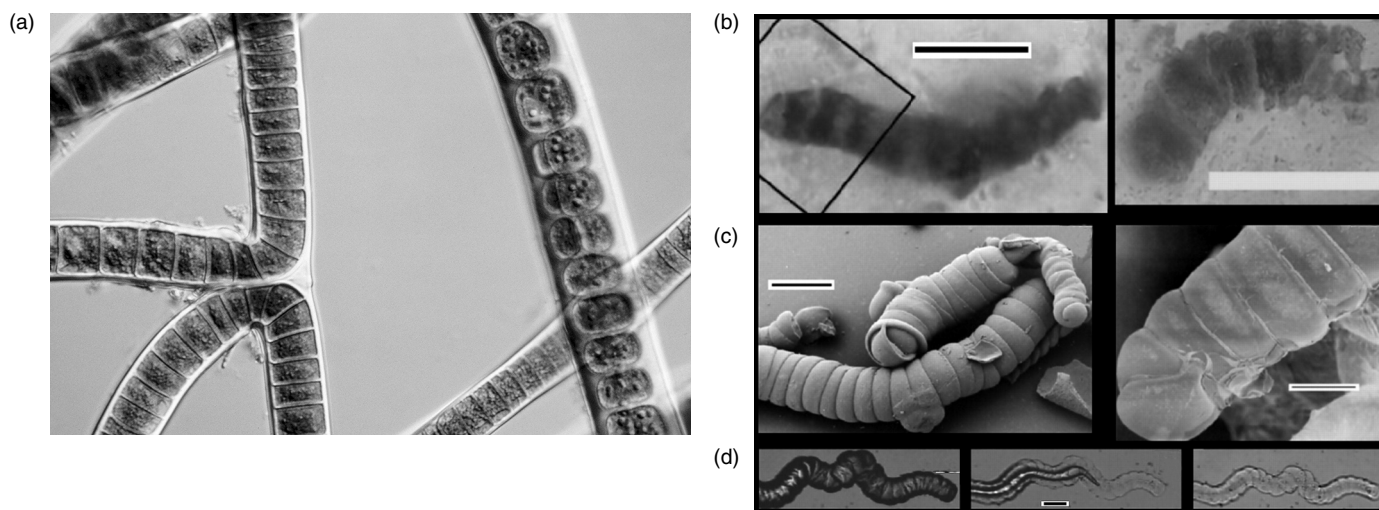


FIGURE 10.32 A montage of illustrations, highlighting the difficulty of identifying cyanobacteria in ancient rocks. (a) Modern cyanobacteria; such filaments are typically tens of μm in diameter. (b) Images of what were thought to be ancient cyanobacteria from the Archean Warrawoona Chert of western Australia (~ 3.5 billion years old), recognized previously as the oldest, direct fossil evidence of life on earth. (c) Microscopic filaments, produced in a laboratory, of silica-coated carbonate crystals, combining materials and conditions that may have been available during the Archean. (d) Progressive dissolution and hollowing, with acid, of synthetic filaments. Compare the image on the left, in particular with the images in part (b). (a) Scale bars in parts (b) through (d) are $40 \mu\text{m}$. (a: *Biophoto Associates/Photo Researchers, Inc.*; b–d: *From Garcia-Ruiz et al., 2003*)

particularly adept at living in extreme, seemingly harsh, environments. Some Archaea, for example, thrive off of carbon dioxide and hydrogen, producing methane in the process.

For these reasons, one wonders whether there was once a window of opportunity for the origin and evolution of primitive life forms on Mars—it is this possibility that has motivated much of the current interest in exploring and sampling the Martian surface. This is where paleontology comes in. While nobody can reasonably expect to see a brachiopod or clam in any of the close-up photographs snapped by the Mars rovers, there is the possibility that one day, more primitive, almost certainly microbial, evidence of past life will be discovered. In the study of the Precambrian fossil record in particular, paleontologists have shown an ever-improving ability to recognize even tiny microfossils representing some of the most primitive life forms on the planet [SEE SECTION 1.2].

Not surprisingly, the search for the earliest, most archaic forms of life on earth has not been without its pitfalls. Evidence from the biogeochemical record, which provides information about the metabolic by-products of life, now suggests that primitive life forms existed on earth as far back as 3.7 billion years ago. And additional, indirect evidence of life is found in rocks that are nearly that old, in the form of **stromatolites**. Stromatolites are layered structures produced by the trapping of sedi-

ment and the precipitation of calcium carbonate within filamentous mats formed mainly by prokaryotic cyanobacteria, other bacteria, and later, eukaryotic algae in aqueous settings during the Precambrian. Today, stromatolites are restricted mainly to environments that are inhospitable to grazing organisms that feed on the mats and thereby prevent stromatolitic development. However, during the Precambrian, before the evolution and diversification of multicellular life, stromatolites were far more common in marine settings and are therefore ubiquitous features of the Precambrian marine record.

Of course, paleontologists would like to find direct fossil evidence of the early inhabitants of earth, and there is evidence of the existence of possible prokaryotic cyanobacteria in rocks dated at 3.5 billion years old, deposited in western Australia (Figures 10.32a and 10.32b). However, in a series of experiments seeking to replicate geochemical conditions at this site of ancient hydrothermal activity, Juan M. Garcia-Ruiz and colleagues (2003) produced an assemblage of microscopic objects that look remarkably similar to the putative prokaryotes collected from the site (Figures 10.32c and 10.32d). While it is possible that Australian specimens are, indeed, the fossil remains of primitive forms of life, the Garcia-Ruiz experiments remind us that it is also possible for nature to produce inorganic structures that look decidedly lifelike [SEE SECTION 1.2].

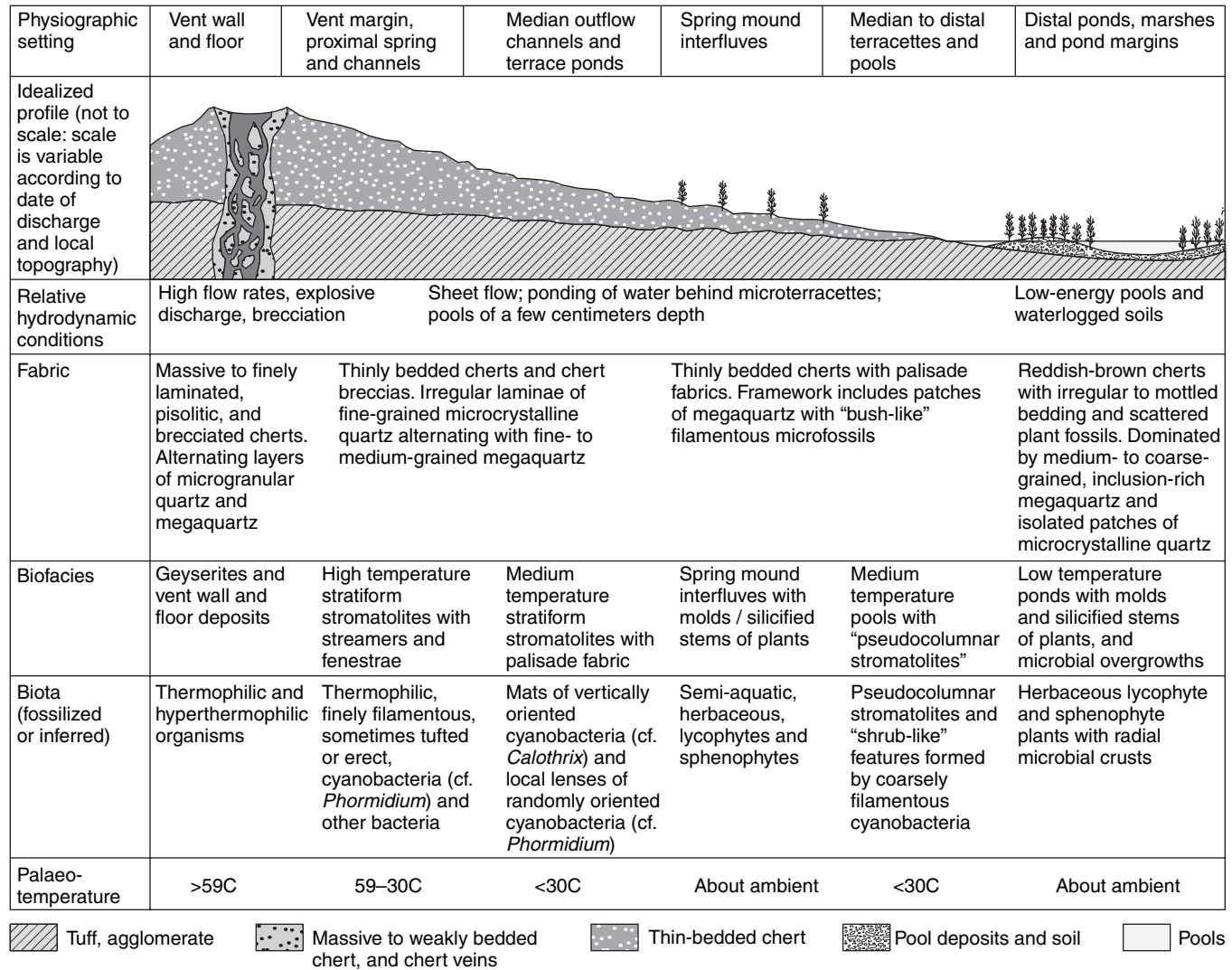


FIGURE 10.33 A summary of physical, lithological, and paleobiological features associated with an environmental gradient at the site of a Devonian thermal spring in Australia. These determinations draw on comparisons with present-day thermal springs. (From Walter et al., 1998)

Nevertheless, there are now numerous instances in which preserved prokaryotic and simple eukaryotic fossil organisms have been recovered from Precambrian and younger rocks, sometimes in conjunction with the collection of biogeochemical data that bolsters, at least indirectly, the claim that the microfossils in question actually are what they appear to be. For the moment, some of the most compelling direct evidence for fossil microbial life in association with ancient hot springs comes not from the Precambrian, but from Devonian strata in eastern Australia. There, microfacies are pre-

served over lateral distances of 100 m in association with a temperature gradient related to hot spring activity (Figure 10.33). Within these microfacies, a variety of microscopic filaments thought to represent various cyanobacteria and other microbes are preserved, although the precise identities of these organisms remain uncertain (Figure 10.34). Based on evidence of the occurrences of Archaea and Eubacteria in present-day hot springs, it appears that some of the organisms found in the Devonian deposits lived at temperatures well in excess of 50°C (122°F)!

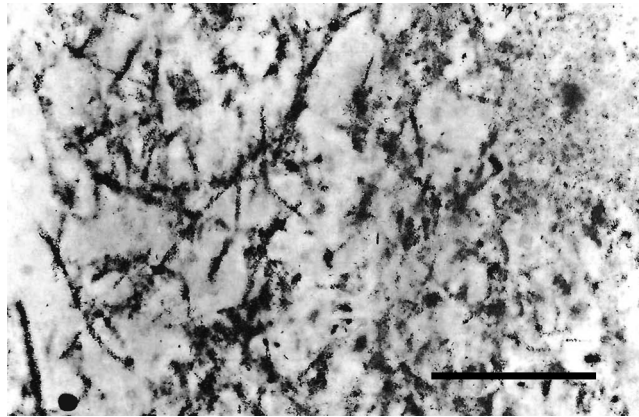


FIGURE 10.34 A photomicrograph of a thin section illustrating tubular molds of what is thought to be a filamentous microorganism, from the site of a Devonian thermal spring in Australia. The scale bar at the lower right is 100 micrometers. (From Walter et al., 1996)

The preservation of these fossils provides a basis for the emerging view of some astrobiologists (or, perhaps more appropriately, *astropaleontologists*) that, in future attempts to sample the Martian surface, we should pay special attention to sites where there is clear evidence not only of the presence of standing water, but also for the existence of hydrothermal activity. It would be surprising if hydrothermal environments did not figure prominently in future scientific missions to Mars.

10.8 CONCLUDING REMARKS

As the foregoing examples illustrate, paleontology sits at the interface of a number of scientific fields, including geology, geochemistry, ecology, evolutionary biology, and

even astronomy. It draws from these fields and influences them in turn. In that sense, paleontology is like nearly all areas of natural science in having become more interdisciplinary in recent years, and it follows that paleontologists need to be more broadly trained than ever before. While one can safely predict that this trend will continue, the particular research questions that will motivate paleontology in the coming years are hard to predict, just as they would have been hard to predict 10 or 20 years ago. We certainly have some ideas as to where the science will be headed next, but, realistically, these are little more than hunches. We can only look to the future with great anticipation!

SUPPLEMENTARY READING

- Aubry, M.-P., Lucas, S., and Berggren, W.A. (eds.) (1998) *Late Paleocene–Early Eocene Climatic and Biotic Events in the Marine and Terrestrial Records*. New York, Columbia University Press, 513 pp. [Overview of the Paleocene–Eocene Thermal Maximum; provides perspective for the many later papers published on this subject.]
- Briggs, D. E. G., Erwin, D. H., and Collier, F. J. (1994) *The Fossils of the Burgess Shale*. Washington D.C.,

- Smithsonian Institution Press, 238 pp. [Richly illustrated overview of Burgess Shale fossils.]
- Conway Morris, S. (1998) *The Crucible of Creation*. Oxford, U.K., Oxford University Press, 242 pp. [An evolutionary interpretation of early animals, with particular focus on the Burgess Shale.]
- Erwin, D. H. (2006) *Extinction: How Life on Earth Nearly Ended 250 Million Years Ago*. Princeton, N.J., Princeton University Press, 296 pp. [Overview of biological and

- geological data surrounding the Permian–Triassic extinction event, as well as possible causes.]
- Gould, S. J. (1989) *Wonderful Life*. New York, Norton, 347 pp. [Discussion of Burgess Shale organisms and some possible evolutionary interpretations.]
- Knoll, A. H. (2003) *Life on a Young Planet: The First Three Billion Years of Evolution on Earth*. Princeton, N.J., Princeton University Press, 277 pp. [Comprehensive overview of Precambrian research and implications for astrobiology.]
- MacPhee, R. D. E. (ed.) (1999) *Extinctions in Near Time*. New York, Kluwer Academic, 394 pp. [Series of papers on extinction in the past 100,000 years.]
- Squyres, S. W., and Knoll, A. H. (eds.) (2005) *Sedimentary Geology at Meridiani Planum, Mars. Earth and Planetary Science Letters*, vol. 240, no. 1, pp. 1–190. [Series of articles on the characteristics and origins of some martian sedimentary rocks.]
- Valentine, J. W. (2004) *On the Origin of Phyla*. Chicago, University of Chicago Press, 614 pp. [Thorough treatment of the nature of animal phyla and their evolution.]
- Whittington, H. B. (1985) *The Burgess Shale*. New Haven, Conn., Yale University Press. [Emphasis on anatomical interpretation of Burgess Shale organisms.]