S279 Our dynamic planet: Earth and life
Science: Level 2

The Open University

Book 2 Part 2
Our Dynamic Planet

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Cover image: Folded layers of a banded iron formation (BIF or banded ironstone). Banded ironstone is a rock formed from alternating layers of the iron oxide mineral hematite (red) and tiger eye and jasper. At greater than 3 billion years of age these are among the oldest rocks on Earth. They were laid down in shallow seas where primitive bacteria may have caused iron to be oxidised and precipitated. Subsequent deep burial of the rocks, and tectonic movements, have caused the rock to alter and deform. This small sample is around 2 cm across. The rock has been cut open to expose the banding (strata), and also polished for display. Many BIFs come from Western Australia. (Dirk Wiersma/ Science Photo Library)

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Chapter 5

Mountains and climate change

In Chapter 4 you looked at plate tectonics and its influence on the climate and habitability of the Earth. In this chapter you will look at a specific aspect of this relationship, namely mountain building. Mountain ranges attract their own microclimates, which tend to be cooler and often wetter than the lowland areas that surround them.

It may strike you as odd that temperatures drop as altitudes increase; after all, the higher the altitude, the closer the Earth's surface is to the Sun. This is primarily because direct solar radiation causes very little heating of the air; most heating is due to radiation reflected back from the Earth's surface. Furthermore, air forced to rise by the presence of a mountain will expand and cool in response to the decreasing atmospheric pressure. Eventually, any water vapour in the air will condense, forming clouds and precipitation, which at high altitudes may fall as snow. Even at low latitudes, high mountains may be capped with snow or ice (Figure 5.1).

Figure 5.1 Mt Stanley (5100 m) from the Rwenzori Mountains, equatorial Africa.

■ How can the extent of mountainous terrain at low latitudes affect global climate?

■ Through its effect on the global albedo. A large area of highly reflective snow at low latitudes (where a large proportion of incoming solar energy reaches the Earth) could lead to a significant decrease in the albedo of the Earth as a whole.

It is difficult to estimate what effect low-latitude mountains may have had on the Earth in the distant past, not least because no one knows for sure where the mountains were or how high they were. Nevertheless, it is something that you should bear in mind, particularly when considering what the climate might have been like when a large proportion of the global land area was at low latitudes, as may have been the case during the Precambrian.

5.1 Mountain building and the carbon cycle

As a result of the density of continental crust being lower than that of either oceanic crust or the mantle, where the underlying continental crust is thickened the Earth's surface is elevated due to isostasy (Box 4.3). The world's large mountain ranges, therefore, reflect the thickened continental crust that supports them with wide regions of thickened crust forming as a result of collision between two continental plates (Figure 5.2). Prior to collision, active subduction of oceanic lithosphere generates two sources of CO_2. The dominant source of this CO_2 is volcanism both above the subducting slab (Figure 5.2a) and at spreading ridges into the oceans, while the second source of CO_2 results from metamorphism of the down-going slab.

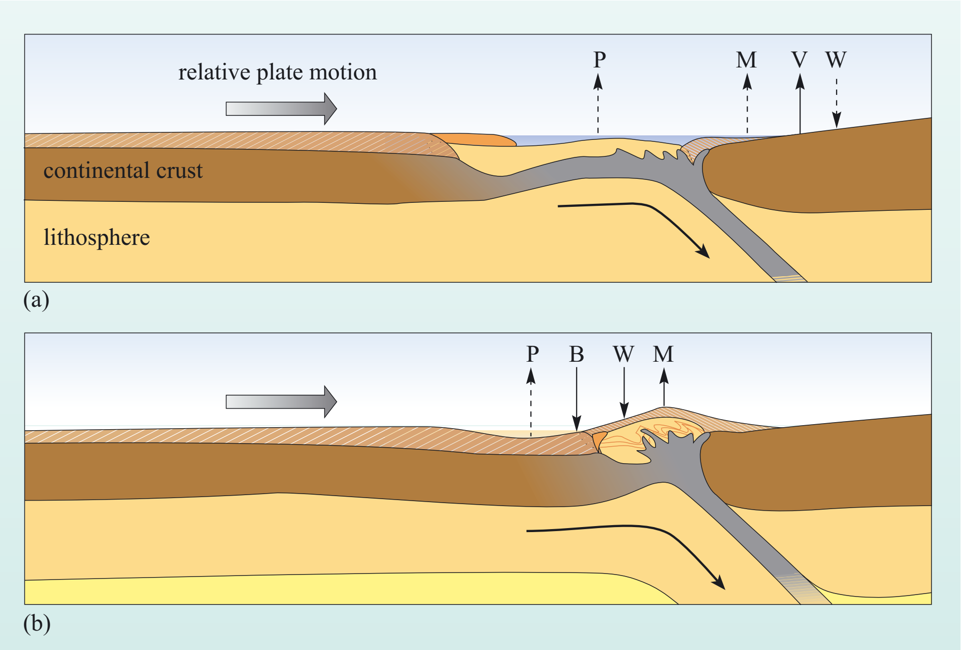


Figure 5.2 Schematic cross-sections showing the formation of a mountain range and the associated carbon fluxes: (a) pre-collision; (b) collision. Increases in atmospheric CO_2 are from volcanic emissions (V), metamorphism (M), and precipitation of carbonates (P). Decreases in atmospheric CO_2 are due to weathering of silicates (W) and burial of organic carbon (B). Dashed arrows indicate relatively minor fluxes.

Eventually, the ocean basin will close due to subduction and the two adjacent continents will collide (Figure 5.2b). Collision will terminate active subduction and the volcanism that results from it. Meanwhile, the CO_2 flux resulting from metamorphism in the thickened crust will probably increase. Throughout the period of subduction in the thickened crust, deep-sea sediments will have been scraped off the surface of the subducting oceanic plate, building up great wedges of sediment at the side of the subduction zone trench, forming accretionary prisms. As the continents collide, these sediments (including calcareous and siliceous remains) will be subjected to increased temperatures and pressures.

If calcium carbonate and silica are heated together at about 400 °C, a **decarbonation reaction** occurs that releases CO_2:

$$\underbrace{SiO_2(s)}_{\text{silica}} + \underbrace{CaCO_3(s)}_{\text{calcium carbonate}} \rightarrow \underbrace{CaSiO_3(s)}_{\text{calcium silicate}} + \underbrace{CO_2(g)}_{\text{carbon dioxide}} \qquad (5.1)$$

■ Where have the silica and calcium carbonate on the descending slab of ocean floor come from?

□ Silica and calcium carbonate are both found in the remains of planktonic organisms (notably diatoms and radiolarians, which are silica organisms, and coccolithophores and foraminiferans, which are carbonate-rich organisms).

Deep-sea sediments are not the only source of calcium carbonate reacting in the decarbonation reactions. At least some products of the shallow-water carbonate factory (e.g. carbonate-secreting algae, corals and bivalve remains) will also be trapped between the colliding continents. Most of the silica in shallow-water sediments is not **biogenic** (i.e. produced by organisms) but in the form of quartz sand, which has been weathered from the land and transported before accumulating on the continental shelf. It is important to realise that decarbonation reactions will only occur when silica and carbonate are mixed together. Although this is the usual situation for planktonic remains in deep-sea sediments, it is not so common for shallow-water sediments where, for example, coral-reef debris is less likely to be intimately mixed with sand. The CO_2 produced by decarbonation reactions due to continental collision is not usually released into the atmosphere via volcanism (as volcanoes are not generally found in such tectonic settings); instead, it seeps out along faults and fractures.

The subduction of sediments of *pure* calcium carbonate (i.e. sediments without silica) will mean that the carbon they contain will not be returned to the atmosphere for millions of years until they are released by weathering processes. Similarly, the ‘piling up’ of carbonate rocks that occurs during continental collision can mean that large volumes of carbon-containing rocks are buried deep in the crust and are prevented from participating in the global carbon cycle for a very long time.

The most significant aspect of climate change resulting from continental collision results from interactions between the rocks exposed at the surface, the hydrosphere and the atmosphere. Following continental collision, the rising mountain range causes the air masses in the lower atmosphere to rise, cool and precipitate rain or snow. The combination of increased precipitation and steep topography results in high rates of **physical erosion**. At the highest altitudes, rocks are shattered by:

- repeated freezing and thawing of water that seeps into cracks (a consequence of the fact that ice occupies more space than the water from which it forms)
- being crushed and ground into small particles by the action of glaciers.

Vast **alluvial fans** are formed at the outlets of steep-sided mountain glaciers (Figure 5.3). In large mountain ranges, huge volumes of mostly sedimentary rocks are broken up by weathering and erosion, transported by water, ice and gravity and buried. Many of these contain a significant component of organic carbon and the burial of this material removes it from further exposure to the atmosphere, which would result in the oxidation of carbon to CO_2.

Figure 5.3 Fragments of rocks forming a vast alluvial fan at the outlet of a river eroding the Karakoram Mountains, located to the north of the western Himalaya.

At lower, warmer altitudes, the wet windward slopes of mountains tend to be regions of strong **chemical weathering**. Rock fragments are carried down in fast mountain streams, accumulate and become chemically altered in reactions with rain and surface waters. The process of dissolving silicate minerals results in the removal of CO_2 from the atmosphere (Section 3.3.2) and, as shown in Figure 3.21, for every two carbon atoms removed from the atmosphere during the weathering of silicate minerals, one carbon atom has the potential of being removed from the atmosphere into seabed sediments, as carbonate remains. By contrast, weathering of carbonate minerals followed by reprecipitation in the ocean does *not* result in any net removal of CO_2 from the atmosphere.

One example of the importance of mountains in enhancing weathering rates is provided by the River Amazon. Even at its mouth, over three-quarters of the dissolved material it carries has been derived from the eastern slopes of the Andes more than 3000 km away – only one-quarter comes from weathering of the vast tracts of bedrock that underlie the Amazon Basin between the source and the mouth of the river.

During subduction, the net effect on atmospheric CO_2 concentrations from processes along the subduction zone is to increase this CO_2 reservoir from volcanic emissions. After continental collision, however, this flux is closed down and the net contribution of this tectonic margin is to deplete atmospheric CO_2 due to enhanced silicate weathering rates and the burial of organic carbon (Figure 5.2). These fluxes are partially offset by increased CO_2 from metamorphism of carbonate rocks within the thickened crust.

Having looked briefly at the general role that mountains play in climate change, the next section will consider a particularly high part of southern Asia, namely the Himalaya and the Tibetan Plateau. You will look at the role the Himalaya and Tibetan Plateau may have played on the climate system during the last few tens of millions of years, and at the effect they have had and continue to have on the global atmosphere and neighbouring seas.

5.2 The uplift of Tibet and the monsoon

The Tibetan Plateau is the highest and largest plateau on the Earth's surface (Figure 5.4). Its southern edge is marked by the Himalaya and several of Asia's other great mountain ranges – the Karakoram, Hindu Kush and Kunlun – decorate its western and northern margins. If continental relief can affect global climate, this is the obvious region to study. This discussion of climatic change over long timescales of millions of years begins with a brief look at climate in this region at the present day.

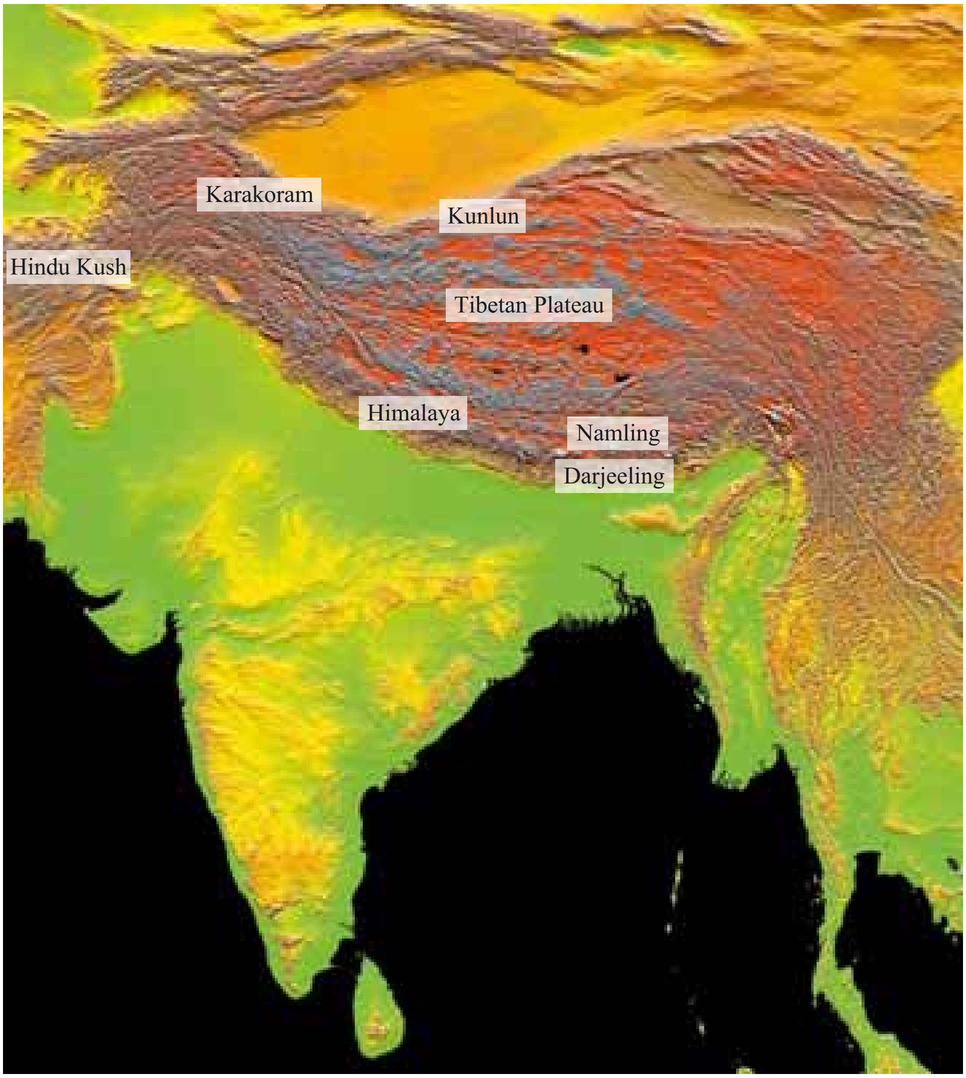


Figure 5.4 Digital elevation map for southern Asia. The Himalaya reach over 5000 m in places; to the north of the Himalaya, the Tibetan Plateau is over 4000 m while to the south, northern India is below 500 m.

5.2.1 Present-day climate across southern Asia

To a large extent, the climate of southern Asia is dominated by the monsoons. In the northern winter, the region is affected by cold, dry northeasterly winds blowing out from the intense high-pressure region over the continent (Figure 1.28). By contrast, in the northern summer when there is a strong low-pressure region over the Eurasian continent, the area receives moisture-laden air in the southwest monsoon.

The whole of southern Asia benefits from the monsoon rains. In particular, the areas of tropical rainforest along southwest India, Myanmar and Sri Lanka (Figure 3.4) are the results of the south-westerlies releasing much of their moisture over high land. On approaching the southern slopes of the Himalaya, the still-moist air mass is driven further upwards, causing summer rainfall over northern India. As a result, annual rainfall in Darjeeling on the southern slopes of the Himalaya is over 3000 mm, of which 88% falls between June and September, i.e. during the southwest monsoon. Less than 100 km away, to the north of the

Himalayan mountains, the Tibetan town of Gyantse receives an annual rainfall of only 270 mm. The contrasting climates result in very different floras and faunas: the southern slopes of the Himalaya are covered by forests (Figure 5.5a) supporting a population density of 200 people per square kilometre; Tibet, which is effectively in the rain shadow of the Himalaya, is characterised by semi-arid **steppe**, and in places is a rocky desert, hardly supporting one person per square kilometre (Figure 5.5b).

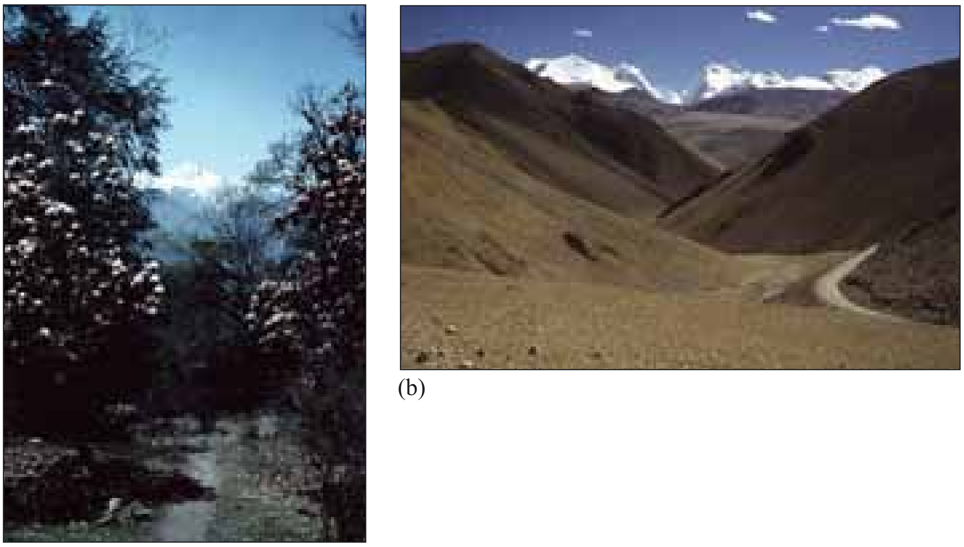

(a)
(b)

Figure 5.5 Two locations only 50 km apart, but on different sides of the Himalayan watershed: (a) rhododendron forests flourish in abundant rainfall on the southern slopes of the Himalaya; (b) rocky desert conditions on the northern side of the Himalaya.

As Figure 1.28 shows, the seasonal shift in the intertropical convergence zone (ITCZ) means that seasonally changing winds (monsoons) affect large parts of the globe at low latitudes. The extreme change in pressure over a large part of central southern Eurasia from intense high pressure in winter (Figure 1.29) to very low pressure in summer means that seasonal changes in the vicinity of southern Asia and the Arabian Sea are by far the most dramatic. It seems that the reason for this may lie in the existence of the Tibetan Plateau itself.

In 1989, the results of a series of experiments were published using a sophisticated computer model of the global climate (a '**general circulation model**' or GCM) designed to investigate the effect on climate of such an extensive high-altitude plateau. Starting with a simulation of present-day climate, the researchers changed just one variable: the topography of present land masses. When the Tibetan Plateau was 'removed', the heavy summer rainfall in northern India all but disappeared. In contrast, an even larger and higher plateau in central Asia greatly *increased* the area of summer monsoon rainfall throughout extensive regions south of the plateau, caused desert conditions over vast areas to the north of the plateau, and *decreased* summer precipitation much further west in the Mediterranean region in Europe.

Of course, such experiments have their critics, many of whom emphasised that no model can take into account all the possible variables. After all, if you think about climate change over the past 60 Ma, uplift of the Tibetan Plateau is not the only change to have taken place within the Earth system. Not only did the Indian land mass move northwards across the globe, traversing climatic belts, but the global climate was itself changing. Nevertheless, the results of the modelling clearly suggested that the uplift of Tibet could have had a dramatic effect on atmospheric circulation and precipitation throughout much of the Northern Hemisphere, and may well have affected the strength of the monsoon winds, particularly those of the southwest monsoon over southern Asia.

The strength of the southwest monsoon is determined by the pressure difference between the high over the tropical Indian Ocean and the low over the southern part of the continent (Figure 1.28). At the end of winter, the large rocky mass of the Tibetan Plateau heats up fast once its high-albedo covering of snow has melted; the overlying air is warmed and the pressure over the continent falls.

Question 5.1

The winds of the southwest monsoon are initially laden with moisture as they have blown across the Indian Ocean and the Arabian Sea. With reference to Section 1.4 (if necessary), why does the release of this moisture as the Himalayan monsoon rains help to intensify the circulatory pattern shown in Figure 1.29b?

The warming of the air over the Himalaya and Tibetan Plateau has a particularly large effect because the air is thin at these high altitudes and its temperature, therefore, is more sensitive to changes in heat.

As discussed in the answer to Question 5.1, the monsoon rains indirectly help to warm the air over Tibet. The condensation of moisture to form rain over the southern Himalaya releases latent heat, and so the summer winds driving from the south into Tibet are not only dry but also warm (Figure 1.29). At this latitude and in the absence of a plateau, the air temperature at 5 km above sea level would be around –20 °C (Figure 1.17); as it is, during the summer months, the temperatures rarely drop below freezing. Nevertheless, the dramatic summer storms that produce rain over the Himalaya may produce hail over Tibet (Figure 5.6). Indeed, the Tibetan Plateau is so high that the subtropical jet stream passes either to the north or to the south of it. The climate implications of this are not well understood, but it is clear that the jet stream would not have been diverted in this way before the uplift of Tibet.


(a)
(b)

Figure 5.6 (a) The Royal Crest of the Himalayan Kingdom of Bhutan. The crossed 'thunderbolts' are a common symbol in Tibetan culture, reflecting the power of summer storms in the Himalaya. (b) Dark clouds preceding a violent hailstorm on a Tibetan summer afternoon. High plateaux like Tibet are notorious for their vicious hailstorms, caused by sudden updrafts within clouds under cold conditions.

The overall effect of the Tibetan Plateau and the Himalaya on atmospheric circulation, therefore, is determined by both their high elevation and their geographical position. Uplift must have caused major changes in atmospheric circulation across the Northern Hemisphere. As far as the southwest monsoon is concerned, because summer heating of the atmosphere over Tibet has increased as the plateau has risen, it is possible that at some stage during its elevation, a threshold altitude was reached above which the monsoon winds were greatly strengthened. Partly for this reason, scientists have been looking for evidence of climate change in southern Asia that can be linked to uplift of Tibet. To find such a link, they need to know something about the timing of both the uplift of the plateau and of climate change in southern Asia over the relevant period.

5.2.2 When was the Tibetan Plateau uplifted?

The elevation of the Tibetan Plateau is the result of a head-on collision between the continental margins of two plates: India, which was migrating northwards, and Eurasia, which was stationary. The collision, which has been dated at around 50 Ma, led to crustal thickening and uplift of the Himalayan mountains and the plateau. It is reasonable to infer, therefore, that most of the uplift has occurred during the past 50 Ma. Can modern techniques improve on this very general estimate?

It is difficult to trace the uplift of a plateau through time because, if there is such a thing as a reliable **palaeo-altimeter**, no one has as yet discovered it. If an attempt were made to plot the change in altitude of the Tibetan Plateau against time, then it would have two (and only two) firm data points:

- the present-day altitude, which on average is 5 km above sea level
- rocks that are now 5 km high were *below* sea level 70 Ma ago because limestones with remains of marine organisms originally deposited in shallow seas at about that time have been found in southern Tibet.

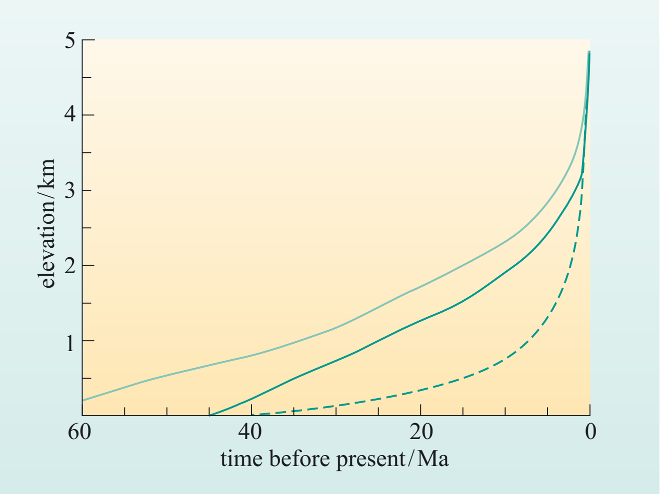


Figure 5.7 The history of uplift of the Tibetan Plateau as determined by studies of three different fossil plant assemblages, using the 'nearest living relative' approach (see section 7.8.2). (Raymo et al., 1988)

Details of the uplift during the intervening 70 Ma, however, are highly uncertain.

One approach to determine the elevation history of the plateau is to exploit the changes in surface temperature resulting from its elevation. The morphology of successful plant species is quite different in cold and warm climates; because temperature decreases with increasing altitude, the higher the altitude, the more cold-climate species are favoured. Palaeobotanists use this fact to infer altitude changes from fossil flora collected from sedimentary rocks deposited over the past 50 Ma. Work along these lines has led to the publication of several quite different altitude–time paths for the Tibetan Plateau (Figure 5.7).

Unfortunately, there are a couple of flaws in this approach. First, even if the region corresponding to the Tibetan Plateau had not been uplifted at all, its climate would have changed considerably over the course of 50 Ma, not least because of the closure of the Tethys Ocean (Figure 4.16).

Furthermore, within the plateau itself there will have been small-scale climatic variations resulting from local topography, with some areas for example being more sheltered or wetter. To some extent, these latter complications can be allowed for, but there is another problem which is more fundamental. As the fossil species found in sediments older than a few million years are usually extinct, some palaeobotanists have adopted the 'nearest living relative' approach. In practice, this involves identifying the nearest living relative to the fossil species concerned, and then assuming that the climatic conditions under which the ancient plants lived were similar to those of their living relatives.

■ Suggest why such an approach might give misleading results.

■ Species evolve and adapt to changing environmental conditions, so the extinct species might have lived under somewhat different conditions from its nearest living relative.

Imagine for example that yaks (currently found across the Tibetan Plateau) are extinct, but that their fossilised remains are well documented by palaeontologists, who have concluded that cattle are the yak's nearest living relative. The inferred habitat of yaks would then be characterised by a temperate or warm climate, similar to where living cattle are found. The truth, of course, is that yaks are adapted to high-altitude, cold conditions (Figure 5.8). In other words, the 'nearest living relative' approach ignores evolutionary adaptation. Clearly, this approach has inherent problems, and the resulting estimates of uplift rates need to be treated with care.

Figure 5.8 Adult yaks on the Tibetan Plateau. Yaks are an example of adaptation to high-altitude, cold conditions. The location is Namling, which is also the site of abundant leaf fossils.

An alternative approach is to examine and classify the shapes of plant leaves that are adapted to different environments (Figure 5.9). By examining the shape, size and margin characteristics of a leaf (**leaf physiognomy**), it is possible to determine the climatic regime under which the plant was growing when it was alive. For example, modern woody, broad-leaved flowering plants tend to have smooth leaf margins in warm climates but toothed, jagged margins in cool

Figure 5.9 Fossil leaves from Tertiary sediments on the Tibetan Plateau.

climates. Thus, since plants live on the Earth's surface, fossil leaves, along with an independent (e.g. isotopic) dating method, can be used to estimate the height of a land surface at any time in the past. This approach is called **leaf margin analysis** and will be discussed in more detail in Chapter 7.

The fossil leaf approach requires very specific field sites that combine abundant well-preserved flora with datable strata, a situation rarely found in nature. So far, only one such locality has been found across the entire Tibetan Plateau (Figure 5.8). From this single site in southern Tibet, 400 specimens, including over 30 species, have been recovered and analysed to yield an estimate of the prevailing temperatures during their growing season. Volcanic strata from above and below the leaf-bearing shales have been dated at 15 Ma using argon isotopes. Finally, a climate model has been run for this period of the Neogene (between 23 Ma and 1.8 Ma) that converted the estimated temperature into an altitude for the latitude of southern Tibet at that time. The result demonstrated that this sedimentary basin in southern Tibet was at an elevation of 4600 ±700 m at 15 Ma, an altitude indistinguishable from its present-day height above sea level (4300 m).

■ Referring to Figure 5.7, how does this conclusion compare with earlier attempts using the 'nearest living relative' approach?

■ The leaf margin analysis indicates that southern Tibet was at an elevation of 4000–5000m much earlier than was previously thought.

The conclusion from leaf margin analysis that southern Tibet has not changed in elevation for at least 15 Ma has been verified by a second technique that exploits the relationship between the fractionation of oxygen isotopes within H_2O, precipitated as rain or snow (Box 4.2), and the altitude. The details of this new isotopic technique are beyond the scope of the book; and unfortunately, the method also carries large uncertainties. Nonetheless, analyses of oxygen isotopes from carbonates in lake deposits broadly confirm the results from leaf margin analysis.

Our understanding of the uplift history of the Tibetan Plateau remains in its infancy. Present knowledge suggests that it began to rise some time after 50 Ma and reached its maximum present elevation by about 15 Ma in southern Tibet. Although there are no direct estimates of the timing of uplift in northern Tibet, dating structures associated with uplift suggest much more recent uplift, perhaps dating back to the past 10 Ma.

5.2.3 Evidence for climate change across southern Asia

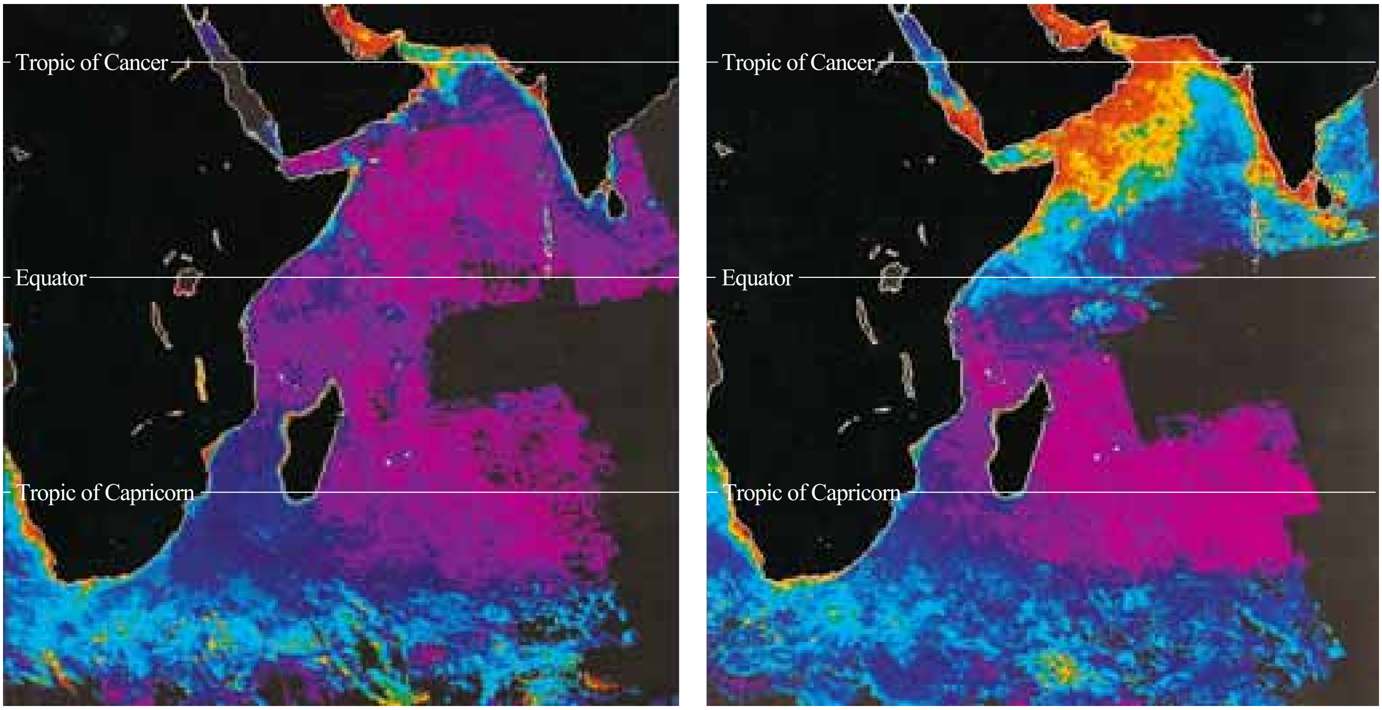
This section will look briefly at some evidence for how climate in southern Asia might have changed over the past 10 Ma, before setting this in the context of global climatic change during the Tertiary Period (i.e. 65 Ma–2 Ma).

Climate change in southern Asia

Evidence for climate change in southern Asia over the past 10 Ma is drawn from a number of different lines of study, including two techniques that use the remains of living organisms:

- zooplankton that lived in the surface waters of the Arabian Sea
- terrestrial plants and the mammals that fed on them.

Take a look at Figure 5.10, which shows the concentration of phytoplankton in surface waters of the Indian Ocean today (a) during the inter-monsoon period, when winds are generally light, and (b) during the summer monsoon, when winds over the northern Indian Ocean and Arabian Sea are strong and from the southwest.



(a) (b)

Figure 5.10 Seasonal variations in phytoplankton concentrations, on the basis of chlorophyll pigment recorded by the satellite-borne Coastal Zone Color Scanner. (a) A composite image for May–June, a period of light winds. The highest concentrations are shown in red (principally in the Persian Gulf and near-coastal areas in the Arabian Sea and around India and Pakistan); the lowest concentrations are shown in pinkish purple (principally in the Arabian Sea and the Indian Ocean area north and south of the Equator from eastern Africa to Sri Lanka). (b) A composite for September–October, during the southwest monsoon. The highest concentrations are shown in red (principally in the southern Red Sea, the Arabian Sea, the Persian Gulf and coastal areas around India, Pakistan and Sri Lanka); the lowest concentrations are shown in pinkish purple (principally in the Indian Ocean south of the Equator to just south of the Tropic of Capricorn). In both (a) and (b) the black areas indicate no data.

■ Without going into details, to what could the different levels of primary productivity in the northern Indian Ocean/Arabian Sea shown in Figures 5.10a and 5.10b be attributed?

▪ The difference could relate to the fact that upwelling is stronger and more widespread in this region during the southwest monsoon, resulting in higher phytoplankton concentrations.

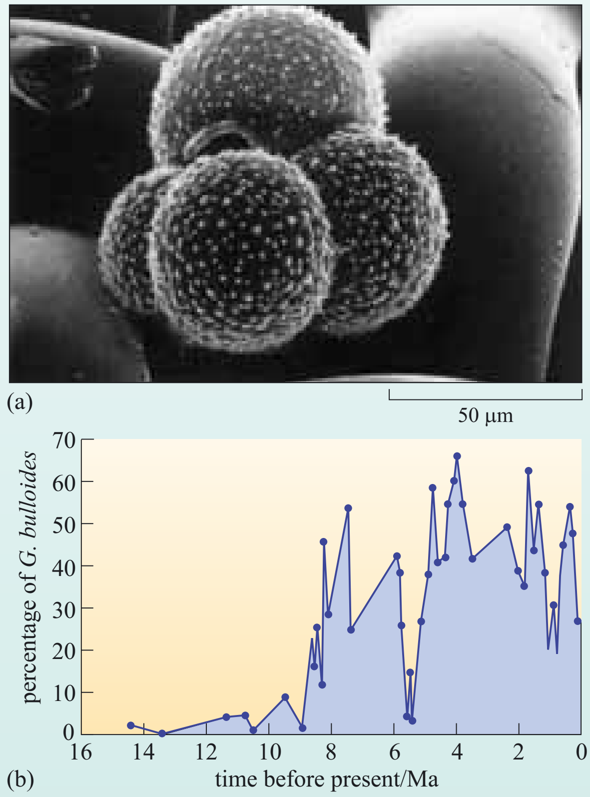


Figure 5.11 (a) The remains of a specimen of *Globigerina bulloides*. The background is the mesh of the sampling net. (b) Variation in the proportion of the microplankton population made up of *G. bulloides* over the past 14 Ma, from a seabed drill core from the Arabian Sea. (Kroon et al., 1992)

As discussed in earlier chapters, upwelling brings nutrient-rich subsurface water into the photic zone, supporting populations of phytoplankton on which zooplankton and larger organisms feed. If you compare Figure 5.10 with the wind patterns shown in Figure 1.28, you will see that the nearshore upwelling occurring here cannot result from longshore equatorward winds (Figure 1.36a) as it does in the tropical regions of the other oceans. Instead, it mainly occurs where surface waters diverge in cyclonic gyres (Figure 1.36b) and at places where surface currents diverge from the coast.

Now back to the discussion of climatic change. The zooplanktonic organism under consideration is a species of foraminiferan known as *Globigerina bulloides* (Figure 5.11a). Its abundance at various times in the past 14 Ma relative to other species of microplankton (i.e. those between 20 and 200 µm across), has been estimated on the basis of its fossil remains in sediment cores drilled from the floor of the Arabian Sea (Figure 5.11b). *G. bulloides* is presently abundant in nutrient-rich tropical waters, and in the Arabian Sea its abundance (expressed as a proportion of the total microplankton population) increases by three orders of magnitude during periods of upwelling.

Question 5.2

(a) In general terms, describe the variation in the abundance of *G. bulloides* over the past 14 Ma.

(b) Bearing in mind the high levels of primary productivity shown in Figure 5.10b, does the plot in Figure 5.11b suggest anything about changes in the strength of the southwest monsoon over the time period in question (i.e. 14.5 Ma to present)?

So, the patterns of relative abundance of *G. bulloides* suggest that the southwest monsoon became stronger several million years after the Tibetan Plateau in the south had reached its maximum altitude.

Organic debris in sediments eroded from the Himalaya provides the second clue to past climate; as the Himalaya rose, so the rate of erosion of the steepening slopes increased. Great rivers flowing southwards deposited much of the eroded material into a large subsiding basin, with the result that these sediments from the Himalaya are now exposed in northern Pakistan and India. Their use as climatic indicators lies in the proportion of the different isotopes of carbon they contain, expressed in terms of the ratio δ^{13}C (Box 5.1).

Box 5.1 Carbon isotopes and δ^{13}C

Carbon occurs in nature as two stable isotopes: ^{12}C and the much rarer ^{13}C. During photosynthesis, fixation of the lighter $^{12}CO_2$ is favoured over that of the heavier $^{13}CO_2$ because $^{12}CO_2$ diffuses into cells more rapidly and more readily takes part in chemical reactions. As a result of this fractionation of isotopes, organic matter produced by photosynthesis is enriched in ^{12}C and depleted in ^{13}C relative to the inorganic carbon in the atmosphere and hydrosphere (i.e. CO_2 gas plus bicarbonate and carbonate ions in solution). Enrichment or depletion of ^{13}C is expressed using the ratio δ^{13}C, which is calculated in an analogous way to δ^{18}O (Box 4.2) to give a value in parts per thousand or ‘per mil’, often written as ‰:

$$\delta^{13}\mathrm{C}\left[\frac{(^{13}\mathrm{C}/^{12}\mathrm{C})_{\mathrm{sample}}}{(^{13}\mathrm{C}/^{12}\mathrm{C})_{\mathrm{standard}}}-1\right]\times 1000 \qquad (5.2)$$

$(^{13}\mathrm{C}/^{12}\mathrm{C})_{\mathrm{standard}}$ is the ratio calculated for a standard carbonate sample, and is 1/88.99.

- If ^{13}C/^{12}C is greater in the sample than in the standard, then the ratio of these ratios will be greater than one, and the expression in square brackets (i.e. d^{13}C) will be positive.
- If ^{13}C/^{12}C is less in the sample than in the standard, then δ^{13}C will be negative.

Higher values of δ^{13}C (or less negative values) correspond to a higher proportion of ^{13}C.

δ^{13}C for atmospheric CO_2 is –8‰; and because of fractionation, plant tissue generally contains a lower proportion of $^{12}CO_2$ by about 20‰. As a result, plant tissue has an average δ^{13}C value of about –(8‰ + 20‰) = –28‰.

■ Does organic material (plant or animal tissue) have a higher or lower value than inorganic carbon?

■ It is always lower (i.e. more negative).

The δ^{13}C of a sample reveals more than just whether it is plant derived. As a result of the different mechanisms of photosynthesis that they use, plants and shrubs that flourish under warm conditions tend to incorporate more of the isotope ^{13}C than those that thrive in colder conditions. Furthermore, as a result of plant respiration through the roots and the accumulation of plant debris, soil acquires a δ^{13}C ‘signature’ similar to that of the plants that grew in it. In particular, carbonates that precipitate in soil have a δ^{13}C value somewhere between that of atmospheric CO_2 and that of the living plants and plant debris in the soil. Measurements of δ^{13}C for carbon (as organic carbon or calcium carbonate) in soils of different ages can, therefore, provide an indicator of the temperatures that prevailed during the growing season.

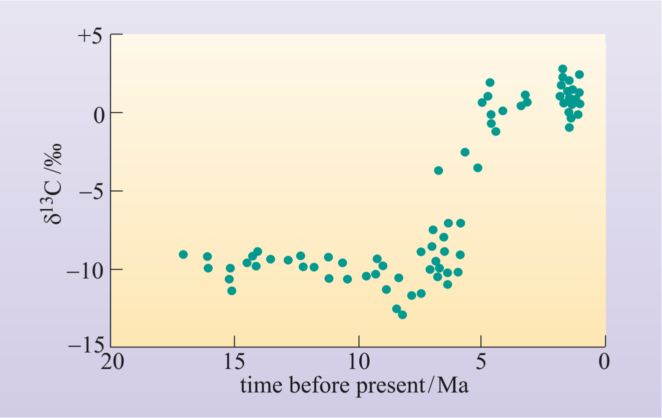


Figure 5.12 Variation of δ^{13}C with time in carbonates in soils formed from debris eroded from the Himalaya of northern Pakistan. (Quade et al., 1989)

The information that you need to take away from Box 5.1 is simply this: the δ^{13}C of plant (and hence animal) tissue is always negative, but is higher (less negative) for the kinds of plants that flourish under warm conditions.

The sediments from the Himalaya referred to above eventually formed soil, within which carbonates were precipitated and, as discussed in Box 5.1, the δ^{13}C of these carbonates reflect the δ^{13}C of organic debris in the soil. Figure 5.12 is a plot of δ^{13}C against time for these soil carbonates.

■ According to Figure 5.12, what marked changes in the δ^{13}C values of organic debris eroded from the Himalaya can be observed during the past 20 Ma?

□ A sharp increase in δ^{13}C values from −10‰ to around 0‰ occurred between 8 and 5 Ma.

The increase in organic material incorporating more ^{13}C has been interpreted by some palaeoclimatologists as an explosion of plant production during the growing season, resulting from increased summer rainfall because of a strengthening of the southwest monsoon at 8–7 Ma. However, because this increase in δ^{13}C values has been recognised in plant remains from other continents and is not a peculiarity of southern Asia, other workers in the field have argued that it marks a spread of plants using a slightly different mechanism for photosynthesis, which evolved within the last 14 Ma. Some modern plant groups including savannah grasses rely on this 'newer' mechanism exclusively, and are referred to as **C4 plants**; the majority (including trees and shrubs), using the original mechanism, are referred to as **C3 plants**. Figure 5.12 might, therefore, chart a transition of plant type that could be part of a global response to climate change that may or may not be directly linked to the strengthening of the southwest monsoon.

Interestingly, the remains of fossilised mammal teeth now preserved in the Himalayan sediments also suggest a change in the vegetation in the region about 8 Ma. The shapes of the teeth suggest that at about this time there was a marked change from browsers (which feed on trees and shrubs, i.e. C3 plants) to grazers (grass-eaters, which feed on C4 plants); furthermore, some identifiable forest-based mammals (e.g. orang-utans) disappeared from the region at that time.

Finally, the *type of sediment* originating from the Himalaya may be used as an indicator of the temperature at which weathering occurred. Before about 7 Ma, the deposits carried down from the Himalaya were predominantly sands and silts; these sediments indicate strong erosional forces (i.e. physical weathering) by freeze–thaw or glaciers acting on exposed rock surfaces that are lacking soil cover. In contrast, sediments younger than 7 Ma include plenty of muds and clays, suggesting chemical weathering, producing thick layers of soil in the source areas of the rivers. Like the δ^{13}C data, the size distribution of sediments in the sedimentary record points towards a sudden increase in summer rainfall in southern Asia around 7 Ma.

In summary, although it is not possible to be precise about the timing of either the uplift of the Tibetan Plateau or climate change in southern Asia, there is evidence that summer rainfall associated with the southwest monsoon increased between 9 Ma and 6 Ma. By this time, the southern plateau had already stabilised at its present elevation for at least 6 million years, but northern regions were just reaching their maximum elevation. Geologists have speculated that by about 9 Ma, the area of the elevated plateau was sufficient to heat the lower atmosphere during the summer months and thus trigger a dramatic increase in the intensity of the monsoon.

5.3 Global climate change during the Tertiary

So far, a possible link between uplift of the Tibetan Plateau and a strengthening of the southwest monsoon has been investigated. Although this may have affected a large part of the globe, it essentially had a regional effect on the climate. If the uplift of this (or any other) high plateau had had an effect on *global* climate, you would have expected the change to have taken place not over the past 10 Ma as the monsoon was strengthening, but over the past 50 Ma, i.e. from the beginning of uplift of the plateau, initiated by continental collision. Before looking more closely at possible global consequences, it is important to understand how global climate has changed since the collision between India and Eurasia.

The variation in global average temperature over the past 120 Ma, deduced from oxygen isotope studies of the remains of deep-sea benthic foraminiferans, is shown in Figure 5.13. Despite the fluctuations, there is a clear downward trend, with a net cooling of nearly 20 °C over the period concerned, with strong independent geological evidence supporting this inference. For example, during the past 50 Ma, the distribution of sediments deposited by glaciers has generally been increasing, with these sediments deposited progressively further away from the present polar regions, reaching their maximum extent during the peak of the present (Quaternary) Ice Age.

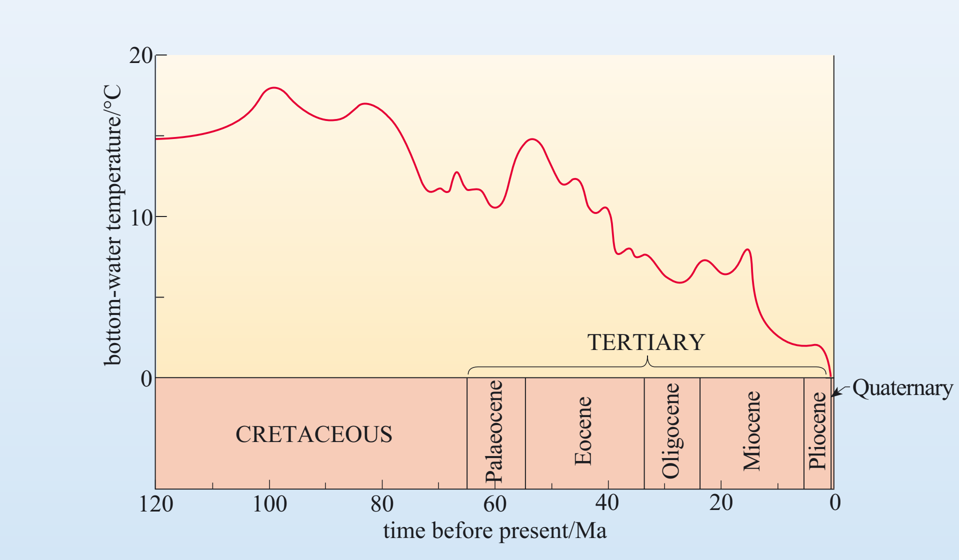


Figure 5.13 Variations in the temperature of ocean bottom waters over the past 120 Ma, estimated using oxygen isotope ratios ($\delta^{18}O$) from deep-sea benthic foraminiferans. (This is an expanded version of the right-hand side of the temperature plot in Figure 4.20.)

What caused this decrease in global temperature? One potential cause may have been the rearrangement of the continents (as discussed in Chapter 4). However, irrespective of how the continents are rearranged, computer-based climate models cannot reproduce the long-term cooling pattern indicated by Figure 5.13. What's more, the climate-modelling experiments that investigated the effects of the Tibetan Plateau on global climate failed to show that the uplifting of Tibet could, by itself, cause long-term cooling. It seems that something else is required to explain this trend.

■ What other factor might have been involved?

■ A change in the composition of the atmosphere; in particular, a long-term *decrease* in the concentration of CO_2.

The reasons behind this are beyond the scope of this book, but you can assume that the temperature variations shown in Figure 5.13 resulted entirely from fluctuations in atmospheric CO_2 concentration. To account for the overall fall in temperature, therefore, the CO_2 concentration would have to have declined from a value of about eight times that of the present day. Many geoscientists believe that the building of large mountain belts in central Asia could well have played a role in bringing about such a dramatic change in atmospheric composition. This particular aspect of mountain building is thought by some to be an important mechanism for changing atmospheric CO_2 concentrations, and hence climate.

5.3.1 The Himalaya, Tibet and atmospheric CO_2

Although bordered by impressive mountain ranges, the interior of Tibet is truly a plateau, with a local relief of generally no more than a kilometre or so (Figure 5.14a). The plateau is the catchment area for many of Asia's great rivers, including the Indus, the Brahmaputra (known in Tibet as the Tsangpo), the Yangtze, and the Mekong (Figure 5.15). These rivers have to descend 5 km before they reach the sea, eroding their way through mountain ranges that are steadily being uplifted (Figure 5.14b).

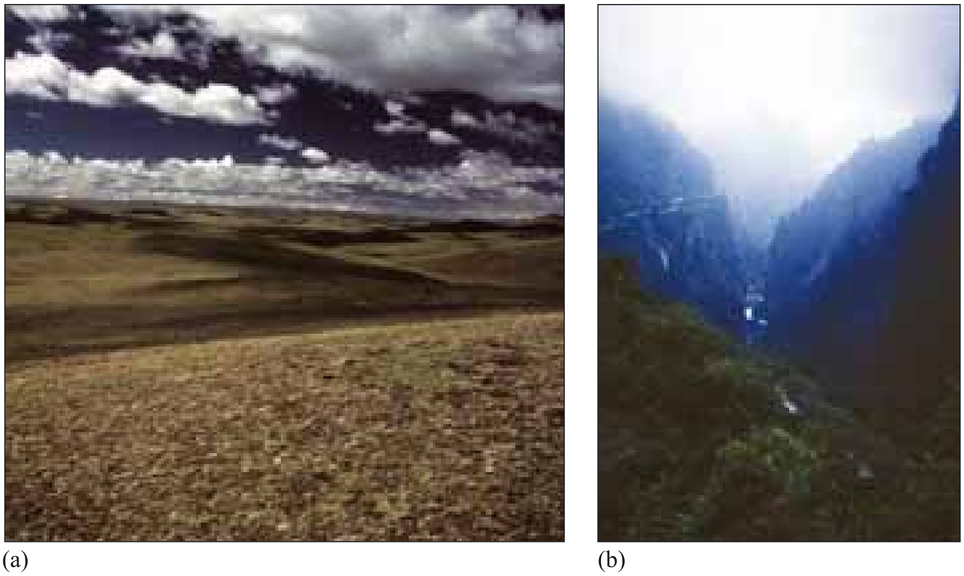

(a) (b)

Figure 5.14 (a) The gentle relief typical of much of central Tibet. (b) A deeply incised Himalayan gorge, carved out by a river flowing south from Tibet to join the Ganges on the Indian plains.

Figure 5.15 The central Asian river system, showing major rivers with sources on the Tibetan Plateau or in the Himalaya.

Question 5.3

Table 5.1 lists the flux of dissolved material of rivers with a source in the Tibet/Himalaya region.

(a) The total flux of dissolved material carried by rivers globally is about 2130×10^6 t y^{-1}, while the global flux of suspended sediment in rivers is about $20\,000 \times 10^6$ t y^{-1}. What percentage of these global fluxes of (i) dissolved material and (ii) suspended sediment are contributed by all the rivers in Table 5.1 together?

(b) The catchment area of the rivers in Table 5.1 (Figure 5.15) represents about 5% of the Earth's continental surface. What do your answers to part (a) imply about weathering rates in the Tibet/Himalaya region in a global context?

Table 5.1 Fluxes of dissolved material in rivers with sources in Tibet or the Himalaya.

River	Flux of dissolved material/10^6 t y^{-1}	Flux of suspended sediment/10^6 t y^{-1}
Ganges	85	538
Yangtze	205	483
Brahmaputra (Tsangpo)	82	668
Irrawaddy	81	260
Indus	28	250
Mekong	124	150
Salween	55	66
Hwang-Ho	19	1 103
Total for Tibetan/Himalayan region	679	3 518
Global flux total	2 130	20 000

It appears that rivers flowing down from Tibet and the Himalaya have great erosive power and carry an unusually large load of fragmented rocks (Figure 5.3) and dissolved material.

■ Bearing in mind the high rates of chemical weathering on the southern slopes of the Himalaya, how could the formation of the Himalaya and the uplift of the Tibetan Plateau indirectly affect the concentration of CO_2 in the atmosphere?

□ Weathering of silicate minerals, followed by accumulation and preservation of organic carbon and carbonates in the ocean, result in net removal of CO_2 from the atmosphere (Figure 3.20). Therefore, if uplift of the Himalaya and Tibet increased total global weathering rates, it would also have increased the rate at which CO_2 was removed from the atmosphere.

Of course, a change in the concentration of atmospheric CO_2 would affect fluxes into and out of other carbon reservoirs, and it would have been some time before a new equilibrium was established. In fact, it has been estimated that reduced atmospheric CO_2 levels would have been re-equilibrated about 1 Ma after the mountain range had been uplifted. Other factors being equal, this reduction in atmospheric CO_2 concentrations would lead to global cooling.

In climate models proposed in recent years, the role of mountain building in the global climate system has been treated in various ways. Two contrasting approaches will be considered, which differ in their assumptions concerning what primarily determines the CO_2 concentration of the atmosphere, and hence what ultimately drives carbon fluxes between the various carbon reservoirs, namely the atmosphere, the oceans and the Earth's crust.

The **GEOCARB model** (as originally conceived by Bob Berner and colleagues at Yale University) rests on two important assumptions:

1. Global temperatures are determined by the concentration of CO_2 in the atmosphere.
2. The concentration of CO_2 in the atmosphere is determined primarily by the volume of gases emitted from volcanoes.

An *approximate* measure of the global rate of emission of volcanic gases can be obtained from the rate of production of new sea floor: volcanoes above subduction zones release CO_2 directly into the atmosphere, while some of the gases from hydrothermal vents and underwater eruptions also eventually escape from the ocean into the atmosphere. There is evidence to suggest that over the past 110 Ma, the rate of production of oceanic crust has decreased roughly to what it was before the eruption of major flood basalts at about 140 Ma (Figure 4.10). Over the past 110 Ma, less CO_2 has been supplied by volcanism, so, according to the GEOCARB model, there would have been global cooling as a result of lower concentrations of CO_2 in the atmosphere.

The second approach, referred to as the **mountain-forcing model**, is preferred by scientists who suggest that changes in atmospheric CO_2 concentrations are driven by changes in chemical weathering rates. This model was pioneered by two geoscientists from the USA, Bill Ruddiman and Maureen Raymo, who extended the idea that uplift of the Tibetan Plateau strengthened the southwest monsoon and suggested that high weathering rates over a region of steep topography affected by high summer rainfall were at least partly responsible for the global cooling that followed the collision between India and Eurasia. If this is true, then uplift of Tibet effectively set the scene for the glacial periods that have characterised the climate in recent geological time.

Question 5.4

Figure 5.13 shows an overall downward trend in temperature from about 100 Ma to present, but there have been fluctuations and the rate of decrease has been variable. On the basis of what you know about the timing of the building of the Himalaya and the uplift of Tibet, along with information in Figure 4.10, to what extent can the shape of the temperature plot in Figure 5.13 be used to support (a) the GEOCARB model and (b) the mountain-forcing model?

The answer to Question 5.4 provides an important insight to the following discussion, which explores in more detail whether weathering of the Himalaya and Tibet *could* have caused global climate change over the past 50 Ma. The first point to remember is that weathering only results in the removal of CO_2 from the atmosphere because some of the carbon carried to the ocean in rivers is *removed* from the oceans and preserved in sediments, i.e. it moves out of the intermediate-scale marine carbon cycle and becomes part of the long-term geological carbon cycle (Figure 3.20). As you may recall, there are two ways in which carbon can be preserved and buried in deep-sea sediments: as carbonaceous sediments (organic carbon) and as carbonates (inorganic carbon).

Beginning with the organic carbon, one factor that would increase the proportion of organic remains preserved in the deep ocean is a large supply of organic debris in rivers. Before the collision of India with Asia, unusually organic-rich sediments were deposited on the continental shelf along the northern margin of the Indian Plate. After collision, the buried sediments were uplifted and exposed at the surface, where they were subject to weathering and erosion. As a result, much of this organic material may have been carried to the sea as particulate and dissolved organic carbon. As discussed in Box 5.1, $\delta^{13}C$ values for organic carbon are lower than those for carbon from other carbon reservoirs. An increase in the flux of organic carbon to the oceans would, therefore, eventually result in a decrease in the average $\delta^{13}C$ value for sediments (both organic and calcareous) being deposited on the seabed. A plot of $\delta^{13}C$ against depth in marine sediments provides a measure of the contribution of organic carbon to the oceans over time. (Note that for reasons that are beyond the scope of this book, marine carbonates always have higher $\delta^{13}C$ values than soil carbonates (Figure 5.12).)

Question 5.5

(a) What would happen to the average $\delta^{13}C$ value of marine carbonates if the global flux of organic carbon from the continents increased significantly?

(b) According to Figure 5.16, when in the past 70 Ma was the largest increase in the flux of organic carbon to the oceans?

■ Why might an increase in the rate of continental weathering result in an increase in the accumulation and preservation of both inorganic and organic carbon?

■ Increased chemical weathering will increase the concentration of a number of constituents in seawater, including the following nutrients: dissolved nitrate, phosphate and silica, and (perhaps more importantly) micronutrients such as iron. An increase in the supply of nutrients to the oceans could result in increased primary productivity of phytoplankton, both with and without calcium carbonate hard parts. This would result in increased accumulation of both organic carbon and inorganic carbon.

An increase in primary productivity in response to increased nutrient supply could also result from increased oceanic upwelling. Vigorous upwelling occurs during the southwest monsoon, so if the uplift of the Himalaya and Tibet caused the monsoon to strengthen then, at the same time, it could have enhanced the rate of preservation of carbon in the deep sea.

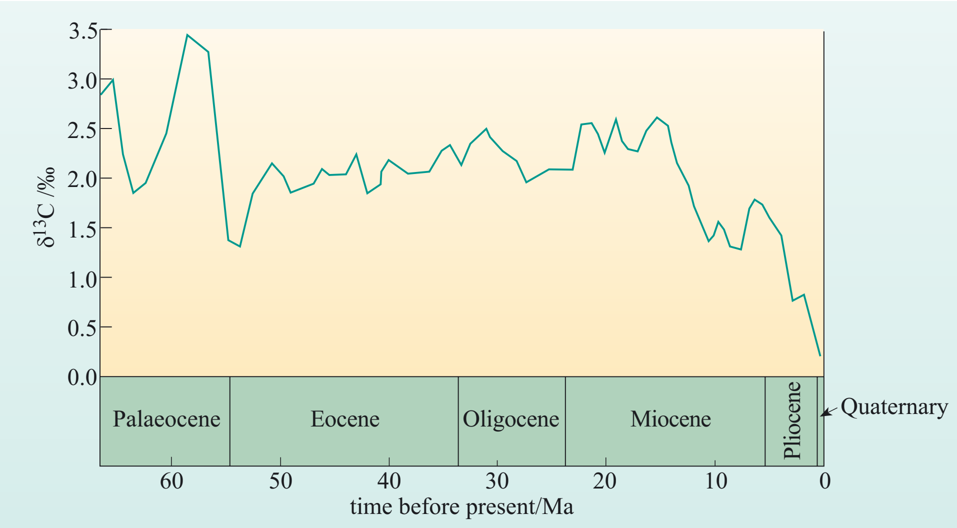


Figure 5.16 The variation of $\delta^{13}C$ in marine carbonates laid down over the past 65 Ma or so, i.e. during the Tertiary and Quaternary Periods.

In fact, some geochemists regard the preservation of organic carbon as more important than the preservation of carbonates. However, it is hard to determine the extent to which the accumulation of organic carbon is driven by weathering rates, especially as marine primary productivity is greatly affected by other influences, notably wind-driven upwelling, and the supply of nutrients generally.

Ironically, the very fact that uplift of Tibet and the Himalaya appears to have such a strong effect on the levels of atmospheric CO_2 could potentially be a problem for supporters of the mountain-forcing model, because it seems to leave open the possibility of runaway cooling occurring, for which there is no evidence in the relevant geological records despite the overall decline in global temperature during the past 100 Ma. According to the GEOCARB model, levels of atmospheric CO_2 would be maintained at more or less the same level over time by a negative feedback process as follows: if more CO_2 is released into the atmosphere as a result of increased rates of production of sea floor, global temperatures will rise. This temperature rise would lead to increasing weathering rates, which in turn would *remove* CO_2 from the atmosphere, thus *decreasing* and returning the temperature towards its original value; and so on (Figure 5.17).

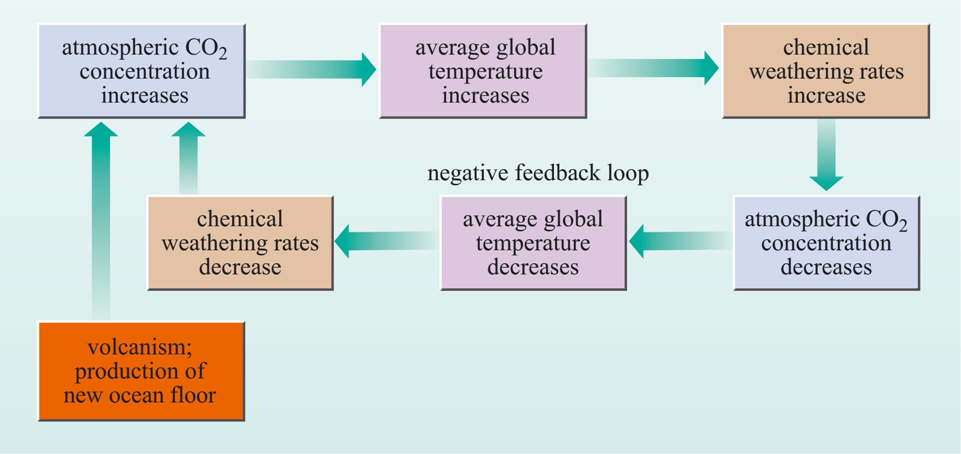


Figure 5.17 The negative feedback loop in the climate cycle derived from the GEOCARB model. If atmospheric CO_2 concentrations *rise* because of *increased* rates of ocean-floor production, then global temperatures will *rise*, leading to *increased* weathering rates. This, in turn, would *remove* CO_2 from the atmosphere, thus *decreasing* the temperature towards its initial value. Similarly, if atmospheric CO_2 concentrations should *fall*, then global temperatures will fall, leading to *decreased* weathering rates. This, in turn, would *remove less* CO_2 from the atmosphere (there would still be various sources of atmospheric CO_2), thus *increasing* the temperature towards its initial value.

On the other hand, if (as assumed by the mountain-forcing model) the concentration of CO_2 in the atmosphere is primarily controlled by mountain uplift, then there is no *direct* link between the rate of operation of the CO_2 sink (i.e. preservation and burial of carbon in the oceans) and the rate of operation of the CO_2 source (i.e. volcanic emission). As a result, there can be no direct stabilising feedback loops of the type described above to prevent runaway cooling.

Estimates of the rate at which weathering of Tibet and the Himalaya has depleted CO_2 in the atmosphere according to the mountain-forcing model show that weathering alone would exhaust all the CO_2 in the atmosphere in only a few million years – something that obviously has not happened. It is important to remember, however, that the processes that eventually lead to mountain building can, at the same time, provide a source of atmospheric CO_2.

■ What is the nature of this source of atmospheric CO_2?

■ *Decarbonation* of carbonates mixed with silica from shallow-water carbonates deposited at the continental margins as well as deep-water carbonates on top of the subducting slab, descending beneath the collision zone.

Overall, during the lifetime of a particular evolving mountain belt, the CO_2 flux from lithosphere to atmosphere as a result of subduction, collision and volcanism will replenish a significant proportion of the CO_2 lost from the atmosphere through weathering. It is important to note, however, that although the operation of source and sink are generally related through the rates of plate convergence at the destructive plate margin and collision zone, decarbonation and weathering are *not* closely coupled within individual zones of mountain building: CO_2 gain to the atmosphere will occur early in the history of the mountain belt when carbonates and silicates are first heated; CO_2 loss will predominate later, with the formation of high mountains and rapid weathering.

A further source of CO_2 associated with the collision of continents is the oxidation of organic carbon in the crust. As mentioned above, after the collision of India and Asia buried carbon-rich sediments were uplifted and eroded. Once exposed at the surface, this organic carbon was oxidised to CO_2 through bacterial activity and by simple chemical reaction with atmospheric oxygen.

In summary, there are at least two mechanisms that would have counteracted any tendency towards a runaway loss of CO_2 from the atmosphere through weathering of Tibet and the Himalaya: decarbonation reactions in rocks heated up as a result of continental collision within the crust, and oxidation of organic carbon at the surface of the crust.

5.3.2 Testing the models

So far, it has not been possible to comment definitively on whether the original GEOCARB model or the mountain-forcing model is more appropriate for the estimation of changes in atmospheric CO_2 concentrations over the past 50 Ma. When scientists need to decide between alternative models, they usually examine specific outcomes or predictions to see how they differ. As far as these two competing models are concerned, a significant difference arises in the contrasting way in which they link climate change and weathering rates.

■ According to the GEOCARB model, how will a high rate of production of new ocean floor affect the rate at which the continents are weathered?

□ According to this model, global temperatures are determined by atmospheric CO_2 concentrations, which in turn are determined primarily by volcanic emissions. *Increased rates of production of new ocean floor will, therefore, lead to higher* CO_2 *levels and higher temperatures*. They will lead to an increase in rates of continental weathering because chemical reactions occur more rapidly at higher temperatures (Figure 5.17).

Implicit in the GEOCARB model, therefore, is the assumption that high rates of weathering of continental rocks would result from global warming.

■ What would be the relationship between global temperatures and high continental weathering rates if the mountain-forcing model were correct?

□ According to this model, atmospheric CO_2 concentrations are driven primarily by continental weathering rates. As weathering of the continents removes CO_2 from the atmosphere, *high weathering rates should lead to global cooling*.

The GEOCARB model and the mountain-forcing models (at first sight at least) have contrasting implications for the relationship between global temperature, atmospheric CO_2 concentrations and weathering rates. The GEOCARB model involves an association between periods of high rates of chemical weathering and *high* global temperatures (high atmospheric CO_2), whereas mountain forcing predicts an association between high rates of chemical weathering and *low* global temperatures (low atmospheric CO_2). This is a significant point because it means that if the rate of continental weathering through time could be measured and compared with the variation in global temperature (Figure 5.13), it might help scientists to decide whether the principal control on climate change (at least over the past 50 Ma) has been the rate of CO_2 released as a result of the production of new ocean floor or due to the formation of high mountain ranges.

Fortunately, geochemists have discovered that certain isotopic ratios in marine sediments go some way towards providing an approximation of rates of weathering of continental rocks. Before illustrating this point, it is necessary to understand some aspects about strontium (Sr) isotopes (Box 5.2).

Box 5.2 The isotopic composition of strontium

The element Sr occurs in nature as several different isotopes. Geochemists are mainly concerned with two of these: ^{86}Sr and ^{87}Sr. The first, ^{86}Sr, is stable and is not the decay product of any other isotope. The other isotope, ^{87}Sr, is known as **radiogenic strontium** because it is the product of radioactive decay of one of the isotopes of rubidium, ^{87}Rb.

Most rocks contain varying amounts of both elemental Sr and Rb. Sr includes both ^{87}Sr and ^{86}Sr; the amount of ^{87}Sr is continually increasing due to the decay of radioactive ^{87}Rb, but the amount of ^{86}Sr remains unchanged. In other words, the ^{87}Sr/^{86}Sr ratio will increase with time in any rock that contains Rb. As a result, geochemists generally refer to the ^{87}Sr/^{86}Sr ratio rather than to the absolute concentration of ^{87}Rb or ^{87}Sr because the isotopic ratios of different rocks (and fluids) provide more insight about the history of the rocks (and fluids) than the total concentration of elemental Sr.

Rocks that make up the continents have variable ^{87}Sr/^{86}Sr ratios, but these values are all greater than the ^{87}Sr/^{86}Sr ratio of rocks from the upper mantle. This is because the rocks that form the continental crust have much higher elemental Rb/Sr ratios than those that make up the mantle.

The ^{87}Sr/^{86}Sr ratio of present-day seawater represents a combination of two components. The first, with a high average value of about 0.7118, comes from rivers that have entered the oceans after flowing over the continents. The second, with a low average value of 0.7035, comes from hydrothermal fluids that have circulated within the upper mantle and escaped at vents along ocean ridges; this lower value is similar to that of rocks of the upper mantle. These two fluxes combine to yield the present-day ^{87}Sr/^{86}Sr value for seawater, i.e. 0.7092, which is an approximation for all the world's oceans because circulation of the ocean water masses is more rapid than the residence time of Sr in seawater and so has homogenised the Sr isotopic ratio by mixing processes.

By measuring the isotopic composition of marine carbonates of known ages, geochemists have calculated the ^{87}Sr/^{86}Sr ratio of seawater over the past 100 Ma. Their results are plotted in Figure 5.18.

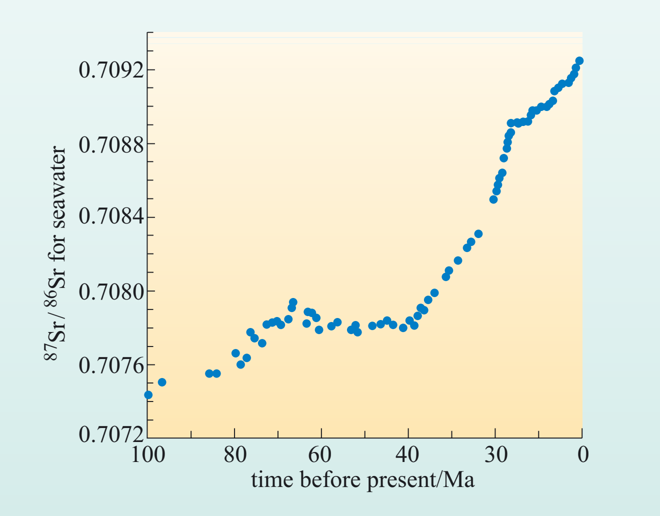


Figure 5.18 The variation in ^{87}Sr/^{86}Sr ratio for seawater over the past 100 Ma. (Richter, 1992)

■ What has been the overall trend in the ^{87}Sr/^{86}Sr ratio of the ocean since the Himalayan collision ~50 Ma ago?

□ There has been a marked increase.

This means that either the rate of supply of hydrothermal fluids (with low ^{87}Sr/^{86}Sr ratios) has decreased or that the flux of Sr from rivers (with high ^{87}Sr/^{86}Sr ratios) has increased, or perhaps a combination of the two. Hydrothermal circulation is driven by the heating associated with sea-floor spreading and other volcanic activity at the seabed. As ocean-floor production has been occurring at roughly the same rate over the past 40 Ma, the trend in Figure 5.18 is unlikely to reflect a marked decrease in hydrothermal circulation. On the basis of the data plotted in Figure 5.18, therefore, it appears that the change in $^{87}Sr/^{86}Sr$ in seawater must relate to an increased flux of high $^{87}Sr/^{86}Sr$ from rivers into the ocean. This in turn could be interpreted as evidence for the rate of weathering of continental crust increasing since the Himalayan collision.

■ If this interpretation is correct, does it support the mountain-forcing model?

■ Yes, because the model predicts that weathering of silicates results in global cooling, and there has indeed been global cooling over the period in question (Figure 5.16).

However, the evidence presented so far linking the uplift of the Himalaya and the Tibetan Plateau with weathering rates via seawater chemistry is entirely circumstantial. More direct evidence can be gleaned from examining the Sr-isotope geochemistry of present-day rivers.

If the $^{87}Sr/^{86}Sr$ ratios of the world's largest rivers are plotted against the reciprocal of the concentration of Sr (i.e. 1/[Sr]), most data points are positively correlated, implying they are essentially mixtures of two contrasting endmember components (a low $^{87}Sr/^{86}Sr$ and a high $^{87}Sr/^{86}Sr$ component) (Figure 5.19). In this case, rocks dissolving into the rivers are either carbonates, which dissolve rapidly and contribute abundant Sr with low $^{87}Sr/^{86}Sr$, or silicates, which dissolve slowly and contribute low concentrations of Sr with high $^{87}Sr/^{86}Sr$. Of all the world's major rivers, there are two exceptions: the Ganges and the Brahmaputra.

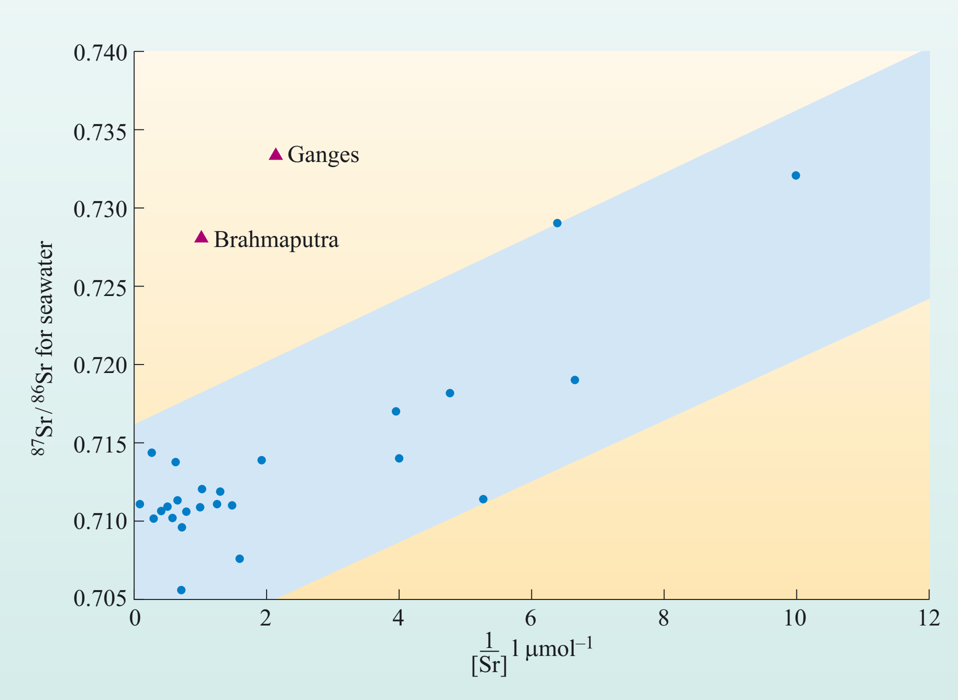


Figure 5.19 The $^{87}Sr/^{86}Sr$ of the world's major rivers plotted against 1/[Sr].

The Ganges and Brahmaputra rivers both flow from South Tibet, across the Himalaya, into the Bay of Bengal (Figure 5.15). Their waters are fed by the southwest monsoon, and their high Sr-isotope ratios, combined with high Sr concentrations, indicate that their addition to the oceans has a marked impact on the Sr-isotope seawater curve (Figure 5.18).

Although the interpretation of the Sr-isotope proxy is complicated by the presence of some unusual rock compositions in the Himalaya, detailed studies of Himalayan rivers suggest weathering rates that are at least triple those of the global average. This conclusion has been taken as evidence to support the hypothesis that uplift of the Himalaya and Tibet intensified the monsoon system and so caused a major increase in the chemical weathering flux of silicates, leading to increased rates of the removal of CO_2 from the atmosphere, thus providing key evidence for the mountain-forcing model.

It is important to emphasise that the Tibetan Plateau and the Himalaya appear to play quite different roles in the climate system. The strengthening of the monsoon seems to be the result of a *large high plateau* being uplifted, as it was this that affected the atmospheric circulation. In contrast, the link between changes in atmospheric CO_2 concentrations and weathering requires increased weathering rates, and it is over the *Himalaya* that these rates become particularly high and not on the Tibetan Plateau, which experiences little rainfall (much of which evaporates) and has relatively modest relief (Figures 5.6b and 5.14a).

So, which is right: the GEOCARB model or the mountain-forcing model? Well the answer is that they both are! The GEOCARB model for the carbon cycle is a **steady-state** model, which means that it assumes the system has attained equilibrium, e.g. it assumes the flux of CO_2 into the atmospheric CO_2 reservoir equals the flux out of it. If such a steady-state system is perturbed, then steady-state conditions will no longer apply (this perturbation is in effect a forcing function) and the system will adjust until the balance of fluxes is re-established. Uplift of the Himalaya and the Tibetan Plateau can be considered a transient event that disturbed the steady-state carbon cycle. It is believed that during this transient event, the chemical weathering rates rather than the rates of production of new ocean floor determined atmospheric CO_2 levels.

So the GEOCARB model provides a satisfactory mechanism for long-term climate change over hundreds of millions of years, while the mountain-forcing model is appropriate for the relatively short-term disturbance to global climate caused by uplift of Tibet and the Himalaya over a period of several million years. Although the two models have been presented as opposing each other, more recent revisions of the original GEOCARB model now include a feedback link between Tertiary mountain uplift and global cooling. In other words, the two models are converging despite operating on different timescales, thus providing a good example of how science advances through the testing of competing hypotheses.

Taking all the potential sources and sinks of CO_2 into account, current estimates suggest that the overall effect of the mountains and plateau of southern Asia is to cool global climate by about 3 °C. Although the role in the climate system of the uplift of the Himalaya and the Tibetan Plateau have been emphasised so as to provide a focus for this discussion, it is highly improbable that a single mechanism could be generally responsible for global climate change. This is not least because the atmosphere is a relatively small reservoir of CO_2 and its size depends on differences between large fluxes. Subtle changes in these fluxes may cause significant climate change. The best that can be said for any supposed cause of climate change is that any specific mechanism *could* result in an observed trend in the climate record; that is not to say that it was unaided, or even that it was the most significant player in such a complex game.

Summary of Chapter 5

1 Over geological timescales, the uplift of mountains as a result of continental collision can affect the operation of the global carbon cycle and hence the amount of CO_2 in the atmosphere, in various ways. Subduction of ocean-floor sediments and collision of continental masses result in decarbonation, in which silica and calcium carbonate react together to produce CO_2, which eventually escapes to the atmosphere. Mountains are also sites of vigorous erosion and weathering: physical erosion at high altitudes and chemical weathering lower down. Chemical weathering (followed by accumulation and burial of carbon in the ocean) results in a *loss* of CO_2 from the atmosphere. In addition, continental collision may result in large volumes of carbon in rocks being removed from contact with the atmosphere for many millions years.

2 Mountain ranges and plateaux affect the climate physically by redirecting air masses around and/or over them. Moisture-laden winds release their precipitation on the windward side, whereas the leeward side (in the case of the Himalaya, the Tibetan Plateau) is dry. The rise of the Himalaya and Tibet is believed to have intensified the strength of the southwest monsoon by providing a source of heat (including *latent* heat) at a critical position in the atmospheric circulation.

3 The rate of uplift of the Tibetan Plateau is not well established; attempts to measure it have made use of fossil plants. There is evidence that the southern plateau reached its present elevation by 15 Ma.

4 Attempts to determine climate change in southern Asia include studies of foraminiferans in the Indian Ocean, studies of $\delta^{13}C$ (to throw light on plant growth) and analysis of the types of sediment eroded from the Himalaya. These provide evidence to suggest strengthening of the monsoon between 9 and 6 Ma.

5 The Earth's climate has cooled markedly over the past 50 Ma. The mountain-forcing model postulates that uplift of the Himalaya and Tibet imposed cooling on the global climate, by strengthening the southwest monsoon and increasing rates of chemical weathering: increased weathering of silicates followed by accumulation and burial of carbonates and/or organic carbon in the ocean is assumed to result in the long-term removal of CO_2 from the atmosphere. To prevent 'runaway cooling', the rapid removal of CO_2 by weathering would need to be partially compensated. Possible mechanisms for replenishing atmospheric CO_2 include decarbonation at subduction zones, and the oxidation of organic carbon from exhumed sediments.

6 The steady-state, carbon cycle model (i.e. the original GEOCARB model) interpreted the role of mountains as providing a negative feedback loop that stabilised fluctuations in temperature resulting from variations in volcanism associated with the production of new sea floor.

7 The isotope ratio $^{87}Sr/^{86}Sr$ of the world's oceans has increased over the past 50 Ma. This has been interpreted as indicating increased weathering rates due to the uplift of Tibet and more especially the Himalaya. This interpretation is supported by the Sr fluxes and isotope ratios of rivers currently eroding the Himalaya.

Learning outcomes for Chapter 5

You should now be able to demonstrate a knowledge and understanding of:

5.1 How the global carbon cycle is affected by plate tectonic processes and in particular continental collision and the uplift of mountains.

5.2 The influence mountain ranges have on the physical characteristics of the climate, altering past and present atmospheric circulation patterns, and in turn how this has influenced the location and intensity of precipitation.

5.3 The various lines of evidence that can be used to determine climate change, including studies of foraminifera relating to nutrient levels and periods of upwelling in the oceans, changes in $\delta^{13}C$ values associated with rates of plant growth, and the types of sediments being eroded, indicative of physical and/or chemical weathering and changing temperature.

5.4 How the mountain-forcing and GEOCARB models can be used to model changes in the Earth's climate over different timescales, and how their apparently conflicting predictions can be deployed to test different feedback mechanisms.

5.5 The isotopic, palaeontological and geological evidence used to demonstrate how and why the Earth's climate has cooled over the past 50 Ma, and the different positive and negative feedback roles that subduction, ocean-floor formation and mountain building have played.

Chapter 6

Life in the Phanerozoic

Reconstructing the pre-Phanerozoic history of life, as discussed in previous chapters, depends upon rather patchily distributed, often problematical, fossils and on somewhat speculative interpretations of other biological, geological and geochemical data. In contrast, the more complete Phanerozoic marine fossil record allows quantitative estimates of the turnover in groups of organisms to be made. Thus, it is possible to identify the timing and scale of **evolutionary radiations** (phases of significant increase in numbers of species within groups of organisms), as well as **mass extinctions**, when abnormally large numbers of species became extinct together. Such information helps to narrow the search for cause and effect in the evolution of life.

The story starts close to the Precambrian–Cambrian boundary. This was arguably the most important interval in the evolution of life on Earth, when complex life emerged. The story of this transition is not, however, completely straightforward. The prokaryote world did not suddenly disappear and the new world order of modern animals and plants did not suddenly appear. Rather, there was a gradual development of highly 'experimental' animals, i.e. the Ediacarans, which persisted for a brief interval of geological time (less than 80 Ma) in the late Precambrian, followed by the diversification of modern **bilaterian** life (i.e. animals with bilateral symmetry) at the beginning of the Phanerozoic, an event that occurred very rapidly and which has been called the **Cambrian Explosion**.

The start of Phanerozoic time (and, therefore, the end of the Precambrian) is set at 542 Ma. The boundary that defines this age – the **Global Stratotype Section and Point (GSSP)** – has been officially placed in an obscure rock outcrop in southeastern Newfoundland. The placement of such an important boundary here, however, is not haphazard. The trace fossils of southeastern Newfoundland are the first record of the Cambrian Explosion.

■ What are used to define boundaries in the sedimentary record?

■ Normally fossils, i.e. the evidence of life. The Precambrian–Cambrian boundary, however, is unusual because the fossils used to define it are trace fossils rather than body fossils.

Recalling that Phanerozoic means 'visible life', to the 19th century geologists who formalised geological time, the situation was very clear-cut: there was a time without life – the Precambrian, and a time with visible life – the Phanerozoic. In fact, Charles Darwin was so worried about the lack of fossils in the Precambrian that he said that people would be entitled to reject his theory of evolution by means of natural selection on those grounds alone. As discussed in Chapter 2, however, during the Precambrian the Earth teemed with prokaryotic life and saw the rise of the cellular innovations that would, in time, give rise to the animals and plants. This process of complex animal evolution *started in the late Precambrian* with the evolution of the Ediacarans. The good news, of course, is that Charles Darwin, if he were alive today, could relax about the issue of the missing Precambrian fossils: they are no longer missing. All that was required to clear up that mystery was another century of investigation!

The transition from the Proterozoic to the Phanerozoic was a time of momentous change, both among organisms and in the conditions at the Earth's surface. To understand how these changes related to one another, it is first necessary to try to establish what took place, and when. Many of the time periods when these changes occurred have been established, largely during the past decade, through the use of high precision isotopic dating techniques.

Figure 6.1 shows the order and timing of events schematically expressed in the form of a 24-hour clock, with midnight being the formation of the Earth at 4.55 Ga and midnight 24 hours later being the present day (0 Ga). This approach is a useful way of understanding the immensity of geological time and the distribution of geological and biological events through that time. Crucial events in the history of life are marked on this diagram.

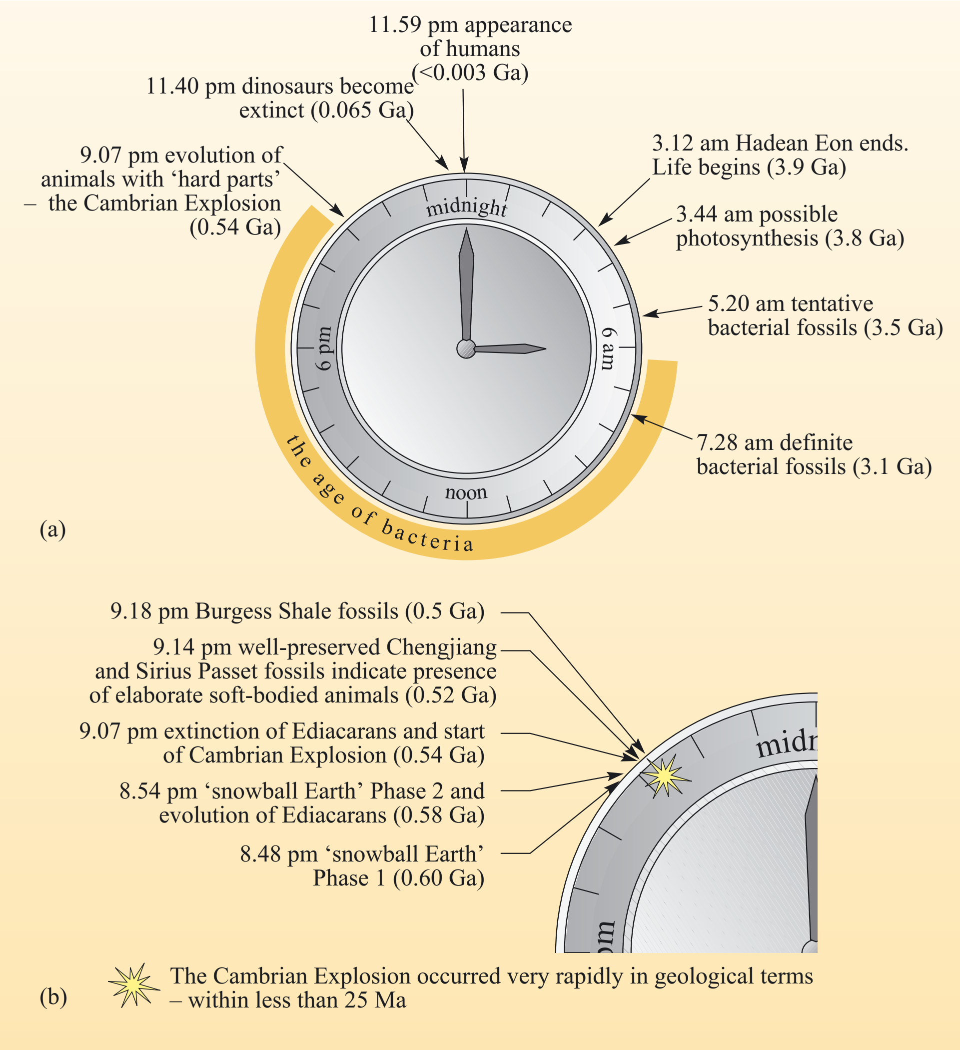


Figure 6.1 The history of life expressed as a 24-hour clock.

Nothing illustrates the importance of the Precambrian–Cambrian boundary more than appreciating how quickly the events associated with it happened when compared with the very long time that the world stayed in the 'age of bacteria' (where 'bacteria' is used loosely here to describe all prokaryotic and single-celled eukaryotic life). Life evolved at about 3.8 Ga (3.12 am on the clock) and persisted at the single-celled level of organisation until about 0.54 Ga (9.07 pm on the clock). At this time, the Ediacarans evolved and were followed by the rapid evolution of the animals of the Cambrian Explosion. Note, however, as discussed in Chapter 2, that the age of bacteria was not without its own crucial evolutionary innovations. Perhaps the most important of these was the evolution of the eukaryotic cell, with sub-cellular organelles such as mitochondria and chloroplasts evolving from more primitive prokaryotic cells.

Interpreting the geological record of the Precambrian–Cambrian transition has been hampered by two major problems. First, correlation of the sedimentary successions in different parts of the world (i.e. recognising beds of the same age from their fossil content or other age-diagnostic features) is extremely difficult; second, no one has yet discovered a complete and unbroken sedimentary succession through this interval.

The last 10 years has seen extraordinary advances in the synthesis of knowledge about this crucial time, and not all of this work has involved palaeontology or geology. Much information has come from genetics, particularly the process by which genetic sequences of different organisms are compared with each other to gauge their level of similarity. These comparisons are known as molecular phylogenies and provide an invaluable test of the findings of the fossil record.

An effect of this comparison process is that it is possible to estimate the times at which major groups of organisms diverged from each other, if one assumes a more-or-less constant rate of mutation (a conclusion that, to a first approximation, appears to be experimentally justified). This 'molecular clock' technique is another way in which the synergy of genetics, palaeontology and geology is revolutionising our understanding of the events around the Precambrian–Cambrian boundary.

One of the major events around the Precambrian–Cambrian boundary was the rapid evolutionary proliferation of animals with readily preservable skeletal hard parts or shells, which allowed better preservation in the fossil record. This innovation occurred while the Ediacarans dominated the oceans just before the Cambrian Explosion.

The oldest examples of these so-called small shelly fossils are some tiny calcareous tubes named *Cloudina* (Figure 6.2), which are common in certain limestones dating from the late Ediacaran (at 550 Ma). This raises a number of key questions, which will form the basis of discussions in Section 6.1, namely: what sparked this explosion? What became of the earlier Ediacaran organisms? What were the ecological and environmental consequences of this rapid evolution? What is striking about the dawn of the Phanerozoic, though, is the sheer diversity of skeletalised organisms that began to appear. Section 6.2 will explore the rich fossil record that followed the explosion to determine any patterns of relationship in time that can be detected between evolutionary radiations, mass extinctions and major environmental changes. This in turn will emphasise the key theme of the nature of the relationship between life and the Earth, as seen from the context of the Phanerozoic record.

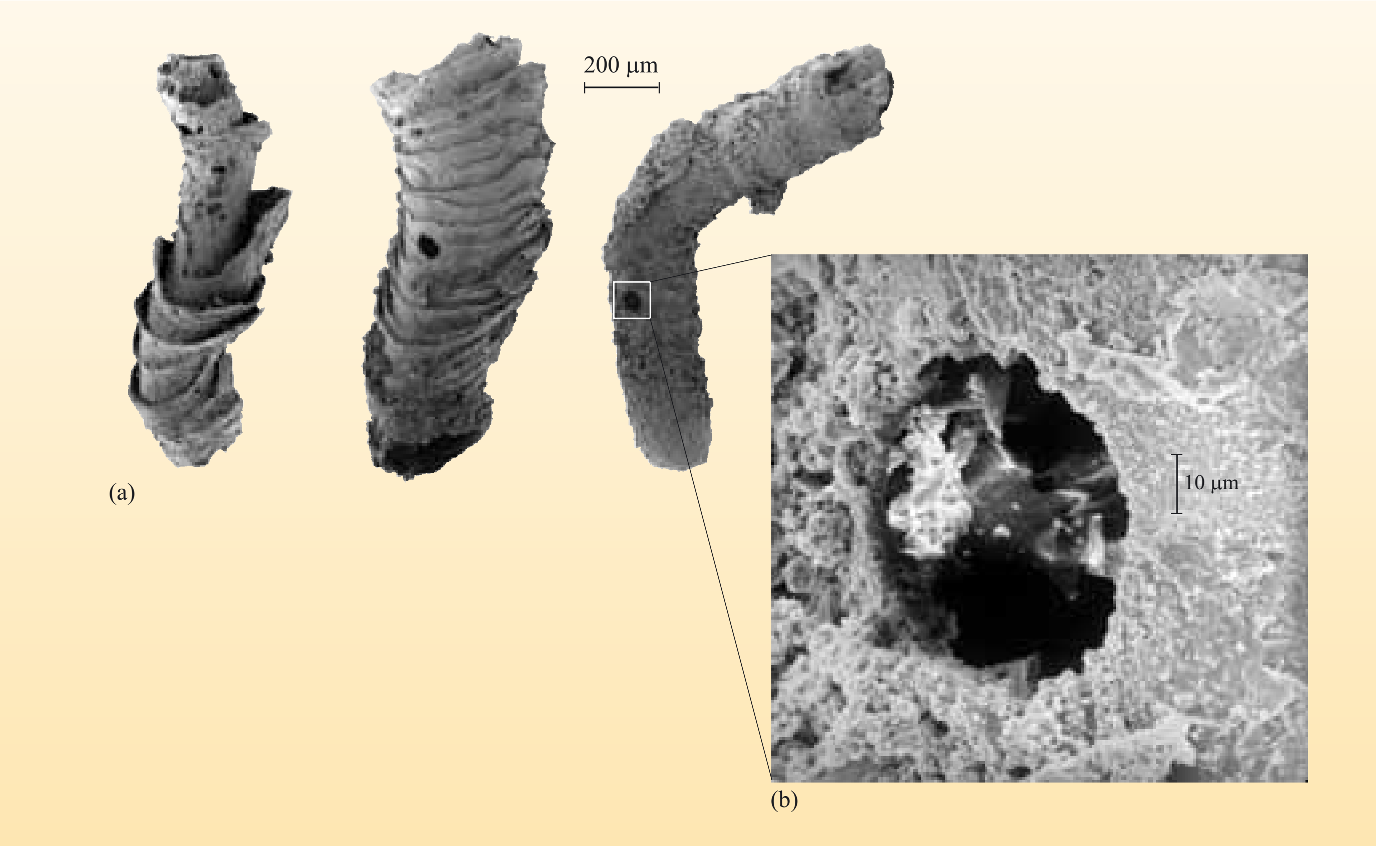


Figure 6.2 *Cloudina* from late Ediacaran age limestones of China. (a) Three isolated specimens. These have been replaced by calcium phosphate following burial and so could be extracted by dissolving the enclosing limestone in acid. (b) Detail showing a hole bored in the wall of one of the shells by a presumed predator. (Bengston and Yue, 1992)

6.1 The Proterozoic–Phanerozoic transition

6.1.1 The snowball (or slushball) Earth

One of the more remarkable ideas to emerge from the study of ancient climates in recent years has been the suggestion by Harvard geologists Paul Hoffman and Dan Schrag that the world was covered from the Equator to the Poles by a sheet of ice several kilometres thick in the late Proterozoic termed **snowball Earth**. They base this extraordinary conclusion on a combination of geochemistry (specifically the isotopes of carbon, as discussed in Box 5.1) and classical geology (understanding the climatological significance of different rock types and how their distribution in time can be used to decode ancient climates).

Evidence for these extreme ice ages has been found in rocks of late Early Proterozoic age from every continent. Evidence from fossil magnetism in the rocks shows that some of these glacial sediments were deposited at low latitudes; so, it is clear that these ice ages were global in extent.

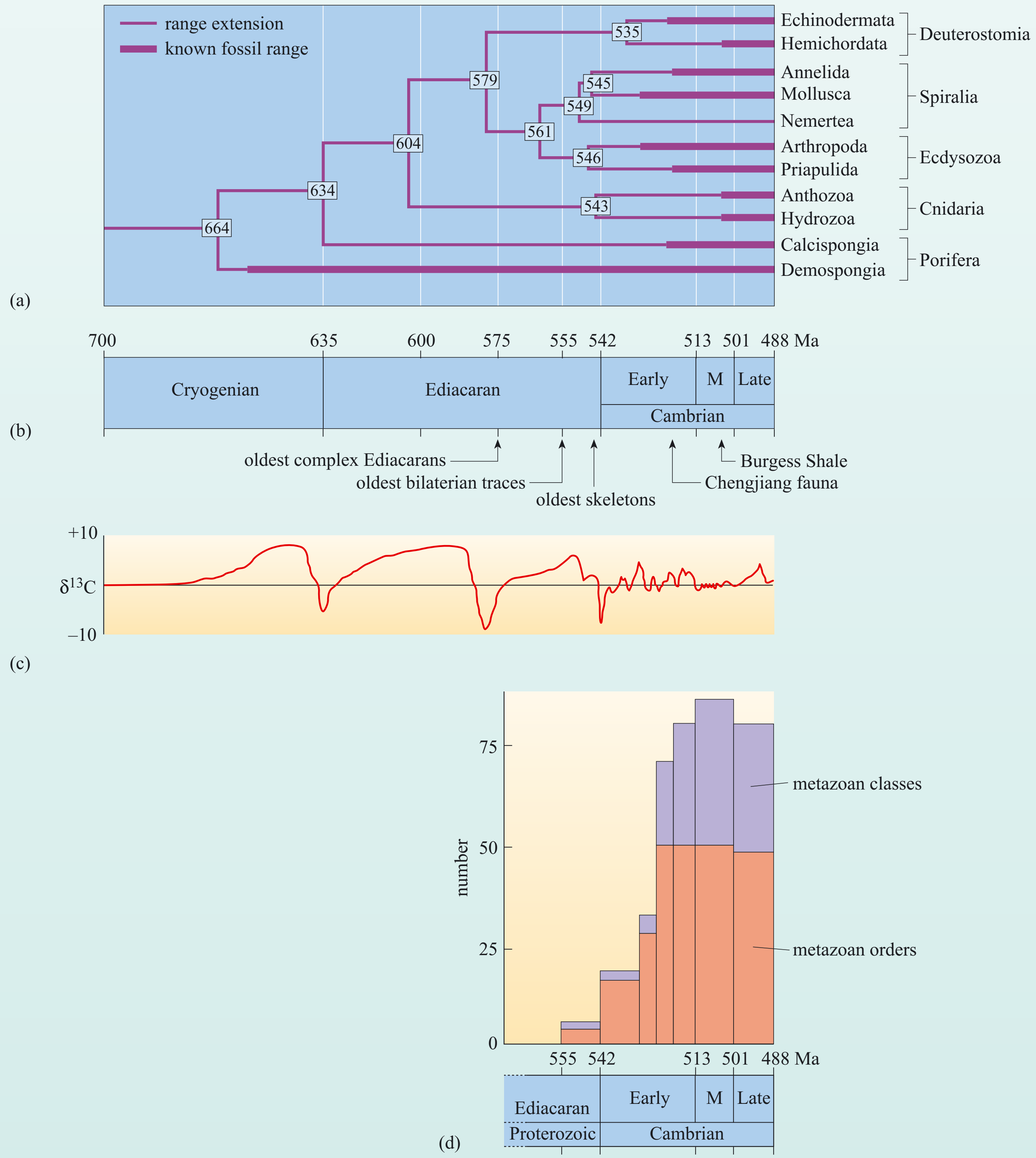


Figure 6.3 Early animal evolution placed in the geological context of the Early Proterozoic/Cambrian transition: (a) the best estimates of the times of divergence of the major groups of animals; (b) timing of major events in the early history of life; (c) the carbon isotope curve indicating times of inferred major glaciation (negative inflections); (d) numbers of metazoan classes (blue, top of bars) and metazoan orders (red, bottom of bars) over the Precambrian to Cambrian transition. Classes and orders are discussed in Box 6.1.

The fluctuations in carbon isotope values imply at least considerable climatic instability at this time. So prevalent were these extreme climatic conditions that the penultimate period of Precambrian time has been named the Cryogenian. Geological and geochemical evidence is unclear, but there may have been as few as two or as many as five Early Proterozoic ice ages; the important point to remember is that the last global glaciation (the Marinoan) occurred at about 635 Ma and marked the end of the Cryogenian. On the basis of glacial deposits in northern China, there is some speculation that there may have been a further glaciation at about 580 Ma (Figure 6.3), but it is generally agreed that this was not a global-scale event.

Not all geologists agree that the Earth was entirely covered in ice during the late Precambrian. Some suggest that the ice sheets extended further south than they did at the height of the late Quaternary glaciations, into the temperate zones, and as this idea is not as radical as the idea of a snowball Earth, it is known as the 'slushball Earth' compromise.

Regardless of the precise scale of the glaciations, there is no doubt that immediately following the Marinoan glaciation the pace of evolution accelerated, generating the Ediacaran organisms first, followed by the bilaterian animals of the Cambrian Explosion.

Question 6.1

Referring to Figure 6.3c, what does the negative excursion between the Ediacaran and the start of the Cambrian (~542 Ma) represent?

It is tempting to think that the rapid diversification of the Ediacarans and the bilaterian animals of the Cambrian Explosion were direct responses to the environmental changes at the time. However, it seems likely that, in addition to the environmental instability, there may have been an internal trigger related to changes in the genetics of these organisms. These questions are considered in more detail below, but first it is important to understand what the first tier of post-Marinoan organisms (i.e. the Ediacarans) actually were.

6.1.2 The Ediacarans

The Ediacarans are an extremely important part of the story for the emergence of the metazoans (animals), so much so that they are briefly discussed here again, along with the history of their discovery.

The Ediacarans take their name from the fossil locality in Australia (Ediacara) where they were first discovered in 1946 by Reginald Sprigg, an assistant geologist to the government of South Australia, who was examining old silver and lead mines in the Ediacaran Hills about 600 km north of Adelaide with a view to prospecting them for uranium.

Apart from his professional interest in uranium, Sprigg was also interested in the possibility that there might be fossils in these Precambrian sequences – an idea that at the time flew in the face of received palaeontological reason. As he approached the old mines he noticed numerous impressions of what he took to be jellyfish outcropping in the Pound Quartzite. He took the fossils home, wrote them up in a scientific paper and then spent years trying to convince the palaeontological community that they were indeed evidence of Precambrian life.

By the late 1950s, additional material had been found in the Flinders Range (also in Australia) and, crucially, from another locality on the other side of the world. In Charnwood Forest, Leicestershire, England, a schoolboy named Roger Mason came across a large fern-like impression embedded in the sandstone. Mason contacted a palaeontologist at the University of Leicester, Trevor Ford, who returned with him to the quarry. Over the next few months they discovered several other fossils, and the Ediacarans were firmly established as a real page in the book of life.

But what are the Ediacarans? The crucial pointer is something that Sprigg noticed instantly: they looked like jellyfish. Jellyfish are a member of a group of animals, namely the cnidarians and the ctenophores, that are united in their common possession of radial symmetry and only two layers of body tissue, which are separated by a layer of jelly. Such creatures are quite different from the rest of the animal world, the bilateria, which are characterised by having bilateral symmetry and three layers of body tissue. Thus, it seemed quite reasonable to the palaeontologist who performed the first in-depth study of the Ediacarans, Martin Glaessner, to consider them as an evolutionary step on the road to the more complex bilaterian animals of the Burgess Shale. This view was, however, rejected as some of the strangest Ediacarans that do not look like jellyfish appear to have no living relatives. For example, *Spriggina* (named after Sprigg) may be a primitive arthropod (although there is as yet no consensus) whereas *Dickinsonia* (Figure 2.12a) certainly has no living relative. This strange creature was probably entirely sessile, living on the seabed and perhaps deriving nutrition through symbiosis with photosynthetic algae. Unlike the majority of the Ediacarans, both *Spriggina* and *Dickinsonia* are bilaterally symmetrical.

Swayed by their apparent similarity to the cnidarians and ctenophores, Martin Glaessner tried to fit all members of the Ediacaran fauna into conventional Kingdoms or Orders. It was only in 1983 that Adolf Seilacher of the University of Tübingen, Germany came up with a different and radical notion. Seilacher noted that the animals of Ediacaran times do not fit into the same basic body plan categories as the animals around today (or indeed those for the Burgess Shale fauna). In his view, the Ediacara consisted of separate segments, similar superficially to a quilted airbed, a plan that is not used in oceanic organisms today. To him, these creatures seemed to show continuous gradations in form between animals that, if they were alive today, would be placed in separate phyla. For example *Spriggina* shares certain features with the Ediacaran sea-pen *Charniadiscus* found in Leicestershire. As such, Glaessner called the Ediacarans the ‘Vendobionta’.

This view of the Ediacarans as being morphologically unique has recently been acknowledged and amplified by Martin Brasier and Jonathan Antcliffe of Oxford University. They have suggested that many of the Ediacaran fossils are different life stages of the same creature and that the radical differences between them can be explained by a process called **heterochrony**, where the characteristics of part of the life cycle are retained into another part of the life cycle of the organism. This, of course, does not help with understanding what the Ediacarans were exactly. There are some who say that they were not multicellular animals at all; recent speculations have suggested that they may have been related to the group that gave rise to the fungi or were perhaps even lichens (a symbiont – an organism that is associated with another in a mutually beneficial relationship – consisting of fungi and algae) in the modern sense of the word. This may seem absurd, but in the **Universal Tree of Life** (Figure 6.4) you can see that animals, plants and fungi are very closely related.

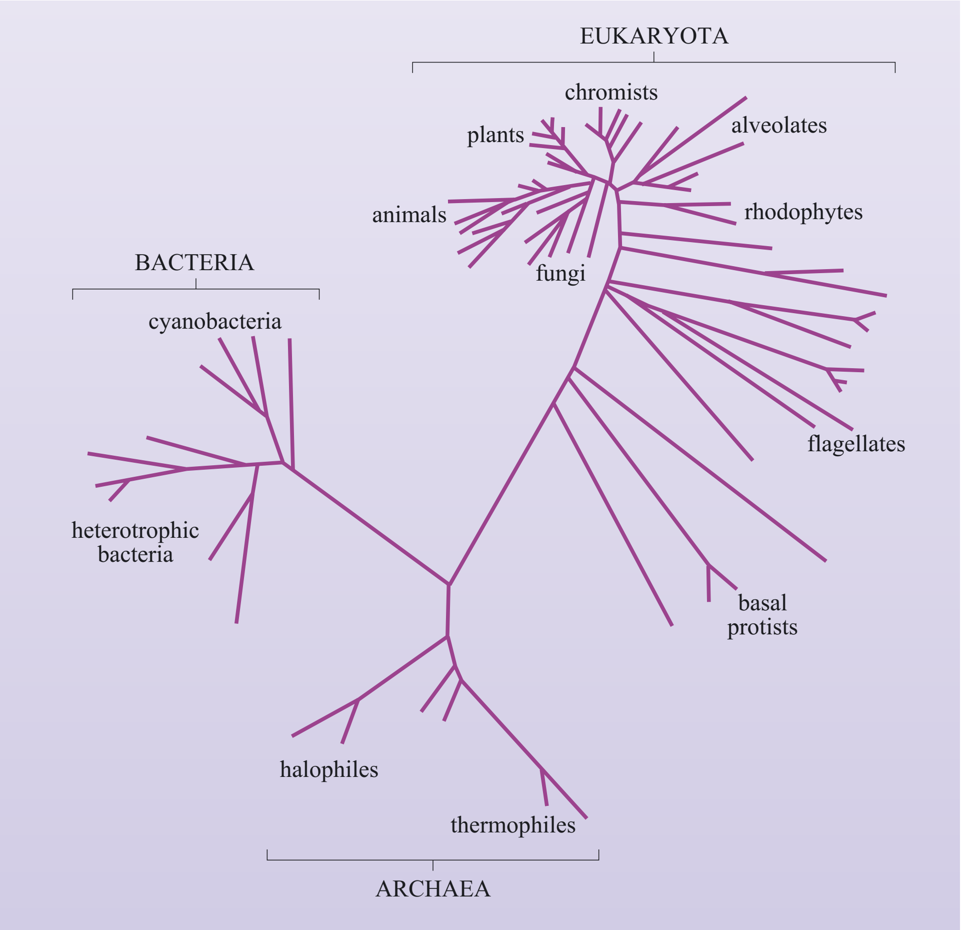


Figure 6.4 Universal Tree of Life showing the relationship between animals, plants and fungi in one branch and the great disparity between this branch and the Archaea and Bacteria branches. The longer the line, the greater the evolutionary distance.

Whatever the truth, the consensus is that the Ediacarans are a group of wholly extinct multicellular organisms that were constructed around a different type of tissue organisation from the rest of the known animal world. To many, these creatures, lacking both head and gut, are a failed experiment in the history of life.

Nothing illustrates the importance of the Ediacarans more than the fact that, in the last few years, the terminal period of the Proterozoic has been renamed after them. The Vendian (from which the Vendobionta took their name) has been renamed the Ediacaran and the end of the Ediacaran marks the end of the Proterozoic and the time when bilaterian animals exploded onto the world stage.

6.1.3 The Cambrian Explosion

At the same time as the Ediacarans were alive, the ancestors of modern bilaterian animals were diversifying with unprecedented rapidity; it is this that is called the Cambrian Explosion.

The Cambrian Explosion represents a time when a large range of different bilaterian body plans appeared in the fossil record in a relatively short period of time. So major were these body plans that they equate to different phyla – one of the highest taxonomic groupings. At this point, a distinction needs to be made between two aspects of the Cambrian Explosion that are often confused: the diversification of complex bilaterians known from a handful of exceptionally well-preserved faunas dotted around the world as opposed to the sudden proliferation of shelly fossils in the sedimentary record.

From the palaeontological perspective, there are only a few localities where the world of the earliest Cambrian fossils may be observed:

- the famous Burgess Shale fauna of British Columbia (of middle Cambrian age, dated to ~505 Ma)
- the Chengjiang (~520 Ma) and Sirius Passet (~530 Ma) faunas of China and Greenland respectively.

The reason why the **radiation** of bilaterians in the early Cambrian is considered an 'explosion' is because no examples of these bilaterian animals have been found at the time of the Ediacarans whilst by ~530 Ma (Sirius Passet fauna) there were abundant examples of animals that can be recognised as ancestral to those alive today. These animals, therefore, appear in the fossil record within a relatively short period of ~12 Ma duration – hence the term 'explosion' (Figure 6.1).

The exact timing of this event has been narrowed down by examining fossils from Siberia where, on the banks of the Kotuikan River, one of the most spectacular Cambrian outcrops in the world can be observed. At river level (where there are only a few unspectacular trace fossils), the rocks have been dated at about 545 Ma. A little higher in the section is a sandstone unit that has been dated as 544 Ma – a difference of only one million years. Starting immediately above this unit, small shelly fossils begin to increase in frequency up the rock section. It is the first evidence of the shelly part of the Cambrian Explosion. Further up the cliff, sediments dated at 530 Ma contain more than 80 recognisable **taxa** (singular taxon), including small shelly fossils, tracks, burrows and trails.

The origins of the Cambrian Explosion

The first 10 Ma or so of the Cambrian was a time when small shelly fossils developed in diversity and complexity. It seems likely that the ancestors of molluscs and an extinct mollusc-like taxon known as the halkierids evolved at this time (Figure 6.5 overleaf). After this 10 Ma period and close to the end of the early Cambrian, **crown groups** (a group of closely related organisms that includes the common ancestor plus all its descendants) of all the major phyla alive today (e.g. annelids, arthropods and brachiopods, and the chordates that ultimately gave rise to the vertebrates and humans), suddenly appeared on the scene.

Obviously, these fossils cannot have appeared fully formed out of nowhere, and advances in molecular phylogenetics and molecular clocks have shed crucial new light on the timing of their evolution. Until quite recently, the molecular evidence seemed to point to an origination time of the crown group bilateria of about 1000 Ma. It has since become clear that the vertebrate genes that were used to calibrate the molecular clock mutate much more slowly than invertebrate genes, giving much older divergence times than are implied by the fossil record. The latest studies indicate that the bilaterians arose between 630 and 600 million years, i.e. between 88 and 58 million years before the Precambrian–Cambrian boundary.

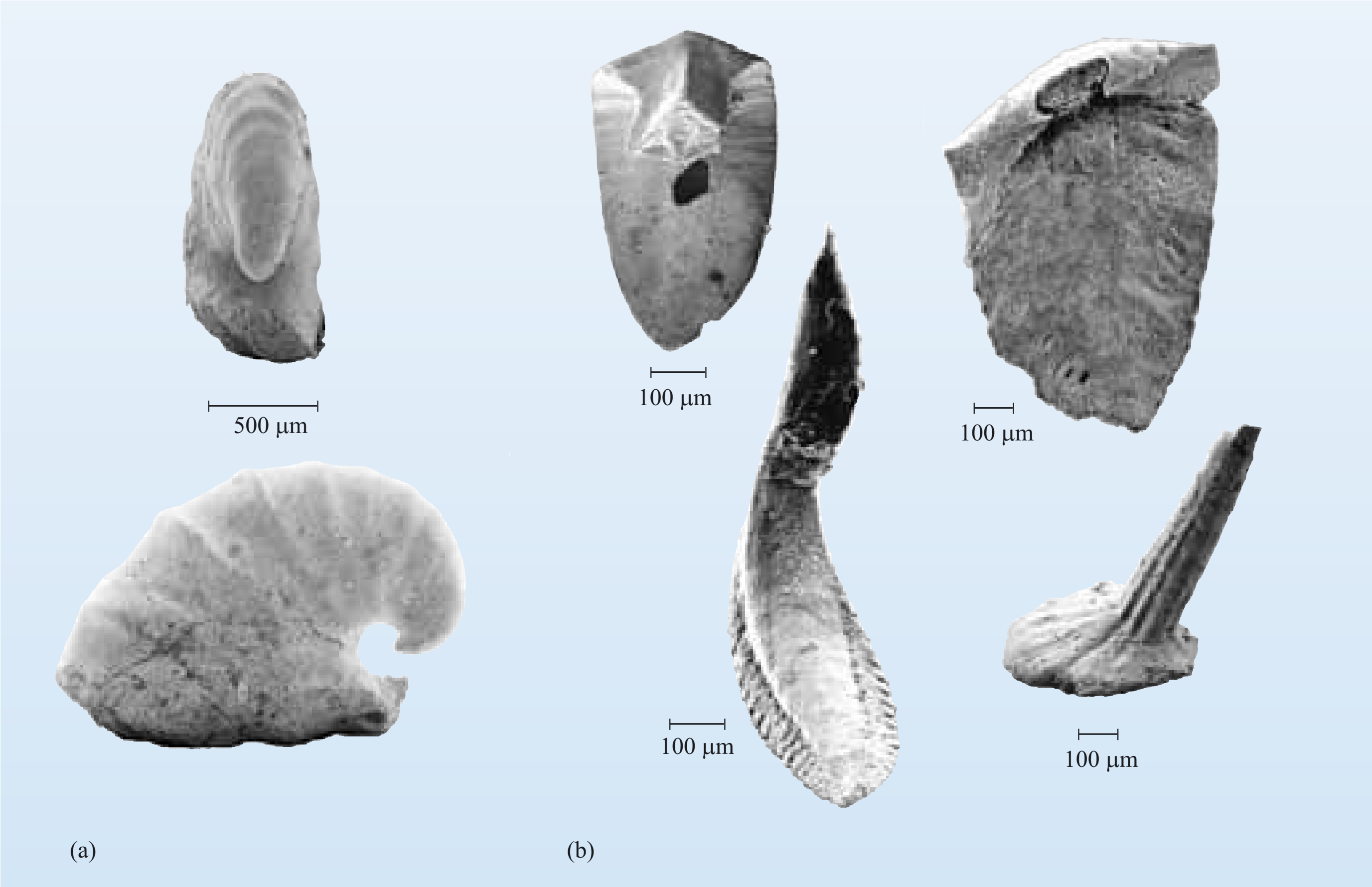


Figure 6.5 Examples of Lower Cambrian small shelly fossils: (a) a mollusc shell; (b) isolated sclerites, an extinct mollusc-like group; (c) chain-mail-like covering of sclerites on a complete organism (*Halkieria evangelista*). The fossil in (c) is about 3.5 cm long.

This clearly implies that the bilaterians were contemporary with the Ediacarans; but, as previously discussed, there is virtually no evidence for this from the fossil record. The reason for this lack of evidence is believed to be because all the late Proterozoic bilaterians were microscopic and, hence, were not preserved in the fossil record. Whether or not the bilaterian animals did originate in the Ediacaran (as seems overwhelmingly likely), it is clear that they evolved very rapidly in the early Cambrian, possibly due to an extinction event that decimated the Ediacarans.

The causes of the Cambrian Explosion

The causes of the Cambrian Explosion fit into two categories: internal (i.e. biological) and external (i.e. environmental) causes. Historically, much effort has been focused on relating the diversification of organisms in the early Cambrian to environmental change. This approach follows on from the work of Darwin, who believed that external influences drove the evolution of organisms.

One of the most exciting developments has been the insight that developmental processes within organisms can, and do, have much responsibility for these changes. One of the most important examples of this has been the recognition of **Hox genes** as an important part of animal development. Hox genes are responsible for *pattern formation*, i.e. the overall arrangement of appendages on the body of an organism. Comparison of the distribution of Hox genes in diploblastic animals (animals having a body made of two cellular layers) and their distribution in the bilateria shows that there are many more varieties of Hox gene in the latter group than in the former. The much higher number of Hox genes in the bilaterians was probably caused by a process known as **gene duplication**. These duplicated Hox genes were subsequently assigned to control the development of other body parts. Hence, it seems likely that Hox genes are implicated in the rapid diversification of the bilaterians in the early Cambrian. Hox genes may be thought of as the ‘coarse’ (as opposed to the ‘fine’) control lever of evolution, and sudden access to it during the early Cambrian drove the Cambrian Explosion.

Some scientists have suggested that the regulation of many new body patterns by Hox gene control allowed the evolution of **macrophagy**, i.e. the ability to ingest and digest food extracellularly by allowing the development of the gut. By allowing the bilaterians to eat and digest food particles that are larger than single cells, organisms were able to grow bigger. This might explain the sudden appearance of the small shelly fossils in the early Cambrian. It would also support the notion that the stem-group bilaterians were contemporary with the Ediacarans. Thus, the bilaterian increase in body size may be ascribed to the development of a novel method of feeding that developed due to the sudden evolutionary deployment of a powerful set of genes. The evolution of macrophagy in turn set up a whole new world of competition, as predators and prey suddenly indulged in the biggest evolutionary arms race of all time.

From the evidence of molecular phylogenetics, it seems likely that the Hox gene revolution occurred sometime between 650 Ma and 550 Ma, precisely coincident with the Ediacarans and the implied hidden beginnings of the Cambrian Explosion.

So far, this section has examined the internal triggers for the Cambrian Explosion. However, there is no denying that the late Proterozoic and the early Phanerozoic were times of enormous environmental change as well. The terminal Proterozoic snowball event (the Marinoan glaciation) finished at about 635 Ma, the same time as when the Hox gene revolution may have been occurring. A heavily glaciated Earth would have forced the early biota into **refugia** (i.e. geographically isolated populations) with limited gene flow between them that could have stimulated rapid evolution and the easy dissemination of novel gene plans like the Hox complex. In addition, it has been suggested that there may have been an increase in deep-ocean oxygen concentration at this time, which would have assisted organisms increasing in size in the rapidly evolving bilateria.

6.2 Radiations and extinctions

6.2.1 Estimating the turnover of life

The Cambrian Explosion is the first of the major evolutionary radiations that can be charted in some detail from the fossil record. Figure 6.6 shows the total numbers of marine animal families (most containing several species; see Box 6.1) based on fossil evidence and estimated to have coexisted at different times through the Phanerozoic. This was initially limited to the marine fossil record, simply because this was relatively more complete than that of land-dwelling organisms.

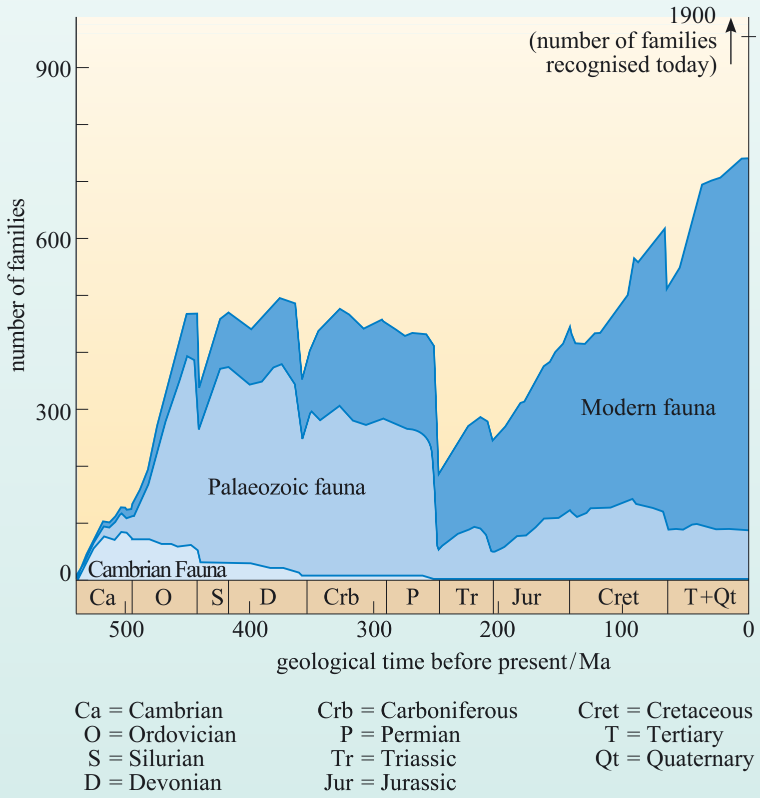


Figure 6.6 Changes in the numbers of families of marine animals through the Phanerozoic, based on fossil evidence. See Section 6.2.3 for explanation. (Sepkoski, 1990)

- What might explain the contrast in relative completeness between the marine and land-based fossil records?
- Most sediment ultimately ends up in the sea, so sedimentary deposition there is relatively more widespread, and less interrupted, than on land.

A later compilation of families (by Mike Benton of the University of Bristol, UK), covering all marine and land organisms, is shown in Figure 6.8a; Figure 6.8b and c show the respective land-dwelling and marine components of that compilation. For all three graphs, minimum and maximum estimates of family numbers are shown

Box 6.1 The hierarchy of classification

Organisms, both living and fossil, are classified into a nested series of increasingly inclusive groups, known as taxa, all the way up to the level of the kingdoms discussed in Box 2.2.

This system, known as the **taxonomic hierarchy**, is ideally intended to reflect evolutionary relationships. Where evolutionary relationships are unclear, a pragmatic scheme has to be adopted instead, which can be subject to later correction in the light of new findings. Taxonomic categories at different levels in the hierarchy are given standard names (e.g. family, species, order), each taxon being assigned its own Latinised name (e.g. Canidae, the dog family). The taxonomic categories employed for animals are shown in Figure 6.7, along with the classification in this system of the domestic cat and dog.

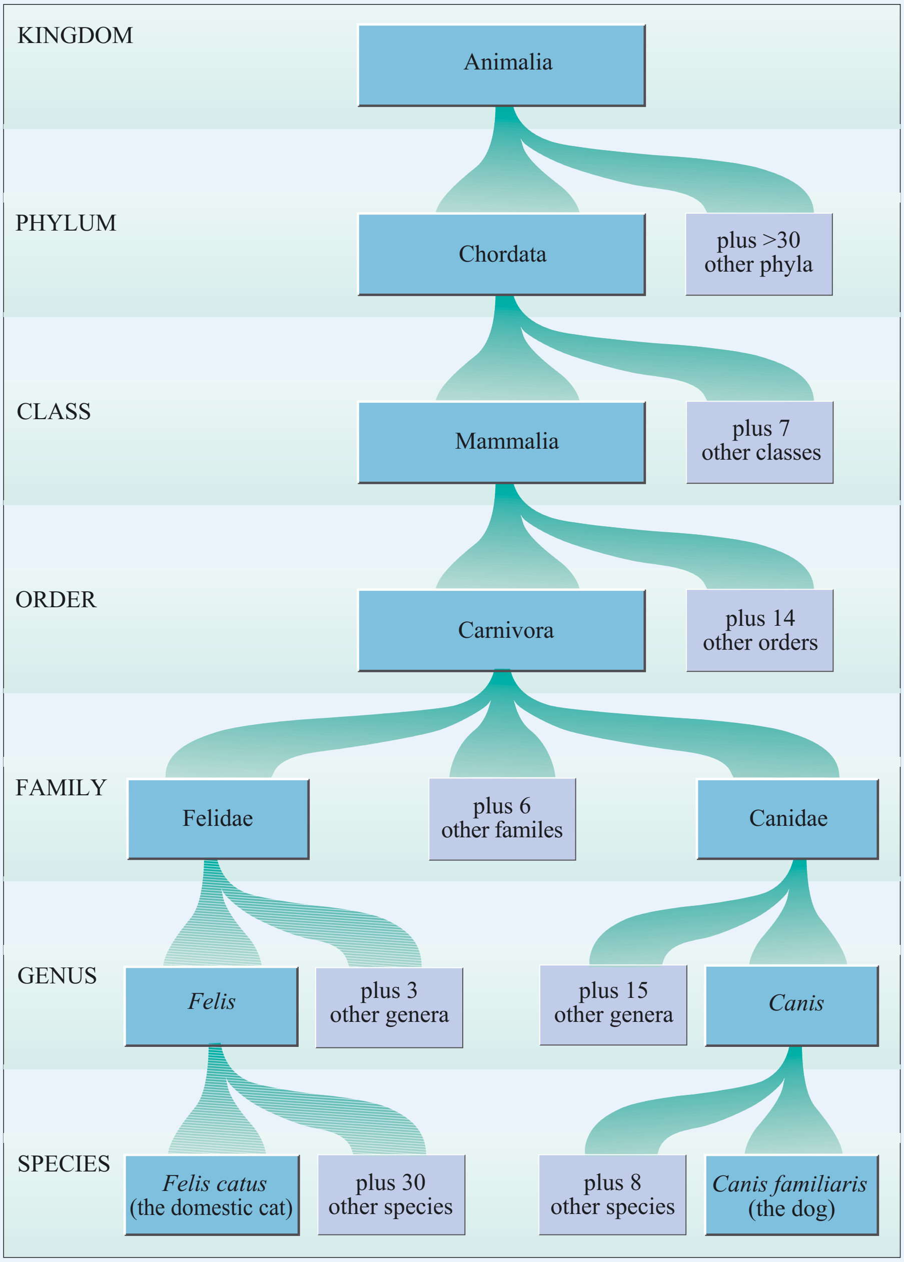


Figure 6.7 The taxonomic hierarchy showing the classification of the domestic cat and dog.

to allow for uncertainties in the number of extinct families and the representation of some fossils in both marine and continental deposits. Notice that Figure 6.8c differs in detail from Figure 6.6, reflecting a mass of slight differences in the family classifications used, and in the estimates of their stratigraphical ranges. These differences provide a useful reminder that such information is not a fixed set of facts, but the result of interpretation both in the classification of fossils and in the correlation of sedimentary sequences. The record is always subject to revision both in terms of new finds and through new analyses of pre-existing data. The similarity of the two marine compilations nevertheless suggests an underlying pattern can be identified and made available for interpretation.

You may wonder why the numbers of families have been plotted instead of the number of species. After all, families are artefacts of classification, whereas species are natural biological units. The reason is that this is the simplest way to cope with the incompleteness of our knowledge; fossils record a fraction of past species, and only some of these have been described and classified. By being more inclusive and using families, it is possible to have a relatively more complete record. A single specimen from one species in a family is sufficient to record the family's presence.

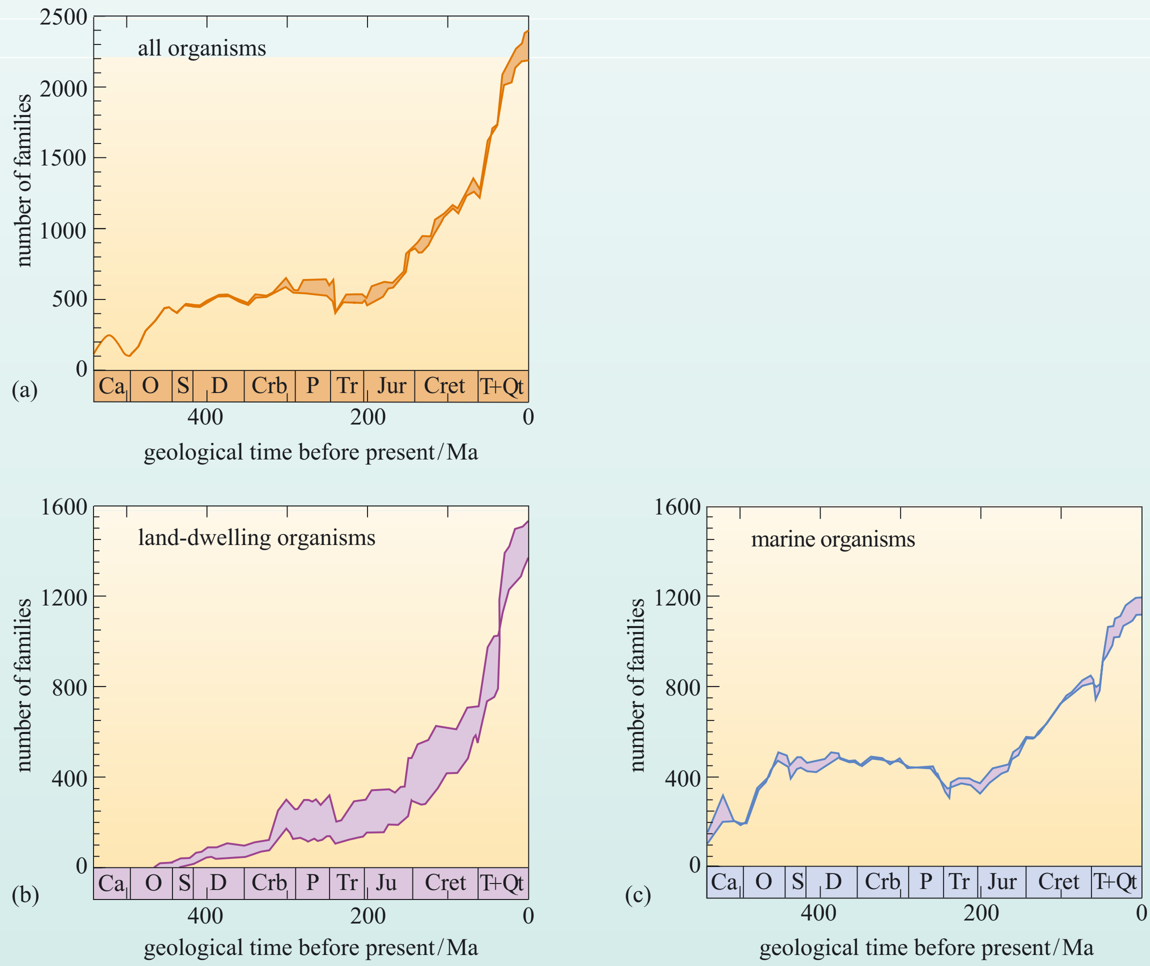


Figure 6.8 Changes in the numbers of families through the Phanerozoic: (a) all organisms; (b) land-dwelling organisms only; (c) marine organisms only. Maximum and minimum estimates are shown. (Benton, 1995)

(By analogy, a single telephone directory would provide you with a fairly comprehensive list of the households in a town, but a great deal more effort would be required to account for each individual.) Families are, therefore, a useful proxy for numbers of species. Of course there is a risk of biased representation because families are of very different sizes. The working assumption, however, is that such inequalities average out, or at least still allow broad patterns at the species level to be revealed, when large enough samples are considered. The skeletal hard-part fossil record represents only a fraction of life, but it at least provides a consistent basis for monitoring the relative variations in family numbers by allowing similar types from different times to be compared.

The steep rise in family numbers on Figure 6.6 throughout the early Cambrian represents the Cambrian Explosion. Throughout this episode, the evolution of new families (i.e. first appearances of species, recognisable by diagnostic characteristics) clearly exceeded the number of extinctions over this time. This illustrates the importance of the evolutionary innovations that occurred in the bilateria during the Ediacaran period and how they fuelled rapid diversification in the early Cambrian.

The pattern has been likened to what happens to numbers of individuals in a population when the birth rate exceeds the death rate.

Question 6.2

Briefly describe an example of the effects of the birth rate exceeding the death rate.

6.2.2 Mass extinctions

Diversity did not increase indefinitely however, and the data in Figure 6.6 suggest a temporary lull in the late Cambrian before diversification rapidly increased during the Ordovician. The reasons for the late Cambrian lull are still unclear. However, more striking is the sharp drop in family diversity (number of families) accompanying the close of the Ordovician, which marks the first of five large-scale mass extinctions during the Phanerozoic as shown by the fossil record.

■ Referring to Figure 6.6, what was the approximate percentage decrease in total numbers of families recorded from fossil hard parts at the end of the Ordovician?

□ The total family numbers fell from around 470 to about 340. Hence, the percentage decrease in family diversity was:

$$\frac{470-340}{470} \times 100 = 28\% \text{ to 2 sig. figs}$$

Two points need to be raised about this result: first, it only represents the net decline in family numbers; given the appearance of new families over the same interval, the percentage *extinction* of pre-existing families would have been somewhat higher. Second, the values of percentage extinction at lower taxonomic levels (i.e. of genera and species), if calculated, would have been higher still. For example, consider a family that lost all but one of its species: it is still counted as having survived, although at the species level there may have been a considerable loss, which must be added to the number of species extinctions in families with no survivors. By sampling well-documented groups at lower taxonomic levels it is possible to estimate these losses, and it has been estimated that ~85% of all species may have become extinct at the end of the Ordovician.

Question 6.3

Referring to Figure 6.6, state the times of the other four great mass extinctions that occurred within the Phanerozoic Era.

Greatly increased rates of extinction over limited periods of time are implicated in all of these mass extinctions, as well as in a number of other smaller scale examples. A temporary suppression in the rate of speciation, and hence origination of new families, is also evident in some cases. By far the most severe mass extinction was that at the end of the Permian, when more than half (57%) of marine animal families became extinct, while the estimated toll at the species level was a staggering 96%. The possible causes of this disaster will be examined later in this chapter, from the context of global change that was occurring at that time.

A postulated link between the mass extinction (including extinction of the dinosaurs) at the close of the Cretaceous and a major asteroid impact (recognisable in the sedimentary record by a sharp peak in abundance of iridium), has generated much debate and popular interest in the casual link between mass extinctions and planetary events. In 1984, Jack Sepkoski and David Raup undertook a detailed analysis of the distribution in time of all detectable mass extinctions. They concluded, for the Mesozoic examples at least, that they all appeared to show a periodicity of approximately 26 Ma, and suggested that this could reflect a regular cycle of extraterrestrial bombardment. A vigorous debate ensued, with opponents criticising aspects of the database and of the analyses, particularly with respect to the recognition of a periodic signal.

There is no dispute that there have been asteroid and cometary impacts (some of considerable size and effect) on Earth as several forms of evidence exist, such as preserved impact craters, deposits of beads known as tectites, **shocked quartz** and other distinctive minerals formed under very high pressures, and tell-tale geochemical signatures (e.g. sharp increases in iridium) in sedimentary sequences. What is open to question, however, is the extent to which impacts have been responsible for mass extinctions and, in particular, whether mass extinctions really show a periodicity that might reflect astronomical 'forcing'. At present, the jury remains out on the latter question, with critics arguing that the observed pattern does not deviate significantly from what can be produced by random coincidence in a model involving numerous unrelated kinds of environmental perturbation (including occasional impacts).

Evidence linking some of the other mass extinctions of the Phanerozoic to impacts is subject to debate, though such evidence has been reported at a couple of modest Tertiary mass extinctions overall. The apparent durations of the various mass extinctions, and their relative effects on different groups of organisms, are by no means consistent from one example to another. Hence, it is likely that a variety of causes may be needed to explain them, and the geological record offers several compelling Earth-bound alternative models (Box 6.2).

One point that is nevertheless clear, is that all five major mass extinctions were brought about by environmental crises of one sort or another. There is no evidence that the rapid diversification of any groups of organisms directly provoked any of these past mass extinctions. Each mass extinction seems to have come as a shock, cutting sharply across any pre-existing pattern of change in diversity, with each one resetting the agenda for subsequent evolution.

Box 6.2 The 'big five' Phanerozoic mass extinctions

In detail, many of the mass extinctions show a more complex pattern than revealed in Figure 6.6.

The main episodes of mass extinction in the Phanerozoic fossil record, together with their main 'casualties' and likely causes, were as follows:

1 Late Ordovician

Two main peaks of extinction towards the end of the period were separated by hundreds of thousands of years. Both plankton (e.g. graptolites) and bottom-dwelling life (e.g. trilobites and reef-building organisms) were affected. Associated events were the growth and decay of a vast ice sheet on the southern supercontinent of Gondwana as it moved over the South Pole, drastically changing the sea level, climate and ocean chemistry. However, the patchy geological record has yet to reveal any record of a clear causal event.

2 Late Devonian

This pattern of extinction is as yet unresolved, but possibly consists of a series of extinctions extending over at least 3 Ma, with the most severe effects ~5 Ma before the end of the period. Shallow marine ecosystems were most affected, with tropical reef-dwellers particularly hard hit. Declines in temperature seem to be associated with widespread anoxia in shallow seas. Although there is no direct evidence for glaciation at this time, sea levels fluctuated and fell overall. A positive shift in $\delta^{13}C$ values in the C_{carb} record would be consistent with burial of organic carbon associated with increased photosynthesis, removing CO_2 from the atmosphere and sequestering it in sea-floor sediments. Alternatively, there is some evidence for meteor impacts provided by glassy fragments found in Belgium, as well as impact swarms in Chad and North America.

3 Late Permian

Increased extinction rates occurred over ~3–8 Ma at the end of the period, although recent findings suggest that these fell largely in two distinct episodes. Marine organisms were particularly devastated (Figure 6.6). At this time the continents had amalgamated into the supercontinent Pangaea and the Earth was emerging from the Carboniferous ice house (Chapter 7). Consequently a complex, probably synergistic, array of causal factors, including biological feedbacks, has been postulated for this extinction.

■ Can you recall from Chapter 4 what other major event coincides with the Late-Permian extinction?

■ The eruption of the Siberian flood basalt province (Table 4.3).

In addition to environmental stresses with largely unknown causes, the eruption of over 2 million km^3 of basalt could have had a significant impact on the global climate, causing periods of cooling, through the emission of SO_2, periods of warming, through the emission of CO_2, and the resultant acidification of the environment. In a global system that was already under environmental stress, the eruption of such a large volume of basalt over a relatively short period of time could have provided the *coup de grâce* of this mother of all mass extinctions.

4 Late Triassic

There were at least two, maybe three, extinction peaks during the last 18 Ma or so of this period. In the sea, both free-swimming animals (especially ammonoids and marine reptiles) and bottom-dwelling forms (including many reef-building organisms) declined. On land, many reptilian groups, including mammal-like forms, were lost, along with large amphibians and many insect families, although there was no marked global extinction of land plants. The marine extinctions, at least, coincided with marked changes in sediment type, strongly suggestive of major climatic change and, in particular, more extensive rainfall. Nevertheless, a huge impact crater in Quebec, about 65 km across, dates from around the Triassic–Jurassic boundary. The late Triassic also coincides with the eruption of the Central Atlantic Magmatic Province (Table 4.3).

5 Late Cretaceous

Two patterns of extinction appear to be superimposed: a gradual decline followed by a rapid collapse. Several groups of marine animals, both free swimming (e.g. belemnites and some marine reptiles) and bottom dwelling (e.g. certain kinds of bivalves) appear to have declined over the last 9 million years of their period. At the end of the Cretaceous an abrupt collapse occurred, especially amongst the plankton. This collapse happened over ~100 000 years or less, and is marked by fluctuations in the carbon isotope record of marine limestones. Ammonites combined both patterns of extinction with a slow decline terminated by the rapid extinction of a sizeable number of the remaining species at the end of the Cretaceous.

On land, the most famous extinction is that of the dinosaurs – though the pattern of their decline is still debated. They were joined in their demise by the pterosaurs (flying reptiles), while flowering plants also suffered major losses at the end of this period, especially at mid-latitudes in North America (as shown by carbon isotopic data from organic residues indicating mass mortality) and at high latitudes in Asia. In the Southern Hemisphere changes in speciation were gradual or non-existent.

A number of other groups were little affected by extinction, including the crocodiles, snakes and placental mammals. Although the final collapse is widely interpreted as impact related (with evidence mounting for the impact crater being buried in the subsurface of the Yucatan Peninsula, Mexico), it affected ecosystems that were already perturbed by other environmental causes, as shown by the gradual background decline. This can be related to substantial changes shown by the continental configuration, global climate change and oceanic circulation patterns at the time. Once again, however, the K–T boundary is marked by the eruption of a major flood basalt province, in this case the Deccan lavas of India.

6.2.3 Evolutionary radiations

Look at Figure 6.6, and in particular the periods immediately following each of the 'big five' mass extinctions.

Question 6.4

What happened to diversity in the immediate aftermath of each of these extinctions? On the basis of what you have read so far in this chapter, suggest a reason for the pattern shown.

This represents the immediate consequences of the mass extinctions, but what longer-term trends can be recognised?

- ■ What happened to overall levels of diversity over the longer term?
- ■ Overall, diversity rose – though not in a continuous fashion. After the Ordovician, an approximate plateau of diversity was established, remaining until the late Permian mass extinctions. Thereafter, diversity started to rise once again and continues to do so at this present time.

After the Ordovician, (and throughout the rest of the Palaeozoic) the recovery of diversity following the mass extinctions appears to have tapered off to similar levels each time, equivalent to between 400 and 500 families. There has been much debate about whether the Palaeozoic plateau of diversity levels reflects some kind of evolutionary equilibrium, with the post-Palaeozoic trend signifying growth to a new, higher, equilibrium level. The implicit assumption of this idea is that increased diversity leads to increased rates of extinction and decreased rates of origination, as a consequence of increased competition between species.

Question 6.5

Describe how the relationship between diversity, rates of extinction and origination could yield an equilibrium in diversity.

It remains open to question as to whether the rate of extinction caught up with that of origination (other than during mass extinctions) to yield the postulated equilibrium levels. An alternative interpretation is that the Palaeozoic plateau of diversity may be the net effect of several major and minor mass extinctions (the latter being below the level of resolution of Figure 6.6), superimposed upon a background level of sustained diversification. This is the current preferred explanation to describe the patterns of change in Figure 6.8. Possible controls on the rates of origination and extinction of taxa, and hence on global diversity, are still, however, vigorously debated.

Whatever the long-term influence of the extinctions on the numbers of families over time, the outcome left an impact on the composition of marine life. This effect is evident in the blue bands in Figure 6.6. These represent sets of major groups (mainly classes) of marine animals, with each set showing a characteristic pattern of family turnover. These sets are referred to as **evolutionary faunas**; their separate diversity histories, along with some of the representatives of the major groups, are illustrated in Figure 6.9. The first set, referred to as the Cambrian fauna, diversified more rapidly during the initial radiations of the Cambrian than the others. However, it soon experienced a decline in numbers of families as the next Palaeozoic fauna began to diversify. The Palaeozoic fauna continued diversifying until the late Ordovician, after which it began a slow decline in numbers, whilst the modern fauna diversified rapidly, eventually dominating the scene in post-Palaeozoic times.

Note that the names of these evolutionary faunas refer only to their times of dominance: all three existed throughout the Phanerozoic (although very few members of the Cambrian evolutionary fauna survived beyond the Palaeozoic). Moreover, the three faunas do not represent discrete sets of animal groups, as in some cases different classes from a single phylum have been allocated to all three faunas, e.g. the molluscs, which consist of bivalves (clams) and gastropods (snails) in the modern fauna and cephalopods (including the ammonoids) in the Palaeozoic fauna.

These broad patterns of change can be explained in terms of a complex version of the equilibrium diversity model outlined above, where each successive fauna (for whatever unknown reasons) had its own characteristic diversity-dependent rates of origination and of extinction of families, and thus its own intrinsic equilibrium diversity level. The details of how this model could explain the histories of the three faunas shown here, and the arguments for and against it, are beyond the scope of this book. Nevertheless, the response of these evolutionary faunas to mass extinctions is worth considering.

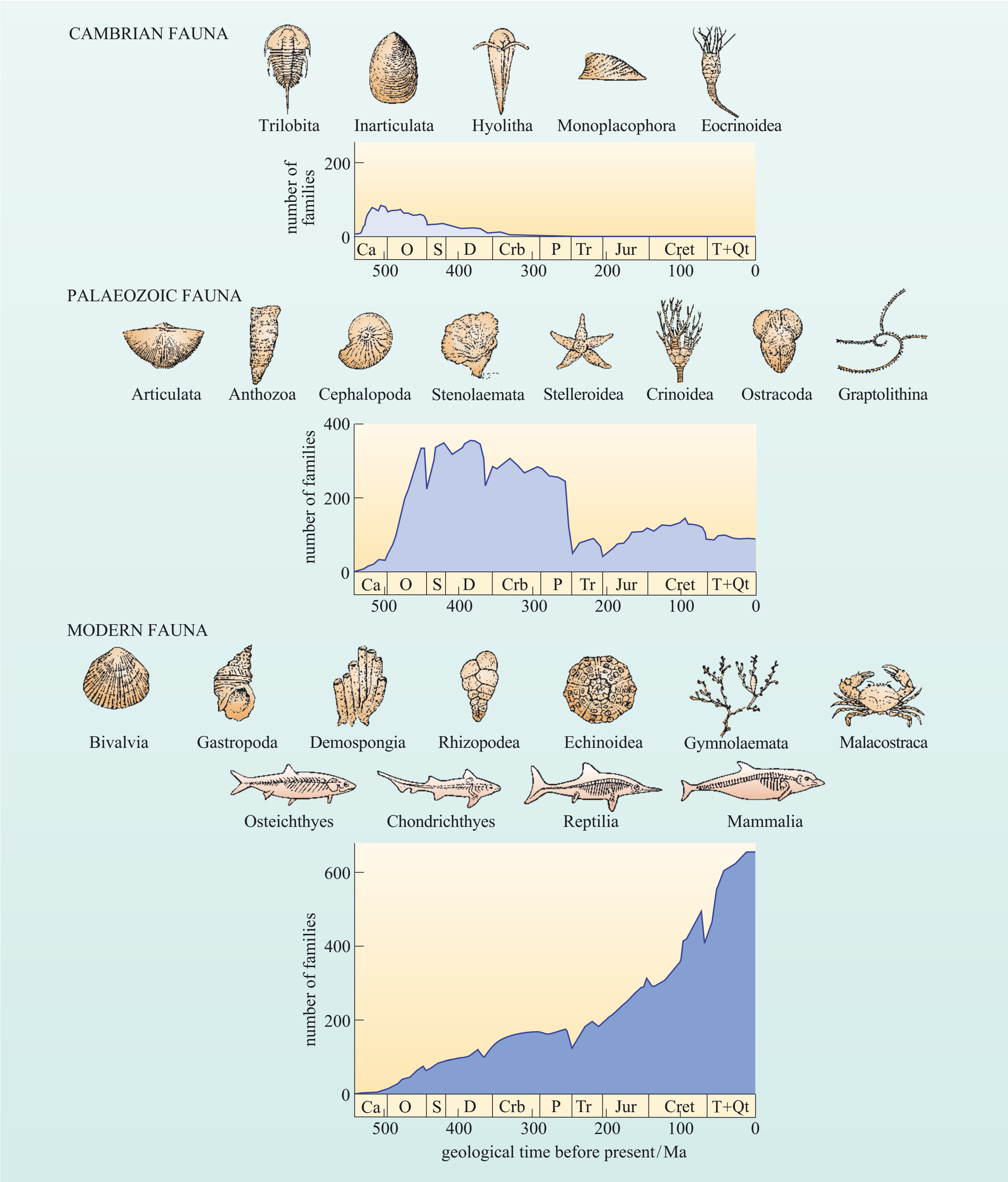


Figure 6.9 Examples of representatives and diversity histories of the three evolutionary faunas of skeletalised marine animals indicated in Figure 6.6.

Question 6.6

Did mass extinction affect all three evolutionary faunas equally? Explain your answer with a reasoned argument.

The ensuing radiations built on the characteristics of the survivors. The complexion of animal groups coexisting at any given time has, therefore, been influenced as much by the devastations of extinction as by the achievements of adaptive evolution. But what were the ecological consequences of these major faunal changes?

6.2.4 Ecological relationships and their consequences

Perhaps the most remarkable of the faunal changes occurred after the late Permian mass extinction and involved predation. Although predation was common in the Cambrian, with some predators even ingesting entire small shelly prey, throughout the Palaeozoic there was an abundance of exposed shelly animals that lived rooted to the sea floor (Figure 6.9) with evidence for predation (e.g. in the form of diagnostic damage preserved in the fossil shells, Figure 6.2) rare. Throughout the Mesozoic, however, the fossil record shows several lines of evidence for a marked increase in the intensity of predation on shelly prey. These include an increase in the frequency of predator damage, the appearance of many new kinds of predators with specialised adaptations for tackling shelly prey, and the emergence of new defensive adaptations by shelly organisms (prey) (Figure 6.10).

Among the newly evolving predators in early Mesozoic seas were crabs and lobsters, along with several groups of fish and marine reptiles, variously equipped to crush, smash or pierce shells. New kinds of starfish evolved the ability to pull open bivalves, insert their stomachs into the opened shell and digest the occupant. In the Cretaceous, these adapted predators were joined by gastropods capable of drilling through shells to reach their prey, while in the Tertiary various shell-breaking birds and mammals evolved.

Although the major groups of shelly prey animals developed a wide variety of protective adaptations, the one notable evolutionary trend was a boom in burrowing, especially by bivalves and echinoids (sea-urchins) to increasing depths in the sediment to gain refuge from predators. The extent of **bioturbation** of the surface sediment was therefore both intensified and deepened. This effect, coupled with an increase in the amount of disturbance at the surface by grazers, detritus feeders, and the number of predators excavating the sediment, made the larval settlement of shelly animals permanently anchored to the surface more hazardous. As a result, these animals, so successful in the Palaeozoic, waned in relative diversity.

These linked ecological changes can be collectively referred to as the Mesozoic marine revolution, transforming the character of marine life to that which can still be recognised today. It could also be said that this revolution helped to provoke the unprecedented rise in marine animal diversity observed in the fossil record from the end of the Palaeozoic onwards. The most profound feedback to biogeochemical cycles, however, came from associated changes in plankton. Starting in the late Triassic, groups of microscopic plankton with calcareous skeletons began to appear, including both single-celled algae (e.g. coccolithophores) and protists (e.g. planktonic foraminifera). One potential

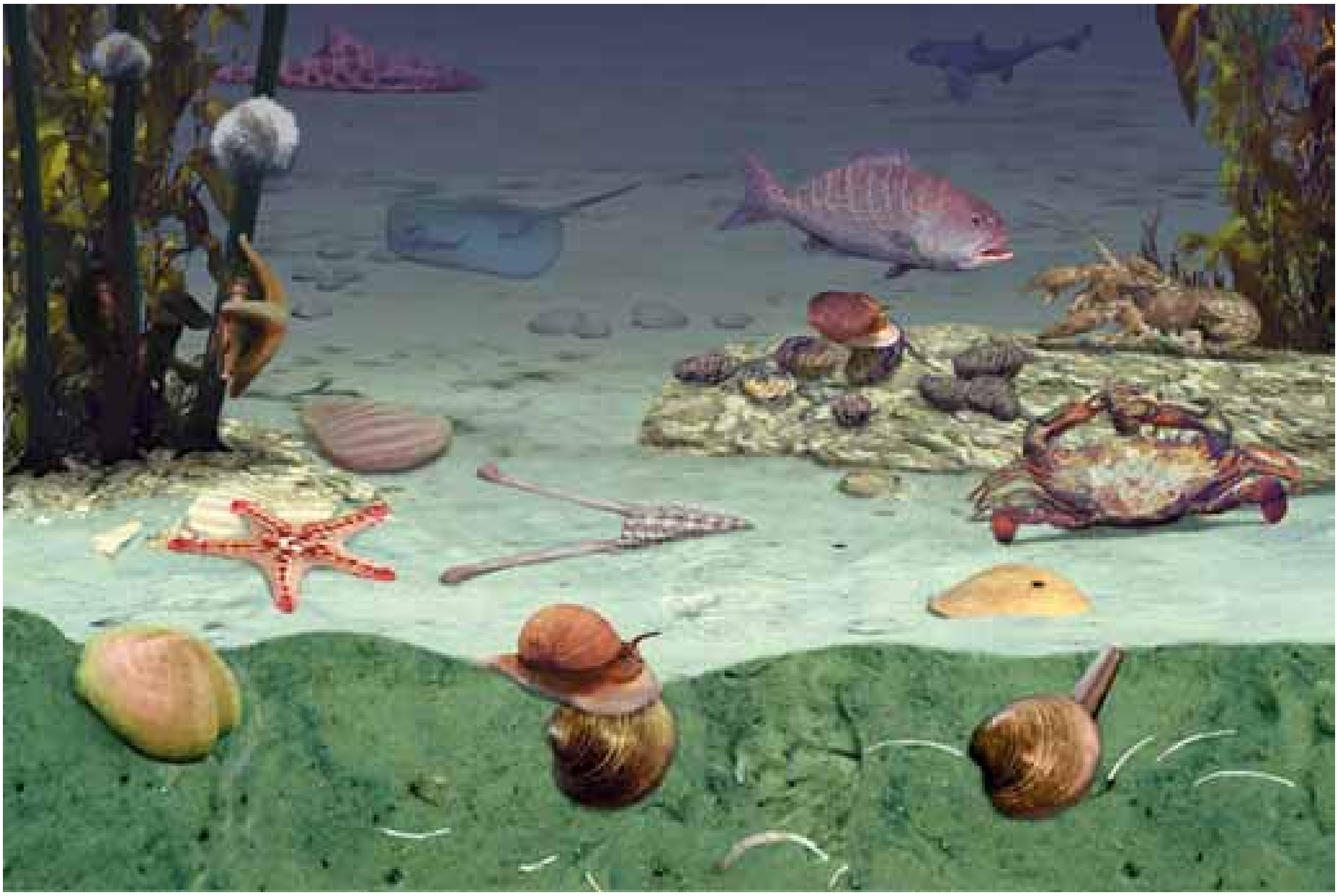


Figure 6.10 Reconstruction of the predators and prey of a shallow Cretaceous sea floor in southern England. In the section of burrowed sediment in the foreground, a burrowing clam (bivalve) is being attacked by a shell-drilling snail (gastropod), while a sea-urchin (echinoid) has burrowed into the sediment for protection. In the middle distance, a starfish tackles a mussel attached to some kelp, while a regular echinoid grazes on some small sessile colonial animals. To the right, mussels and oysters (both bivalves) are being attacked by another drilling gastropod, a crab and a lobster (both arthropods). Various shell-crushing fish hover in the background, and the jaw of one (a shark), with its pavement of flat teeth, lies on the surface in the centre foreground. In the foreground, the remains of some bivalve shells with tell-tale gastropod drill-holes can be seen.

interpretation of this simultaneous adoption of calcareous skeletons (or toughened organic walls in some other planktonic groups) by both groups is as a defensive adaptation against increased grazing pressure.

Question 6.7

What effect might the evolution of calcareous plankton have had on the distribution of carbonate sediments?

Going back again in time, however, some quite different evolutionary changes during the Palaeozoic had even more considerable environmental consequences – perhaps the most profound since the oxygenation of the atmosphere in the Proterozoic. These were the changes that allowed plants and (ultimately) animals to invade the land.

6.3 The greening of the land

6.3.1 Beginnings

So far, this chapter has investigated the emergence of metazoans in general terms. In this section, the focus will turn to a specific evolutionary change that occurred during the Palaeozoic that was of major importance for the distribution of life on Earth and its eventual effects on climate – namely the colonisation of the land by plants. It is generally accepted that the main colonisation of the land by green plants took place in the Silurian or late Ordovician. However, there is evidence that bacterial mats and possibly fungi were prolific enough on damp land surfaces to have formed primitive soils as early as the late Proterozoic. This is not hard to imagine because there is a present-day analogy: the sandy desert floors of the southwest of the USA are partially stabilised against erosion by crusts of cyanobacteria. Either way, though these early soil-forming microbial communities would have altered the colour of the local landscape and incorporated some organic matter into the land substrates, they would have had a minimal to negligible effect on global climate, unlike the changes that took place during the Silurian and Devonian, as will shortly be discussed.

The first convincing evidence that plants had begun to adapt to a dry-land environment comes in the form of microscopic fragments of tube-like structures, cuticle and **spores** (Box 6.3).

Box 6.3 What is a spore?

'Spore' is a generic term; a commonly known example is pollen. Reproduction in some plants is achieved by the formation of spores instead of the production of separate male and female gametes directly (Figure 6.11).

A spore consists of a living cell surrounded by a tough water- and chemical-resistant outer coat. The cell is haploid and develops into a haploid individual which, in turn, produces gametes by mitosis. Fusion of two gametes yields a new diploid individual that goes on to produce a new generation of spores by meiosis.

The spore coat protects the haploid generation during dispersal and, because the coat is so tough, the spore has a high probability of being preserved in the fossil record. Many sedimentary rocks contain thousands of fossilised spores in each cubic centimetre, and the diversity of spore contents of rocks allows stratigraphic correlations to be made.

Pollen grains are specialised male spores in which the development of the haploid generation is highly abbreviated: the sperm cells are released directly and then fuse with egg cells to produce seeds. In this way, seed plants have effectively curtailed the haploid generation in favour of the development of diploid individuals.

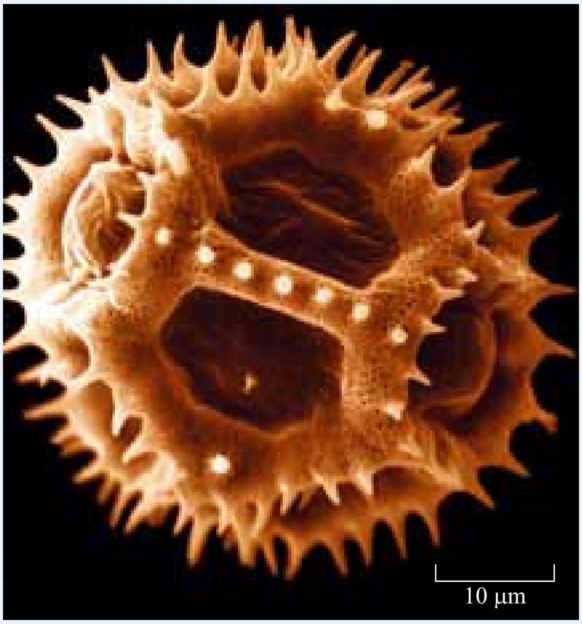


Figure 6.11 Scanning electron micrograph of a specialised male spore, or pollen grain, of chicory (*Cichorum intybus*). The complex ornamentation (i.e. the spikes on the surface) aids in dispersal by insects and can be used for spore identification.

6.3.2 Interpreting the structure of early land plants

The move from an aquatic to a terrestrial environment was accompanied by fundamental changes in plant architecture. Initially, land plants were low-growing, sheet-like structures that existed almost entirely within a relatively still and humid layer of air next to the ground: the **boundary layer**. In other words, if a wind is blowing (or air currents are in motion) and the free air (i.e. air that is well above the ground surface and unimpeded by, for example, trees and buildings) is moving relative to the ground at a certain speed, then close to the ground the air will be moving much more slowly because of the effect of friction (viscous drag) caused by the ground surface. The wind speed will, therefore, decrease progressively towards the ground surface; immediately above the ground there will be a relatively still layer, i.e. the boundary layer (Figure 6.12).

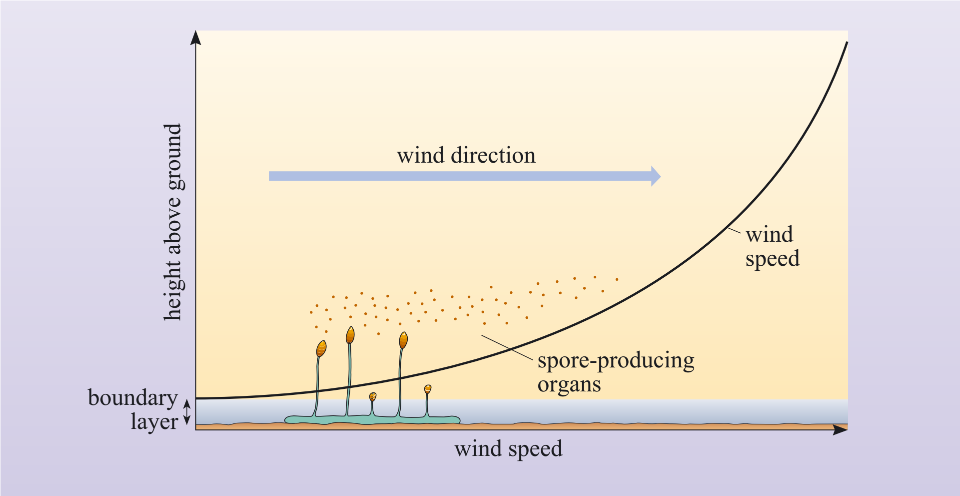


Figure 6.12 Variation in wind speed with height above a surface over which air is flowing. Superimposed on this plot is a diagram showing the height and characteristics of a typical early low-growing land plant, such as *Sporogenites*, which has only its spore-producing organs projecting above the boundary layer.

The thickness of the boundary layer will depend on the speed at which the free air is moving and on the roughness of the surface. Typically, the thickness of the boundary layer over a sand or gravel surface will be of the order of a few centimetres. If the ground surface is moist, then the boundary layer can become saturated with water vapour. This in turn means that it will have a higher relative humidity than the free air above it (unless, of course, all the air is water saturated).

A plant growing within the moist boundary layer would tend not to dry out because of this high humidity. Moreover, it would not need to expend energy and resources developing internal methods of storing moisture, enhancing its mechanical strength to cope with changing water contents and hence internal strength, or making cuticles to prevent loss of H_2O through evaporation. Yet, the lack of flowing air or water around the plant body in the boundary layer would be disadvantageous for dispersing progeny. By contrast, any plant capable of growing up into the moving air above the boundary layer would not have this problem of spore dispersal (Figure 6.12) and so taller early land plants would have had an advantage in the race to colonise the land surface.

Accordingly, in early land plants the ground-hugging body of the plant remained in the boundary layer, while stalks with special pouches containing the spores grew upwards (Figure 6.13). These spore-producing organs exploited the moving air

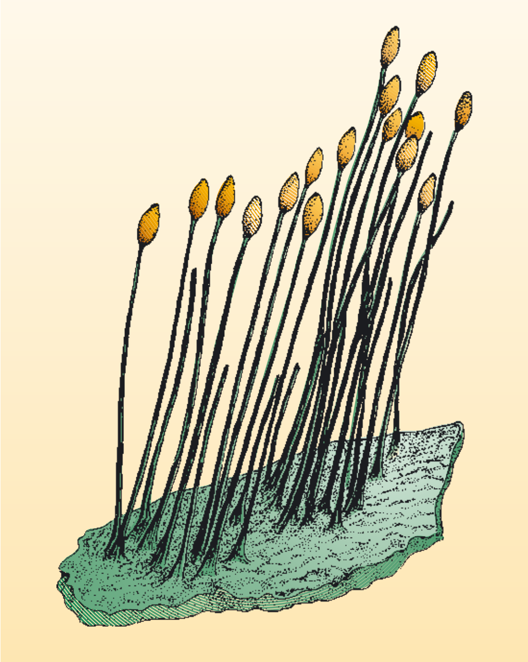


Figure 6.13 *Sporogenites exuberans*, an early Devonian plant (about 2 cm tall), reconstructed from fossil specimens. The pouches that contained the spores are clearly visible at the tops of the stalks. (Stewart and Rothwell, 1993)

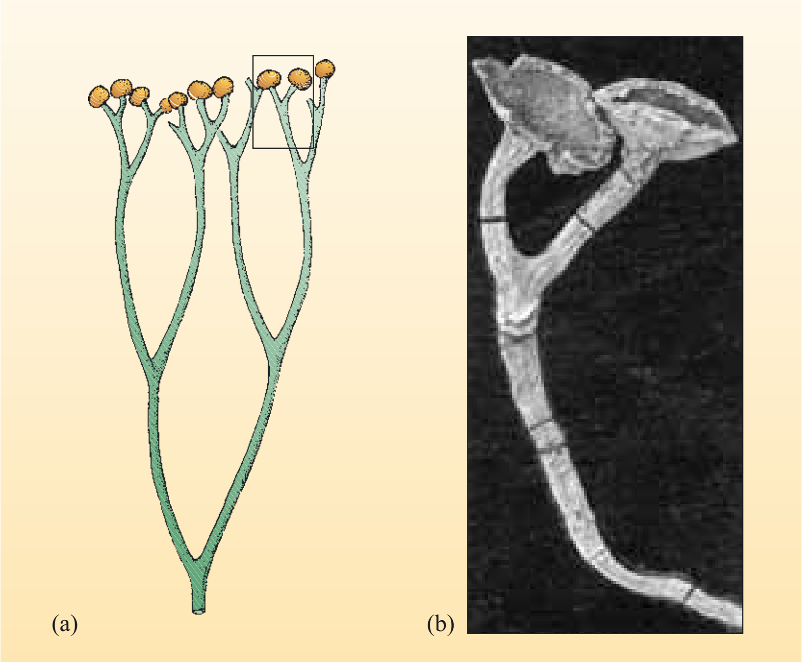


Figure 6.14 (a) Reproductive units (about 7 cm long) of *Cooksonia caledonica*, a late Silurian plant, reconstructed from fossil specimens such as that shown in (b). The specimen in part (b) is 4 mm in length. No specimen of the rest of the plant has been found. ((a) Stewart and Rothwell, 1993)

currents above the boundary layer to carry the spores away on the wind to colonise new territories, and if the spores were small enough, they could travel great distances quickly.

Reproductive units are preferentially preserved in the rock record because the presence of a waxy cuticle enhances their preservation potential. As such, many land-plant fossils consist of isolated reproductive units only, whereas the rest of the plant remains unknown (Figure 6.14).

- How might the increasing vertical height of early plants have affected the thickness of the boundary layer?
- The presence of taller plants would have, in effect, increased the roughness of the ground surface and hence the thickness of the boundary layer.

This positive feedback loop would have promoted vertical growth because a higher boundary layer would have extended favourable moist growing conditions upwards, permitting greater plant growth and requiring greater projection of spore-producing organs above the boundary layer. With vertical growth would have come an increase in the cost of construction, because greater structural strength would have been required. In addition, a mechanism by which to move fluids up (water) and organic molecules in solution down (sugars produced by photosynthesis) through the plant body would have been needed. This increase in construction cost would, in turn, have necessitated more food production – in other words, more photosynthesis. More photosynthesis would have required more gas exchange with the atmosphere, more plant mass and, therefore, a larger (and possibly higher) surface area to intercept light. The result of this positive feedback was the construction of branching and shading plants, and the need for more vertical growth.

To cope with the competition, many plants adapted to minimise their energy expenditure while still growing tall. All common early land plants and representatives of the groups of taller plants in the Silurian and Devonian shared a number of similarities (Figures 6.15 and 6.16); all had a prostrate stem, known as a **rhizome**, with small root-hair-like appendages (**rhizoids**) that anchored the rhizome to the substrate, and all also had vertical stems sprouting up from the rhizome at varying intervals (Figure 6.15a and b). As the horizontal rhizome branched out over the substrate, a single plant could occupy several square metres with numerous vertical stems, increasing the chances for successful reproduction. Thus, in an early Devonian landscape there would have been patches of vegetation composed entirely of extensive thickets no taller than a few tens of centimetres.

The vertical stems of early plants were often branched and, at or near the apex of the vertical stem, were the spore-producing **sporangia**. Stems on these early plants bore no leaves, but often had hooked or spine-like outgrowths (Figure 6.15c; Figure 6.16b and d). These outgrowths were quite small and poorly supplied with fluid transport tissue and as such, their role in increasing the plant's photosynthetic area was probably minimal unlike leaves on modern plants.

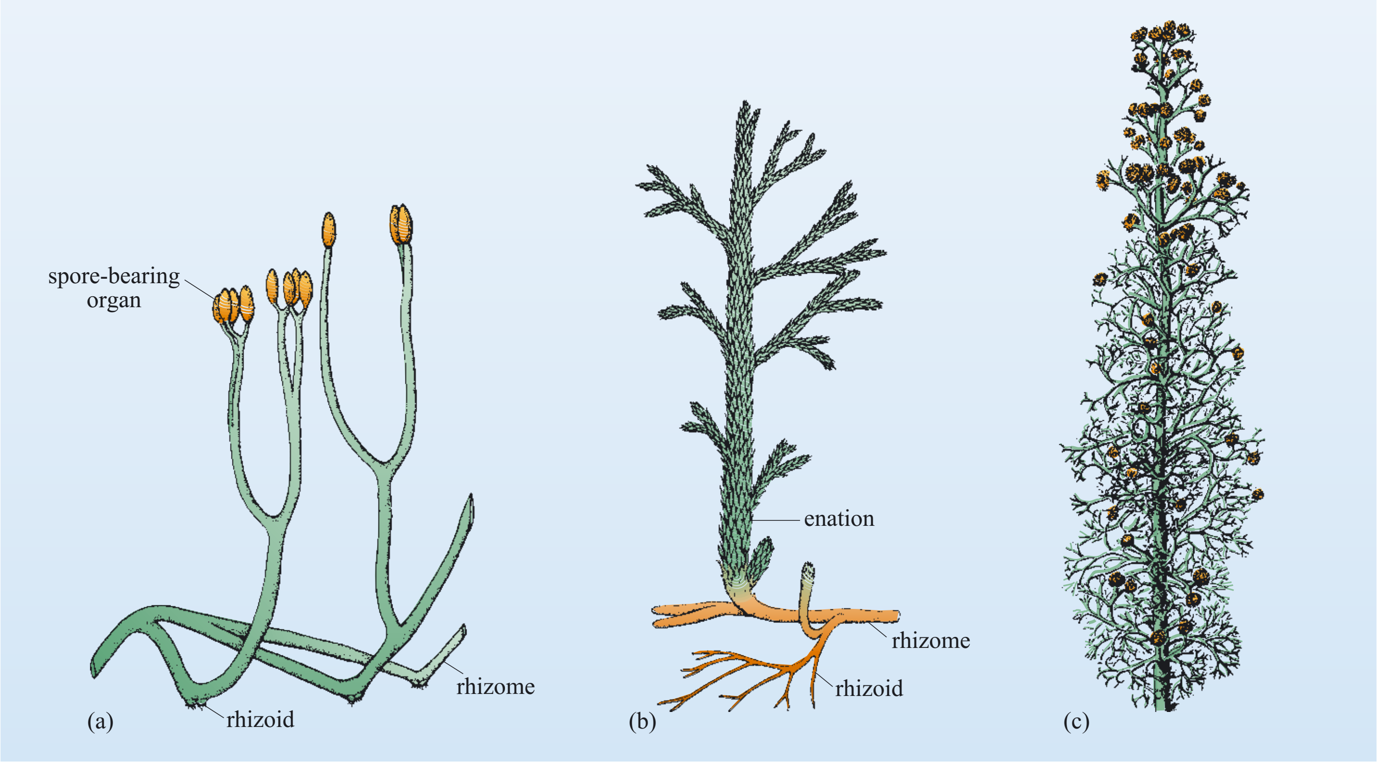


Figure 6.15 Reconstructions of some common early land plants, showing various structural features. (a) *Aglaeophyton major*, Early Devonian (about 50 cm tall). (b) *Asteroxylon mackiei*, late Early Devonian (about 30 cm tall); enation was a special kind of outgrowth from the stem that functioned as a small leaf. (c) *Pertica quadrifaria*, Early Devonian (about 1 m tall overall).

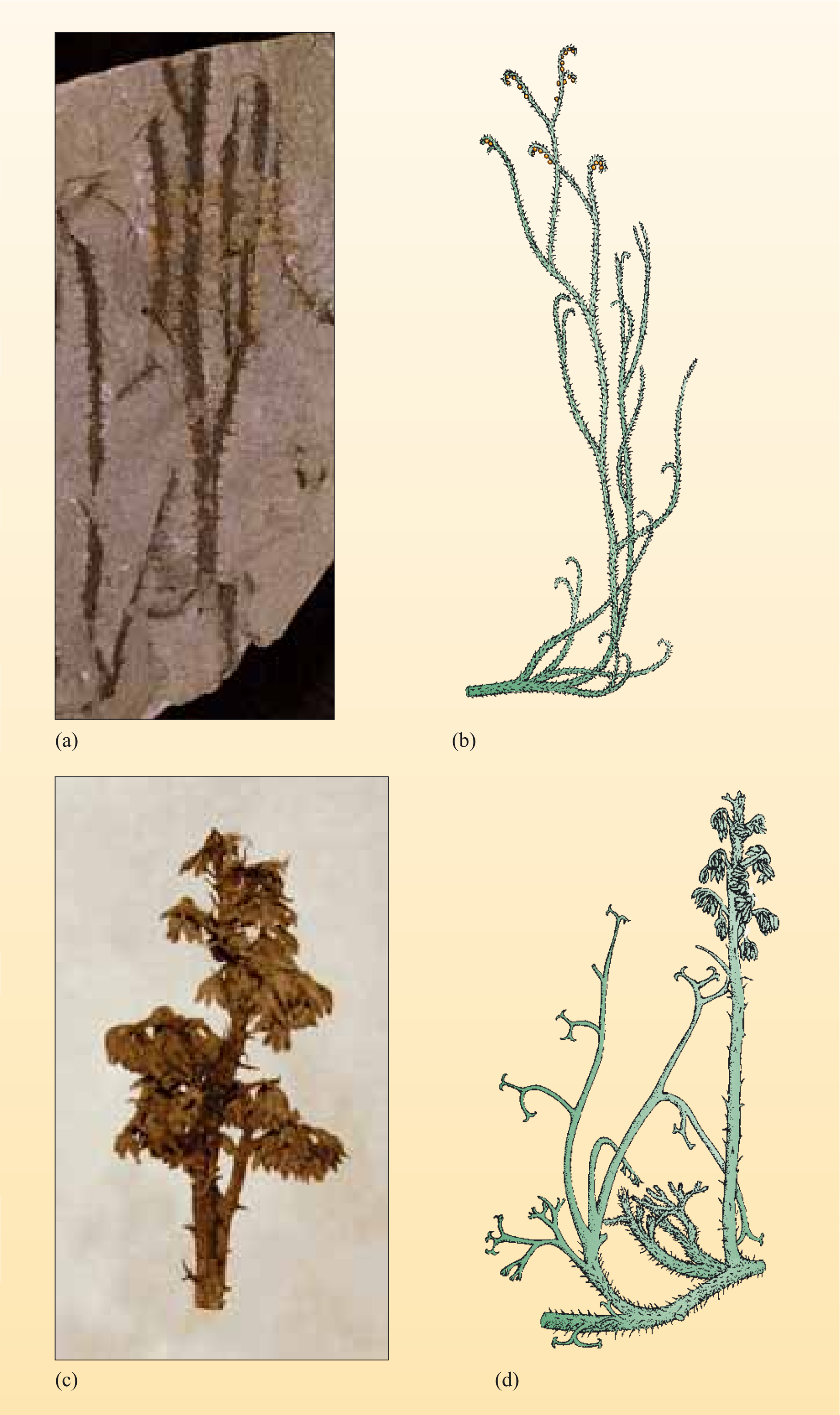
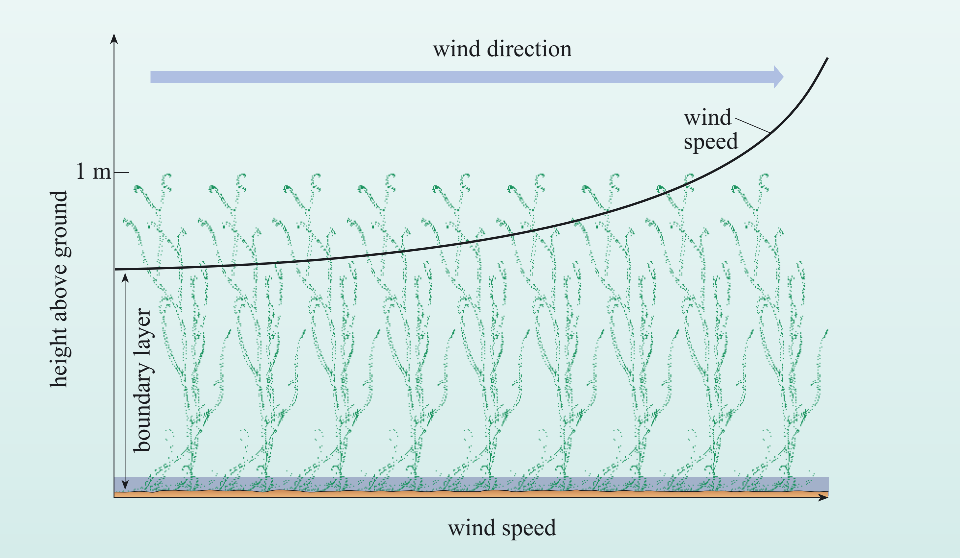


Figure 6.16 Fossil and reconstruction of: (a) and (b) *Sawdonia ornata*, Early Devonian (about 50–90 cm tall); (c) and (d) *Psilophyton dawsonii*, Early Devonian (about 50 cm tall). (Stewart and Rothwell, 1993)

Instead, their curled or hooked form suggests that their main function was to enmesh neighbouring stems, thereby providing mutual support. Upright growth was aided further by the crowding of the stems, which increased the height of the boundary layer. A modern-day analogy of this crowding effect can be seen in a field of wheat: a single stalk has very little mechanical strength and, if exposed to wind on its own, would quickly be blown over; many stalks growing closely together, however, can survive upright throughout an entire growing season.

To summarise, surface roughness and, hence, the height of the boundary layer increased as land plants evolved, their growth driven upwards by reproductive advantage and mutual shading (minimises loss of moisture) (Figure 6.17). Beneath this canopy of vegetation a humid environment was maintained, so that the need for thick cuticles to help retain water content was reduced.

Figure 6.17 *Sawdonia* heath superimposed on an increased boundary-layer profile. As in Figure 6.12, two diagrams are superimposed here: one shows the height and characteristics of the plant and the thickness of the boundary layer, and the other shows the wind speed in relation to the height above the ground.



The simple, leafless architecture of the earliest land plants conveys little about the climate of the time. The naked branching stems with limited **vascularisation** make them similar to modern desert plants. This simple internal structure would have allowed the plants to grow in a wide range of environments; indeed, each genus known from Devonian sediments has been found over several continents, suggesting an ability to colonise a range of climatic environments. At this point it is important to note that fossil species can only be defined by their morphology; it is not possible to deduce if they were genetically related.

■ Why is it important to state that the species have been defined by their morphology alone?

■ Species alive today are usually defined (at least in sexually reproducing organisms) in terms of their capacity to cross-pollinate freely with other members of the same species. In fossils, particularly those of primitive plants, data on the pollination limitations of the original plants is unavailable, so species have to be defined from a purely morphological perspective. Similar-looking plants might, therefore, have been genetically distinct and so unable to cross-fertilise.

Box 6.4 The evolution of the leaf

By the Late Devonian, multi-layered forest ecosystems were fully developed, populated by plants with broad, flattened leaves with high leaf areas. Evaporation and **transpiration**, and hence the cycling of atmospheric water over land, must at last have approached present-day levels. Although earlier Devonian heaths of plants such as *Sawdonia* would have had a major impact on reducing erosion and sedimentation rates due to the binding action of the rhizoids and rhizomes, their effect on the hydrological cycle would by no means have been as great as that caused by the advent of leafed plants. Without the evolution of the leaf, our present world could not exist.

A leaf can be thought of as a flattened organ that produces food for the plant by photosynthesis. Leaves are generally green due to the colour of the light-trapping pigment, chlorophyll. Leaves come in a variety of shapes and sizes, and their architecture varies with the species and the environment. The environmental constraints on leaf architecture will be discussed later, as fossilised leaves provide a powerful tool for determining past climates; first it is important to consider why the leaf evolved and why it is found on the vast majority of terrestrial plants.

Take a leaf from any common plant – preferably one that has leaves that are partially transparent. What do you notice? One of the most obvious features is that most leaves are very thin, often not more than a fraction of a millimetre thick. This ensures that all the cells in the leaf are close to the atmosphere with which the plant has to exchange gases. Where leaves are thicker, this is a specialisation that has developed to increase the plant's ability to conserve water, reducing the plant's surface area to volume ratio. Some leaves may also have thicker than usual coverings of cuticle or waxes, which enhance water conservation. Overall, the size, shape and thickness of a leaf are a compromise between conflicting demands, e.g. maximising light capture and minimising water loss.

Another notable feature of leaves is their network of veins (Figure 6.18). Usually, the network consists of a **midvein**, or **primary vein**, from which a series of thinner **secondary veins** branch. These in turn have even thinner **tertiary veins** running between them. Sometimes even finer orders of veins criss-cross the leaf until very small areas of the leaf are enclosed by veins.

The veins of a leaf have two functions:

- to supply water and nutrients and distribute the carbohydrate products of photosynthesis to the rest of the plant
- to provide structural support for a web of photosynthetic tissue that makes up the leaf; it can exceed a square metre in area.

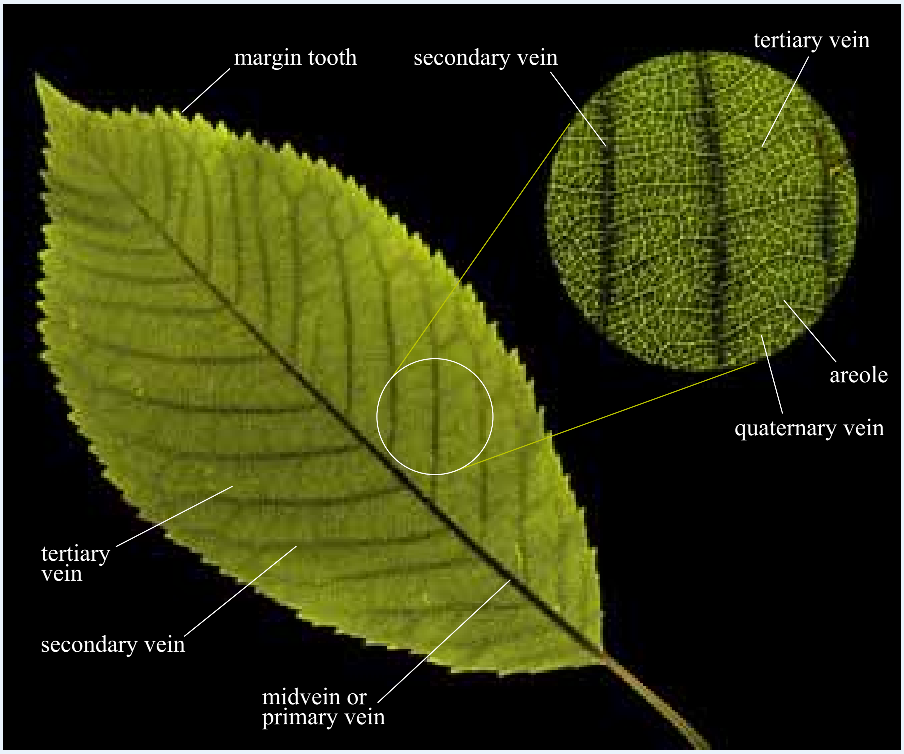


Figure 6.18 The vein system of a modern leaf.

The branching pattern of veins is reminiscent of the branching pattern of a tree. This similarity is not altogether accidental, for it appears that almost all the leaves present today, whether from an oak tree or a fern, were derived from modified branches. The only exceptions to this are the leaf-like **enations** of some primitive plants, such as club mosses or *Asteroxylon* (Figure 6.15b), which are outgrowths of the stem.

So, how did leafed plants evolve? Examine Figure 6.19, which attempts to summarise what is known about the evolution of the plant characteristics that have been significant in increasing the gas-exchange, carbon-fixation and water-cycling processes in early land plants. The important point to extract from the figure is that there appears to be a broad correspondence between the drawdown of atmospheric CO_2 and the innovations in land-plant architecture. As time progressed, plants increased in size and their simple naked branched stems developed a single main stem with side branches. These side branches eventually became flattened and webbed with tissue to form large photosynthetic surfaces (leaves).

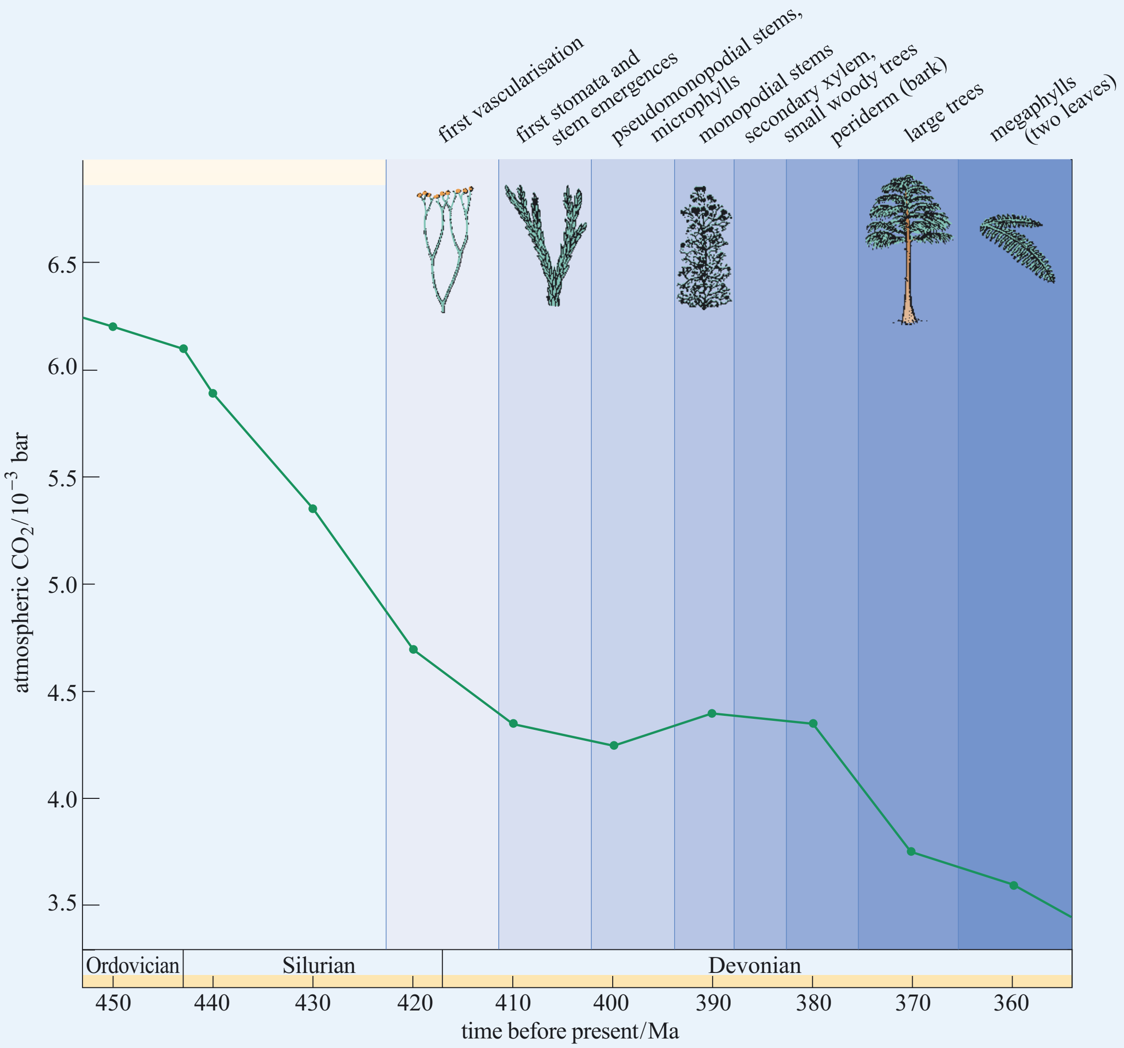


Figure 6.19 Major innovations in land-plant architecture with respect to the atmospheric CO_2 level. Pseudomonopodial stems refer to a single vertical stem made up of unequal branches, whereas monopodial stems denote a genuine main stem. Microphylls are small outgrowths of the stem, whereas megaphylls are true leaves. Secondary xylem is the tissue that makes up wood, whereas periderm is similar to bark.

This increase in leaf area demanded greater fluid movement in the plant body, so vascular systems became more complex and more efficient to deal with demand. In turn, this provided more fluids and nutrients to the leaves, which became even larger, allowing more carbon to be fixed and providing more carbohydrates with which to build larger plants. This positive feedback loop was eventually moderated (i) at the point at which atmospheric CO_2 concentrations became limiting in the context of temperature, water availability and other factors, and (ii) when the structural costs of building larger plants became prohibitive, if not in absolute terms, then in competitive terms.

Figure 6.19 shows that, in the Devonian, atmospheric CO_2 was estimated to have been about ten times higher than present levels of 0.38×10^{-3} bar. If correct, this high concentration of CO_2, coupled with the relatively small biomass of plants, would have meant that CO_2 was unlikely to have acted as a limiting factor on photosynthesis at that time. Instead, the primitive vascular systems in plants coupled with the fact that there was less water than now being cycled through the atmosphere, suggest it is likely that water rather than CO_2 may have limited photosynthesis in a large number of plants. Intriguingly, in many early Devonian plants, **stomata**, which in the absence of leaves would have been scattered over the stems, were rare compared with their prevalence in today's plants and those in the Carboniferous.

Question 6.8

Why do you think early Devonian plants could have functioned with only a few stomata?

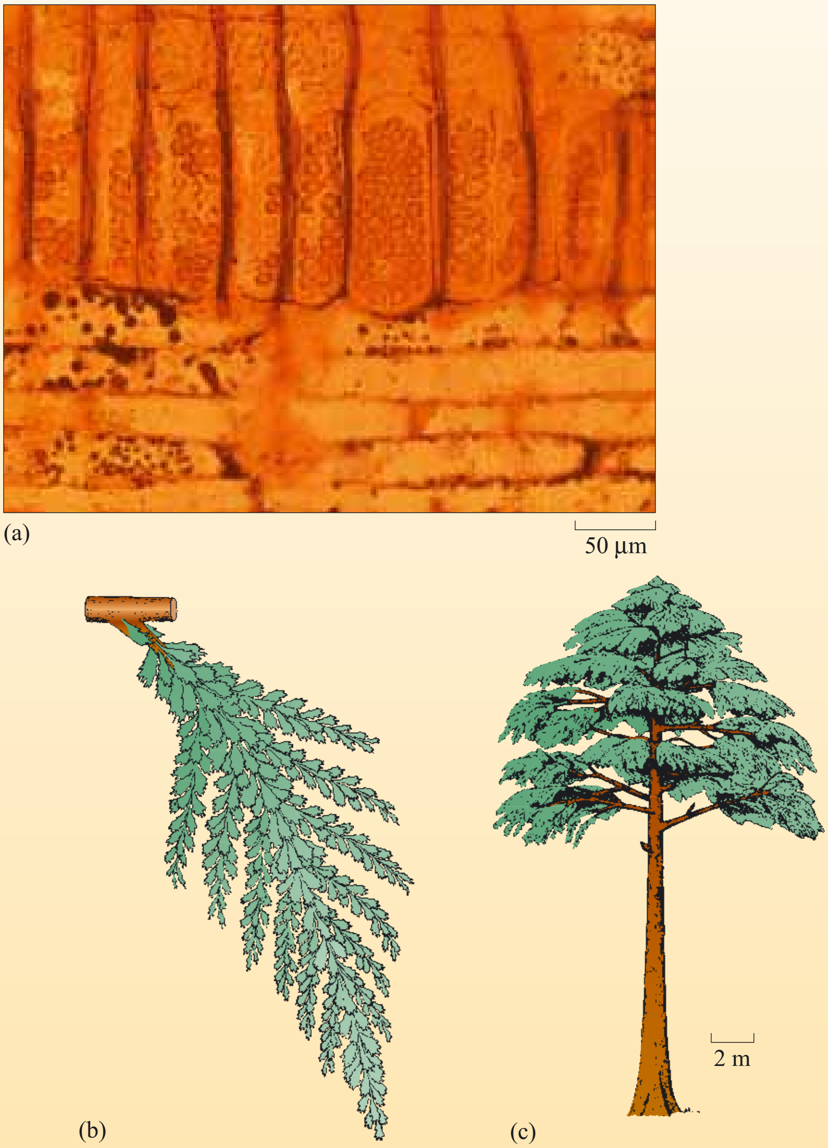
The evolution of leaves in the Late Devonian greatly increased the surface area for gas exchange and also for the evaporation of water vapour into the atmosphere, thereby causing the atmosphere to cycle water at a greater rate. The evolution of leaves also contributed to the cycling of carbon because many long-lived plants discarded their leaves and replace them numerous times during their lifetimes, enhancing carbon transfer from the atmosphere to the soil and the sediments. The innovation of leaf loss and replacement appears to have evolved in the Devonian. As the land surface became increasingly enriched with organic matter, so rates of chemical weathering increased, and rich soil profiles developed across the land. In summary the carbon, water and other biogeochemical cycles can be inextricably linked by the photosynthesis of land plants.

6.3.3 The first forests

The Late Devonian saw a major diversification in land plants and most of the main groups of plants (with the exception of the flowering plants – the **angiosperms** – and the **cycads**) appear to have had their origins in Late Devonian times. One of these early groups, the **progymnosperms**, was especially important as it represented a further increase in carbon sequestering.

The progymnosperms were the dominant canopy formers in the earliest forests. The story of their identification is of interest because it provides an example of why it is important not to be too restricted in the concepts of ancient organisms, i.e. it can be misleading to interpret ancient plants only in terms of plants that are living today. The progymnosperms produced wood for the first time that had all the characteristics of the wood of modern conifers (which, together with other primitive seed-bearing plants, are referred to as **gymnosperms**). However, other progymnosperms were found to have foliage that looked like the modern fern and which bore reproductive structures that produced spores like a fern, rather than seeds like the modern conifers. As the wood and foliage were initially found unattached to each other, it was thought that they came from different plants, and as such, they were classified as belonging to different groups. The wood, given the generic name *Callixylon* (Figure 6.20a), was classified as belonging to the gymnosperms, whereas the foliage, assigned to the genus *Archaeopteris*, was thought to belong to the ferns (Figure 6.20b). In 1960, the American palaeobotanist Charles Beck described fossil specimens that showed the wood and foliage attached to each other, reconstructing the *Archaeopteris* 'plant' as a forest tree, about 20 m tall (Figure 6.20c), so creating the progymnosperm class.

Figure 6.20 (a) *Callixylon*, showing general characteristics of secondary xylem. (b) *Archaeopteris* foliage. (c) Reconstruction of the *Archaeopteris* tree. (b and c: Beck, 1962)



It seems unlikely that the *Archaeopteris* tree would have retained its leaves throughout its life; they were probably replaced many times, so enhancing the flux of carbon from the atmosphere to the soil. Moreover, the wood of *Callixylon* is made up of significant amounts of the complex organic polymer **lignin**, which decays more slowly than most non-woody plant tissues. The lignin in woody plants results in them having a higher probability of being represented in the fossil record over non-woody (**herbaceous**) plants, as well as increasing the probability of them contributing to long-term carbon sequestering.

The progymnosperms are, therefore, significant because they illustrate the innovations in land-plant biology that brought about significantly increased rates of carbon sequestering from the atmosphere. This effect may in turn have led to the global cooling in the late Carboniferous and early Permian.

Summary of Chapter 6

1 The geological record for the late Ediacaran suggests a number of environmental upheavals during this stage involving a global fall in sea level and marked fluctuations in the rate of burial of organic material (i.e. climatic instabilities). This was followed by lowered rates in the Cambrian. Nevertheless, the Ediacaran faunas persisted to the end of the Ediacaran, reaching a maximum diversity in the final 6 Ma, with a few forms surviving into the Cambrian. It is unclear whether the majority of Ediacaran animals underwent a mass extinction at the close of the Vendian or whether they were simply ecologically displaced by newly evolving animals.

2 Exceptionally preserved fossil assemblages of soft-bodied animals from the Cambrian reveal anatomical advances over the earlier Ediacaran fauna. Many of the Cambrian forms exhibit greater differentiation of body parts, including the concentration of food-trapping organs around a 'head' end, the appearance of limbs and of discrete tubular, two-ended guts. These innovations may have been fuelled by Hox gene duplication.

3 A revolution in feeding relationships accompanied these anatomical changes. In particular, the rapid proliferation of skeletal hard parts may reflect the rise in predation, and hence multi-tiered food chains.

4 The proliferation of shells from early Cambrian times impinged upon biogeochemical cycles, leading to increased deposition of limestones in offshore open marine environments. Phanerozoic seas thus saw a shift in emphasis from the burial of carbon in organic material to the fixing of carbon in carbonate rocks. Increased burrowing in offshore sediments also helped to reduce the extent of organic carbon burial there.

5 The fossil record for families of marine animals with hard parts provides a general guide to Phanerozoic mass extinctions and radiations. The early Palaeozoic radiations are consistent with a relative ecological 'vacuum'. Subsequent diversification was interrupted by a succession of mass extinctions, of which five were notably severe, occurring in the late Ordovician, the late Devonian, the late Permian (the most devastating), the late Triassic and the late Cretaceous.

6 Although periodic extraterrestrial impacts have been proposed for these and other smaller mass extinctions, differences in the relative durations and the effects of the extinctions, together with other geological data, suggest a mixture of Earth-bound and extraterrestrial causes.

7 Each mass extinction was followed by a relatively rapid rise in family numbers. Over the longer term an overall increase in diversity levels occurred, though whether this was the result of successively higher

equilibrium levels or merely the effects of a dynamic interplay between ever-rising diversity and numerous extinction events remains unresolved.

8 Within the pattern of diversification of marine animals, three ‘evolutionary faunas’ may be distinguished: the Cambrian fauna that dominated the initial radiations; the Palaeozoic fauna that continued diversifying through the Ordovician, but then commenced a long slow decline; the modern fauna that slowly but relentlessly, expanded, rising to dominance after the Palaeozoic. Each successive fauna was less drastically affected by mass extinctions than its predecessor. The extinctions left a biased line-up of survivors.

9 Post-Palaeozoic faunas show an intensification of predation, especially upon shelly prey. One major defensive adaptation appearing among the prey animals was deep burrowing into the sediment, which led to yet further churning of surface layers. These, and other linked changes, are collectively referred to as the Mesozoic marine revolution. The associated rise of various planktonic groups with calcareous skeletons in the Mesozoic enhanced carbonate sedimentation in deeper water, increasing the oceanic carbonate sink.

10 Most of the Earth’s non-bacterial biomass is in the form of green land plants. The evolution of terrestrial vegetation had a profound effect on the Earth’s surface systems.

11 Plants adapted to this environment initially by growing close to the substrate surface and so staying within the boundary layer where they were not subject to the more intense desiccation that might occur in the faster-moving free air above.

Learning outcomes for Chapter 6

You should now be able to demonstrate a knowledge and understanding of:

6.1 The factors that may have led to the diversification of species that mark the transition from the Proterozoic to the Phanerozoic Era.

6.2 How evidence from exceptionally preserved fossil assemblages has been used to investigate the potential cause(s) of rapid expansion in the number of species during the Cambrian (referred to as the Cambrian Explosion), and the associated differentiation in body parts and functions, feeding mechanisms, level of predation and rise in hard external skeletal parts.

6.3 Why mass extinctions and radiations are best investigated by examining changes in the number of families (rather than species) over time.

6.4 How each of the five major mass extinctions was followed by a relatively rapid rise in diversity levels and the impact these extinctions had on each of the faunal successions.

6.5 How the structure and complexity of land plants developed over time in response to competition for light and nutrients as well as changing environmental conditions, and how this in turn resulted in the specialisation and adaptation of leaf structures and new reproductive mechanisms (changing from spores to seeds).

Chapter 7

The Earth at extremes

During the history of the Earth, the climate has swung to hot and cold extremes compared with today's climate. This chapter will look at the Earth in the late Carboniferous and Permian, an interval spanning over 70 Ma (323–251 Ma), focusing on the late Carboniferous–early Permian glaciation before moving on to look at the greenhouse world of the Cretaceous. Although these two periods have very different climatic regimes and the biota that inhabited them were different, they are both linked by the role of CO_2 in controlling planetary temperatures. You will look at the changes in the geography, climate and life, and proposed theories linking them. The aim of this chapter is not to describe every aspect of life during these times, but to concentrate on those organisms that contributed most and/or which were most affected during each event in order to understand how very different climatic regimes and their influence on the Earth's biota can be explained by various atmospheric and geological processes.

7.1 The icehouse world

7.1.1 Geographical perspective

Students of geology living in Europe (or in North America) might tend to think of the Carboniferous as a time of warm, humid conditions, when the Earth was covered in lush vegetation. Recent history would have been very different without the fortuitous accumulation of Carboniferous plant remains across these regions some 300 Ma ago, as these provided the coal reserves upon which the 19th-century industrial revolutions of the developed world were based. By contrast, the same students might tend to think of the Permian as a time of dry and desolate conditions, on a planet of deserts and salt lakes. An Australian or Brazilian student of geology, however, would have a different perspective, as the evidence shows that their countries were at times covered by extensive ice sheets during the Carboniferous, while major coal reserves formed during the Permian across parts of Australia, South Africa and India.

So the perception of the Carboniferous world, seen from a European or North American perspective as warm and wet, and the Permian as hot and dry, is overly influenced by the local to regional geological record. The coal deposits of those continents were produced under tropical conditions, not because the whole planet was warm but because Europe and North America were in low latitudes at that time. In fact the late Carboniferous and early Permian represent a cooler phase in the Phanerozoic from a global viewpoint.

To make sense of these varying perspectives, you only need to look around the world today to see the enormous variety of climate, environments and life-forms, ranging from tropical rainforests through deserts, temperate forests and tundra to ice caps. So it is logical to expect to find a similar scale of heterogeneity in the Carboniferous and Permian worlds. During these times, however, the continents were arranged very differently from the way they are today (Figure 7.1).

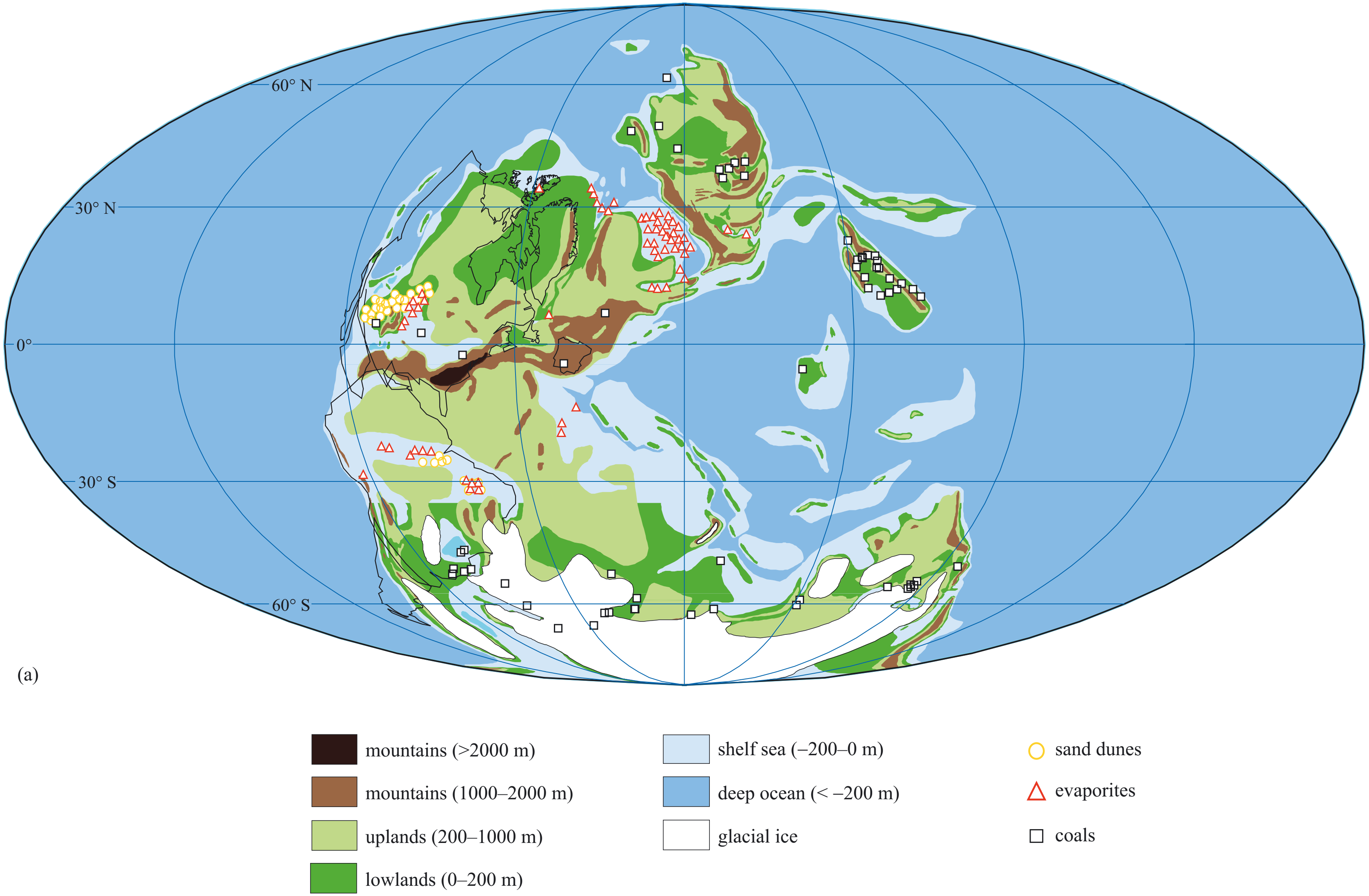


Figure 7.1(a) Pangea in the earliest Permian (281 Ma).

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Figure 7.1(b) Pangea in the Permian (251 Ma).

Question 7.1

From Figure 7.1, what was the most striking aspect of the continental arrangement during the Permian compared to that today?

Figure 7.1 shows the position of Pangea at the beginning and the end of the Permian, and illustrates the changes in location of this supercontinent and the shift from glaciated to ice-free conditions. These maps, compiled by Fred Ziegler and colleagues at the University of Chicago, represent the most detailed palaeogeographical synthesis to date of a vast array of data. Figure 7.1a can serve as a general reference map for the Permo-Carboniferous (i.e. the late Carboniferous to early Permian) icehouse world.

Life on Pangea was very different from that of today: there were no flowering plants and no mammals. As far as the oceans were concerned, there were no calcareous plankton, predation on shelly organisms was less intense than it is today, and **sessile** shelly forms lying exposed on the sea floor were commonplace. Yet there are a number of similarities in terms of the broad effects of global climate change, including the response of organisms to it, which might inform our understanding and speculations about the effects of climate change in the future.

7.1.2 Geological evidence

The distribution patterns of climatically sensitive deposits, such as evaporites, **red beds,** glacial **diamictites** (non-sorted mixtures of rock interpreted as being of glacial origin, previously known as tillites), fossilised wood and coals can provide important clues to past climates.

The formation of evaporites (salt deposits) requires that evaporation exceeds precipitation. Ideal conditions occur in arid regions, where formation can take place in enclosed basins with high temperatures and low rainfall. Modern evaporites occur mostly in subtropical regions centred around latitudes 25° to 35° in both hemispheres. A similar distribution can be seen in Figure 7.1 with respect to the inferred palaeogeography of the Permian. Much the same pattern can also be seen for desert sand dune deposits.

Red beds are sedimentary rocks containing hematite (Fe_2O_3) that formed under oxidising conditions in hot climates. The original source of iron in these rocks was often exposed igneous or metamorphic rocks that had been intensely chemically weathered. This iron was then remobilised (as Fe^{2+}) in anoxic groundwater and reprecipitated in desert sediments as iron oxide, as a result of evaporation drawing the water up towards the surface. Modern red beds form largely within 30° of the Equator (reflecting **Pleistocene** shifts between humidity and aridity), and most Palaeozoic red beds seem to have had a similar distribution, being commonly associated with evaporite deposits. Of course, such ancient red beds may be eroded to yield red soils at a later date in a different latitude, as can be seen, for example, in the countryside of Cheshire, England.

In contrast to these indicators of climatic warmth, most diamictites are considered to have been deposited by glaciers. Their widespread occurrence in southern areas of Pangea during the Permo-Carboniferous indicates that large areas experienced glacial conditions at least some of that time.

The formation of coal requires a net surplus of precipitation over evaporation, sufficient warmth and light for plants to grow, and isolation of buried plant material (or peat, the precursor to coal) from the oxidising atmosphere. Rainfall and plant productivity are closely linked, while periods of drought strongly affect preservation because falling groundwater levels permit oxidation of organic matter (through aerobic decomposition or burning).

Further clues come from growth rings in trees, which can also serve as climate indicators (Box 7.1). Fossil Carboniferous tree trunks from low palaeolatitudes lack or have only faint evidence of growth rings, indicating that they grew in near-constant conditions of humidity and warm temperatures, and therefore most Carboniferous coals almost certainly formed under tropical conditions at low latitudes. By contrast, thick coal deposits also formed in the Permian within 5° to 30° of the present South Pole. These coal deposits contain fossilised tree trunks with prominent growth rings, implying seasonal growth.

Box 7.1 Tree growth rings

Growth rings are formed when a tree grows at varying rates over time. Typically, variations in wood growth are caused by environmental changes such as water availability, temperature or light regime (day length). Away from low latitudes such variation is usually tied to the annual cycle of the seasons. Wood cells with large internal cavities are produced early in the growing season, when the availability of, and the demand for, water is high. These cells comprise the **earlywood**. When water is less available and demand is less (in late summer and autumn), the water-conducting space in the cell becomes constricted as the cell walls thicken. These **latewood** cells are mechanically stronger than earlywood cells, but less efficient at water conduction. No cells are produced during the period of winter ‘shutdown’ or dormancy of the tree. The change from large cells to small, thick-walled cells corresponds to seasonal changes in tree growth, forming a single growth ring. In non-seasonal environments, such as in tropical rainforests, there is less of a fluctuation in climate conditions through the year (though there may be some variation in rainfall) and growth is consequently more uniform, with rings being absent or only weakly developed. The ratio of wall thickness to cell cross-sectional area for water conduction is a compromise to meet both the water demand and the need for structural strength.

By combining knowledge of the present-day distributions of different climatically sensitive deposits and the climate conditions under which they form, it is possible to infer similar conditions when similar features are encountered in the geological record.

The next section will focus on some of the more important aspects of the Earth and its life within the interval spanning the late Carboniferous and early Permian.

7.2 Permo-Carboniferous glaciation and subsequent warming

7.2.1 The available record

The late Carboniferous and early Permian interval is interpreted as having been a time of pronounced cooling. This was apparently followed by a shift back towards warmer conditions during the rest of the Permian, with global climate eventually becoming warmer than at present.

So how much is really known about Permo-Carboniferous conditions? The answer is a fair amount. Even though it is often harder to work on rocks of that age than on more recent rocks – a bit like walking in the dark with a light only occasionally being switched on to give an idea of what's around – a reasonable picture has been built up by studying the available evidence. Some of this will be discussed in the following sections.

7.2.2 The link between atmospheric CO_2, vegetation and climate

It is now widely acknowledged that anthropogenic build-up of atmospheric CO_2 (and other greenhouse gases) is implicated in current rapid rises in global warming. Over a longer timescale (hundreds of thousands to millions of years), atmospheric CO_2 levels also appear to have varied throughout the Earth's history and such variations must have had an effect on global climate.

Two major routes by which CO_2 can be removed from the atmosphere are through direct uptake by plants (during photosynthesis) and by dissolution in water. So long as the rate of photosynthesis exceeds that of respiration, then the longer term net effect is sequestration of atmospheric CO_2 as a consequence of the burial of organic material. On land, buried organic material is first converted to peat, then coal, so that a reservoir of organic carbon builds up, locking it away from the atmosphere. Section 3.3 described how CO_2 is highly soluble in water, and this provides the second major route by which it is removed from the atmosphere. The overall reaction between CO_2 and water to form a weak acid, carbonic acid (H_2CO_3), can be expressed as:

$$CO_2 + H_2O \rightleftharpoons H_2CO_3 \qquad (7.1)$$

Carbonic acid dissociates to release a hydrogen ion (H^+) and a bicarbonate ion (HCO_3^-), which in turn dissociates to form the carbonate ion (CO_3^{2-}) and a further hydrogen ion. The high levels of CO_2 in vegetated soils (from respiration of plant root systems and microbial decomposition) mean that CO_2 concentrations are typically 10 to 100 times higher in the soils than in the atmosphere, and it is the acidic water in soils that is mainly responsible for the weathering of minerals in soil and rock.

Question 7.2

(a) What are the two main rock-weathering reactions involving dissolved CO_2?

(b) Which of these is considered to lead to a net drawdown of CO_2 from the atmosphere when precipitation of carbonate occurs?

A third weathering reaction that needs to be considered is that involving exposed deposits of peat and coal. In contrast to the weathering reactions just discussed, the oxidative process in this case *releases* CO_2, while using up oxygen from the atmosphere.

Plants are responsible both directly and indirectly for considerable drawdown of atmospheric CO_2. The Permo-Carboniferous interval seems to have been outstanding in terms of the direct effects of vegetation on climate. Two significant things occurred: firstly the spread of land plants – and in particular trees – provided a large pool of organic matter, some of which was then buried; secondly, since their first appearance in the Devonian (416–359 Ma), plants have greatly increased the rate of soil and rock weathering. The result of this weathering process was an increased transfer of CO_2 from the atmosphere to the oceans in the form of bicarbonate ions (see the answer to Question 7.2) and ultimate burial there, as limestone, then lowers atmospheric CO_2 levels. Although CO_2 is returned to the atmosphere through volcanism and weathering of exposed organic deposits, it seems that this reverse process was greatly outweighed during the late Carboniferous and early Permian by CO_2 drawdown mediated in one way or another by land plants. Models for the change in atmospheric CO_2 levels, based on the estimated balance of carbon fluxes, show a marked fall in CO_2 for this interval (Figure 7.2). This in turn would have resulted in a lowering of mean global temperatures.

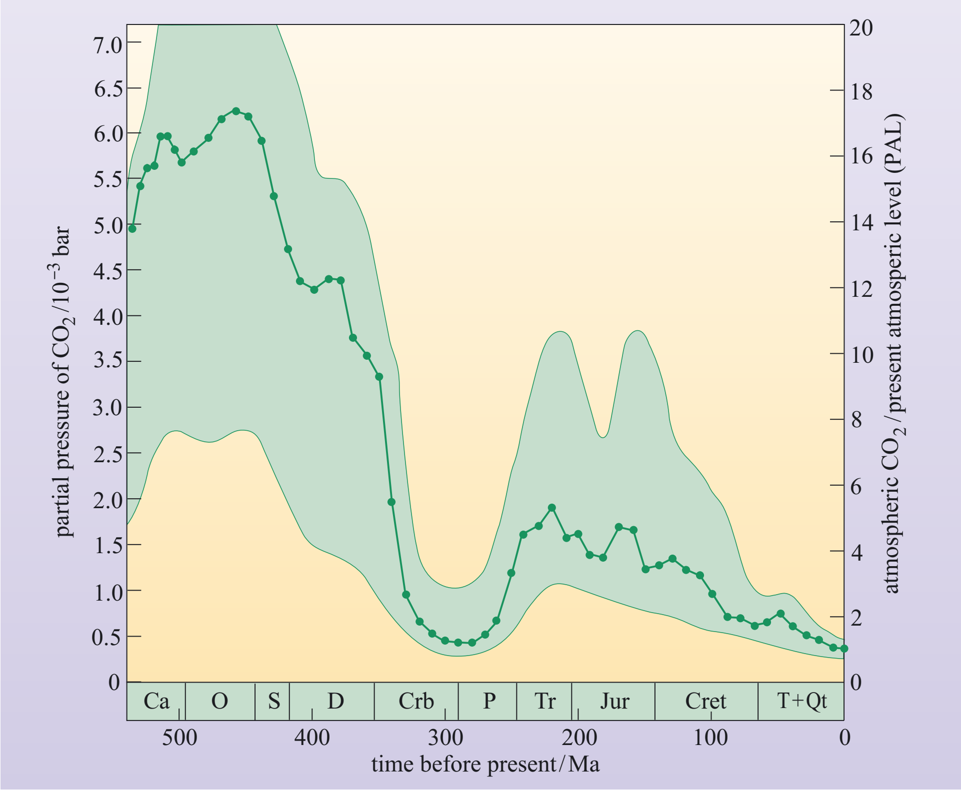


Figure 7.2 Variation in the level of atmospheric CO_2 (absolute and as a factor of present atmospheric level (PAL)) over the Phanerozoic as calculated from the 'GEOCARB' model (Section 5.3). Note the pronounced fall in CO_2 levels around the Permo-Carboniferous boundary to levels similar to those of today. Shaded area is the uncertainty in the data. (Berner, 1994)

Other mechanisms may also have contributed to globally cool conditions during this time interval, in particular the effects of the location of the southern part of the Pangean land mass over the South Pole, and the effect that the assembly of such a supercontinent might have had on climate. To understand this, it is important to investigate the influence of plate tectonics on global climate.

7.2.3 Continental motion and climate

The following aspects of plate tectonics are relevant to the Permo-Carboniferous icehouse world:

- the configuration and position of land with respect to the poles, and their effects on ocean circulation
- volcanic activity related to mid-ocean ridge and subduction processes
- collisional processes causing uplift and mountain belts
- eustatic changes in sea level.

As will be seen shortly in the following discussion, each of these can affect climate, both locally and globally.

As noted above, the cause of the Permo-Carboniferous glaciation has, in some cases, been ascribed to the positioning of a part of the Pangean land mass at that time over the South Pole.

Modelling of a 'cap world' (Box 4.1) configuration leads to a markedly cooler (south) polar region. If snow precipitation exceeds **ablation** (in areas of maritime influence, with moist air coming off the ocean), then its accumulation would lead to the formation of an ice cap. A counter argument, however, is that during the Earth's history land masses were positioned over the poles at other times, including much of the Cretaceous, when global climate was warmer than today. So the onset of glaciation and subsequent melting of the polar ice cap might not be explained solely by movement of the Pangean land mass onto and away from the South Pole.

An arrangement more reminiscent of a 'slice world' was reached in the Triassic (251– 200 Ma), when the land mass was symmetrical about the Equator. This had developed gradually over millions of years through the northward drift of Pangea. Western equatorial regions of Pangea started to become more arid at the very end of the Carboniferous, with arid conditions spreading eastwards as the monsoonal system developed and disrupted zonal circulation. This change can be seen in the rock record, with indicators of wetter conditions such as coals progressively replaced by those indicative of aridity (e.g. evaporites and red beds). Thus, conditions became progressively drier at low latitudes during the Permian, with the development of a monsoonal system most probably contributing to this. These changes do not, however, explain the overall trend of deglaciation and global warming.

If there was only one Pangean supercontinent during the Permo-Carboniferous, then it follows that there was only one superocean. However, some Asian microcontinents continued to drift around at this time (Figure 7.1), some of which presumably had small spreading ridges between them. Nonetheless, compared with times of greater continental fragmentation, the total length of mid-ocean ridge systems and corresponding subduction zones would have been less than at other times, delivering less CO_2 to the atmosphere. Though this may help to explain the glaciation (through net drawdown of CO_2, as discussed earlier) it does not help to explain the subsequent retreat of glaciers during the Permian.

There is a third tectonic factor to consider in the Pangean supercontinent and its effect on global climate, i.e. the collision of all the plates that contributed to its formation, and the consequent mountain chains this created. The assembly of

Pangea from its constituent parts was akin to a multitude of continent–continent collisions. Numerous mountain ranges were built, though whether anything like the Tibetan Plateau formed is open to conjecture.

Question 7.3

What effect would mountain building on such a scale have had on the rate of CO_2 drawdown from the atmosphere?

Without compensation for any such increased drawdown, the consequence would have been global cooling. It is known that major mountain chains generated by such collisions did exist in the late Carboniferous and early Permian, as the eroded relics of these still form many upland areas in northwestern Europe (e.g. the Ardennes and Harz Mountains) and in the USA (the Appalachian Mountains), for example. This raises the question as to whether the effect of their formation on CO_2 levels and climate can be evaluated.

High $^{87}Sr/^{86}Sr$ ratios occur in the weathering products of continental rock, whereas low ratios occur in the hydrothermal effusions associated with sea-floor spreading. Since all of this material ultimately ends up in the oceans, the values that are preserved in marine carbonate rocks containing strontium reflect the relative inputs of continental weathering and sea-floor spreading through geological time. Figure 7.3 shows a compilation of strontium isotope ratios throughout the Phanerozoic. In the long term, many factors are likely to have been involved in the overall pattern; for the time being, focus your attention on the Carboniferous, and the approaching late Carboniferous–early Permian glaciation.

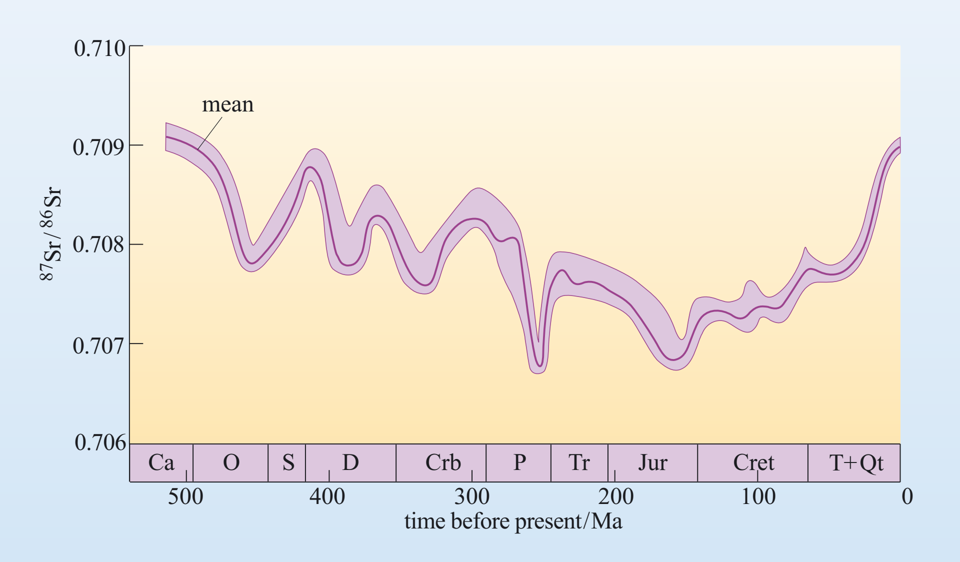


Figure 7.3 $^{87}Sr/^{86}Sr$ ratios in marine limestones through Phanerozoic time. The shaded area represents variation in values. (Reymo, 1991)

Note the relatively high $^{87}Sr/^{86}Sr$ ratios during the late Carboniferous–early Permian with respect to the late Devonian to early Carboniferous (before the main continental collisions involved in the formation of Pangea), reflecting increased continental weathering relative to sea-floor spreading.

Thus, mountain building may also help to explain the globally cool conditions through increased drawdown of CO_2 during weathering of exposed rocks. The relationship is not quite so simple in detail as continental weathering rates also vary with temperature (as do most chemical reactions). Hence, it is to be expected that increased continental weathering rates (yielding high $^{87}Sr/^{86}Sr$ ratios) are associated with *high* atmospheric CO_2 levels and global warming. The drawdown of CO_2 would then regulate atmospheric CO_2 levels, and hence climate. The converse compensation should also occur, with lowered CO_2 levels leading to global cooling and reduced weathering rates. Figure 7.3 indicates that *increased* weathering rates have been inferred during a time of globally cool conditions. So how can this apparent paradox be explained? It seems that the sheer volume of rock made available (through major uplift) for weathering was the overriding factor. It is known from the Himalaya today that much of the *chemical weathering* of the eroded sediment eventually takes place in lowland areas flanking the mountains. If analogous to conditions during the Permo-Carboniferous, such a large area of weathering, combined with the large-scale effects of vegetation, could have resulted in abnormally high continental weathering rates in the late Carboniferous to early Permian, global cooling notwithstanding, therefore enhancing the icehouse conditions.

Finally, tectonic processes can also cause global sea levels to change, which may in turn affect global climate. Sea-level variations can occur through changes in the volume of the ocean basins. This is caused, most directly, by changes in the volume of mid-ocean ridges. Low sea levels would result in the emergence of areas of former continental shelf, and lowland swamp forests would have expanded, with a consequent rise in sediment weathering rates and drawdown of CO_2 through peat accumulation. Global sea levels would have been lowered yet further due to the accumulation of polar ice locking up large volumes of water. Although this does not explain the initial formation of the polar ice cap, it may have been a factor in maintaining icehouse conditions.

So there are several tectonic factors intertwined with the effects of vegetation and CO_2 levels on climate, each of which may help to explain the conditions seen in the Permo-Carboniferous icehouse world. Section 7.3 will focus on the effect of vegetation on the climate, but first it is important to briefly take an ‘external view’ of the Earth and climate change.

7.2.4 Extraterrestrial causes of climate change

Another factor involved in climate change that needs to be considered is the increase in solar radiation throughout the Earth’s history. The solar flux during the Palaeozoic has been estimated as being 3–5% lower than that of today. This might not seem much, but an increase in solar radiation of only 2% has an effect on mean global temperature that is equivalent to a doubling of atmospheric CO_2 levels. Therefore 3–5% less solar radiation should account for a considerable lowering of mean global temperatures, relative to today. As Figure 7.4 shows, the combination of low atmospheric CO_2 levels (derived from the GEOCARB model in Figure 7.2) and reduced solar radiation results in an even sharper contrast between the Permo-Carboniferous icehouse world and other geological intervals (over the Phanerozoic). So, lower levels of solar radiation can also be invoked to explain, in part, the Permo-Carboniferous climate. If, however, solar radiation has increased only gradually through time, then it cannot fully explain both the marked global cooling of the late Carboniferous and early Permian *and* the relatively rapid subsequent warming during the Permian.

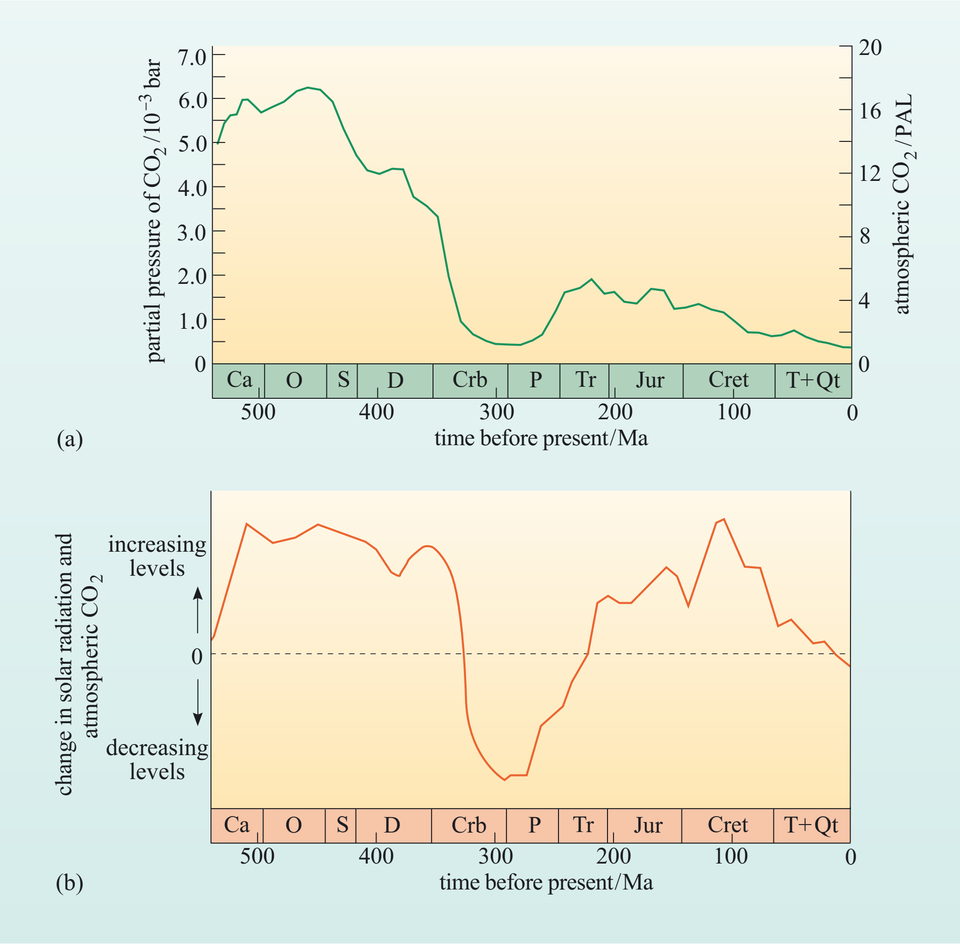


Figure 7.4 (a) Phanerozoic atmospheric CO_2 levels derived from the GEOCARB model shown in Figure 7.2. (b) Combined plot showing net forcing effect of CO_2 and increasing solar radiation on climate through the Phanerozoic relative to the present level. Note the significantly lower levels around the Permo-Carboniferous boundary compared with those of today. (Crowley, 1993)

7.3 The impact of land vegetation

7.3.1 Land plants in the Carboniferous and Permian

Given the striking effect that Permo-Carboniferous land vegetation appears to have had on CO_2 levels and global climate, it is now time to look at this in more detail. Much diversification and the appearance of extensive low-latitude forests dominated by plants that were a bit like very large versions of living clubmosses (lycophytes) and horsetails (sphenophytes) occurred during this time. Many of these grew as tall trees dominating the low-latitude swamps.

■ Why can height be advantageous to a plant?

□ Height enables a plant to compete successfully for access to light and to disperse its spores by winds over a wider area. Consequently, a tall plant would have a distinct advantage over its shorter competitors.

There was a plentiful supply of water at these low latitudes, and many plants evolved and thrived. As a result, thick peat deposits formed in the late Carboniferous low-lying wetland areas, eventually producing the major coal reserves exploited today across the Northern Hemisphere.

Towards the end of the Carboniferous, the lycophyte trees were dominant in only a few areas, with seed plants such as conifers taking over in a number of habitats. Seeds are able to survive periods of drought, germinating when external conditions become favourable: with a seed, an embryo is shielded and nourished by nutritive tissues within a protective coating. These changes in vegetation signalled the gradual loss of most low-latitude, peat-forming swamps and their widespread replacement by drier, well-drained environments in the early Permian.

7.3.2 *Lepidodendron*: a typical swamp dweller

Rather than comprehensively surveying the kinds of trees that made up the late Carboniferous swamp forests, this section will concentrate on the features of one in particular, namely *Lepidodendron*, which is a typical example of a lycophyte tree and is one of the most thoroughly studied of all Carboniferous plants. Not surprisingly, it figures prominently in Carboniferous swamp forest reconstructions (Figure 7.5), and there are examples of these in the Fossil Grove in Glasgow.

Lepidodendron formed the dominant forest canopy during the Carboniferous and grew between 30 m and 40 m in height when mature, only developing a branched crown when in its reproductive phase. In spite of its large size, it had a simple structure in that it had very little woody tissue. Instead of wood, the trunks were largely supported by bark, suggesting that each tree may have lived for only one or at most a few seasons before falling over and perhaps being buried. The vigorous growth and short lifespan of these plants help to explain why so much peat accumulated in these swamps, eventually to become coal. Peat accumulates if the rate of production exceeds that of decay. Studies of modern trees show that bark contains chemicals that make it more resistant to biological decay; they can also inhibit decay of other substances, such as carbohydrates and forest litter. Consequently, there is little sign of decay in late Carboniferous plants, allowing the short-lived *Lepidodendron* trees to be buried in the swamps; some examples of their fossilised remains are shown in Figure 7.6.

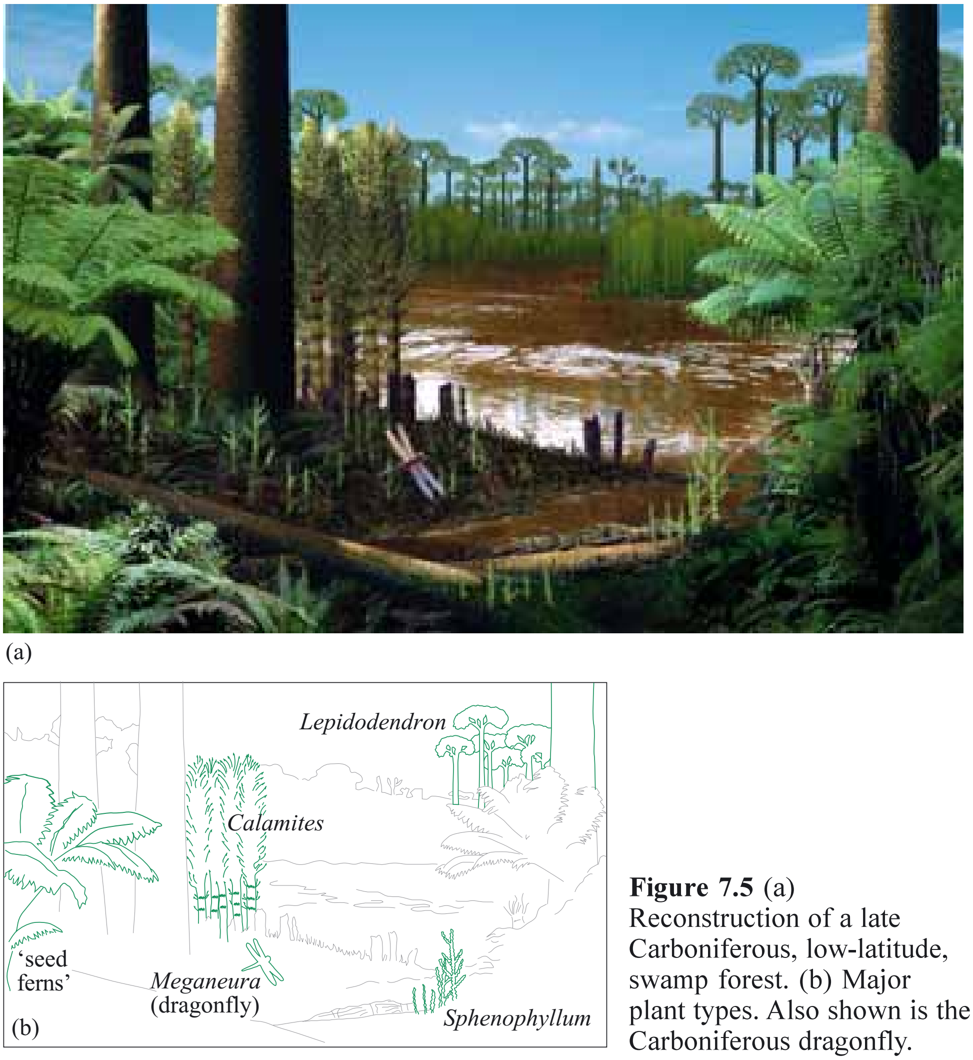


Figure 7.5 (a) Reconstruction of a late Carboniferous, low-latitude, swamp forest. (b) Major plant types. Also shown is the Carboniferous dragonfly.

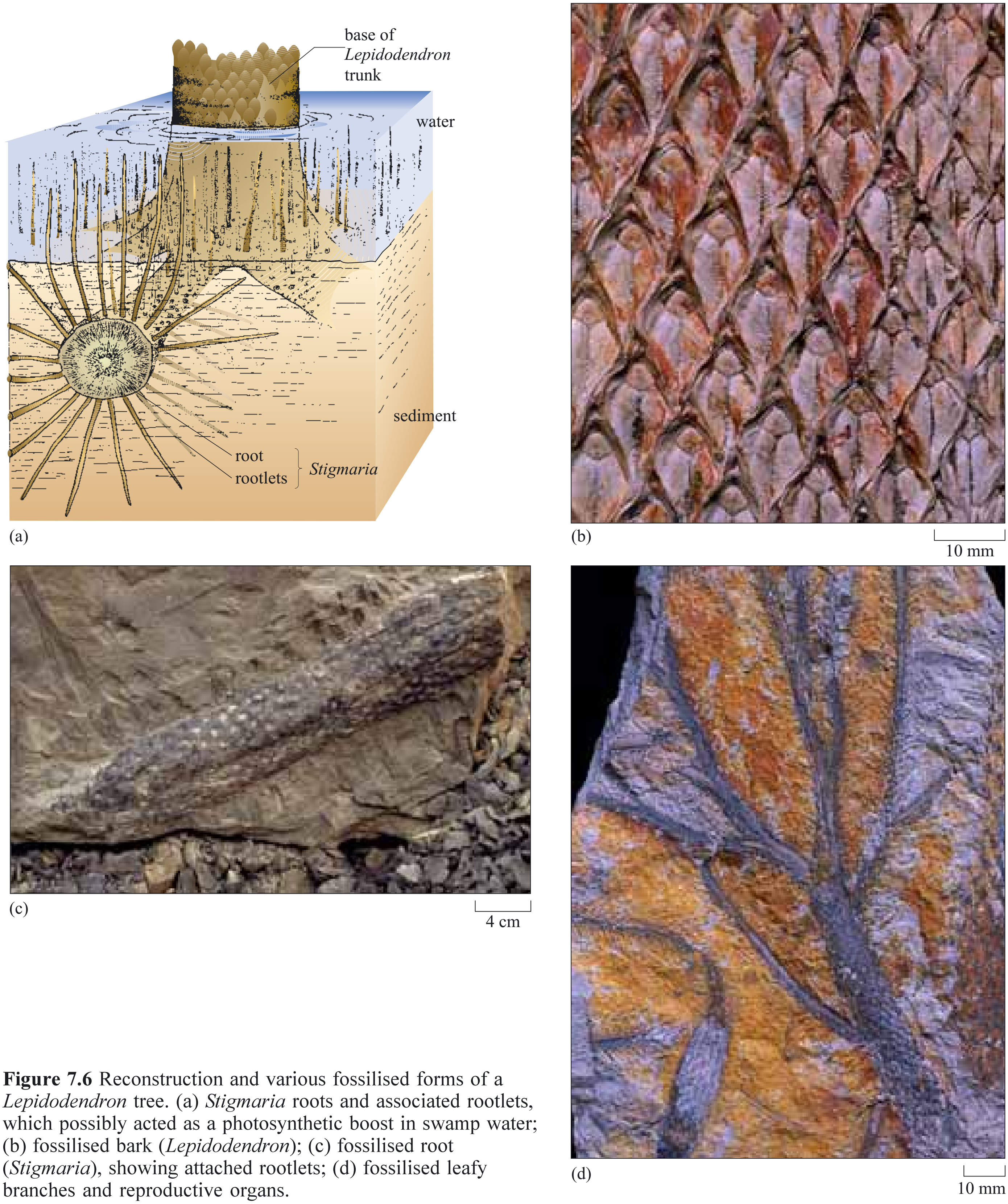


Figure 7.6 Reconstruction and various fossilised forms of a *Lepidodendron* tree. (a) *Stigmaria* roots and associated rootlets, which possibly acted as a photosynthetic boost in swamp water; (b) fossilised bark (*Lepidodendron*); (c) fossilised root (*Stigmaria*), showing attached rootlets; (d) fossilised leafy branches and reproductive organs.

Near the base of the *Lepidodendron* trunk, the primary water-conducting tissue (**xylem**) was restricted to a cylinder only a few centimetres in diameter. Although there was not very much of it, the xylem must have been able to conduct water and nutrients from the roots up to the top of the tree. Compared with modern trees, *Lepidodendron* appears to have had no or extremely little **phloem** in its trunk. Phloem is the vascular tissue that enables movement of the products of leaf photosynthesis (such as sugars) to the rest of the plant, including the roots. So how did the root system (and the rest of the tree) get its food?

The rooting structure of the *Lepidodendron* tree (their fossils are known as *Stigmaria*) terminated in numerous finger-width hollow rootlets that were helically arranged on root branches (Figure 7.6a and c). In many respects, these projections appear to be more similar to leaves than roots, but leaves that have been modified for anchorage. Furthermore, as the root systems were shallow, some of them could have been exposed to sunlight filtering through water in the swamp. As the three vital ingredients for photosynthesis (H_2O, CO_2 and energy) would have been available in the shallow swamp waters, it is possible that the roots and leaves photosynthesised and nourished the plant independently.

7.3.3 The legacy of the forests

Plants like *Lepidodendron*, which were superbly adapted to and dominant in low-latitude swamp environments, were important because they enhanced CO_2 drawdown from the atmosphere. So why did they become extinct?

Although these lycophytes are only remotely related to seed plants, they had developed a reproductive structure similar to a seed. Indeed, differences between a lycophyte reproductive structure and a ‘true’ seed are largely technical. Referring back to the advantages mentioned earlier of seed plants and their ability to survive and even thrive in drier habitats, suggests that the lycophytes should have been able to adapt to a changing environment as the swamps dried up and the climate changed. As discussed above, the *Lepidodendron* had highly specialised rooting organs that spread out in shallow sediments and were well adapted to support a tree living in waterlogged habitats. The overly specialised adaptations of their underground organs were therefore the most likely cause of their extinction, rather than the failure of their reproductive systems. There are probably two reasons for this: growth in drier and firmer soils would seem to have been very difficult, if not impossible, for the shallow-rooted *Stigmaria* with its presumably delicate rootlet apices; and, by being buried, the rootlets would have lost the energy (sunlight) needed to nourish themselves. Thus, with the demise of lycophytes such as *Lepidodendron*, the way became open for the remaining seed plants to dominate and diversify. Some of these early seed plants developed leaves adapted to life in dry environments and became dominant elements of lowland European and North American vegetation in the early Permian. As can be seen in Figure 7.7, a number of these already existed in the late Carboniferous, but were marginalised in drier habitats on the fringes of the wetlands; once the lycophytes died out, they seized upon the opportunity to spread across the low-latitude areas of Europe and North America.

It should be stressed that these changes in low-latitude vegetation and climate did not all occur at the same time on a global scale. Further east, in Asia, broad-scale patterns of vegetation and climate remained similar from the Carboniferous until

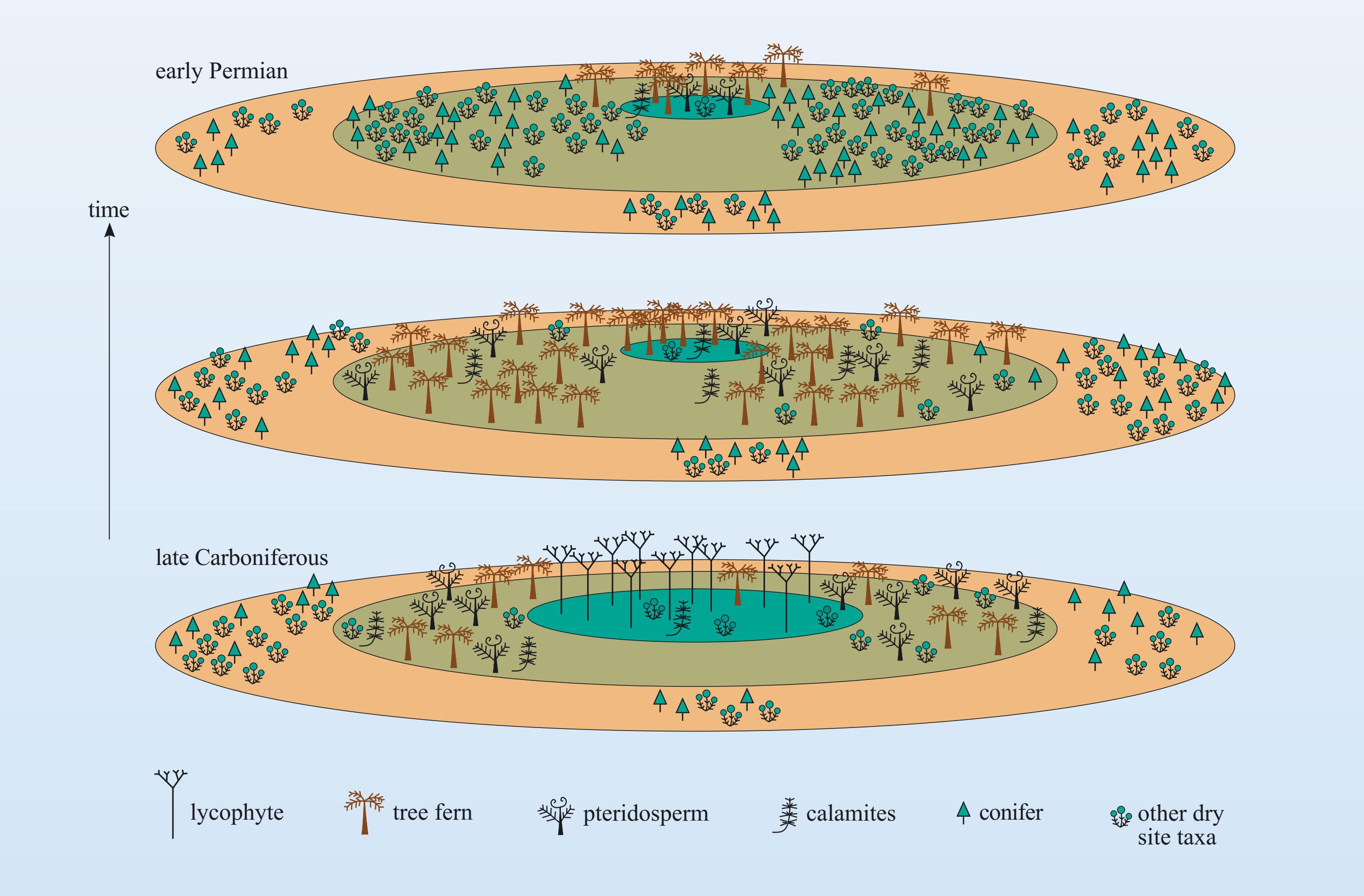


Figure 7.7 Late Carboniferous–early Permian change in equatorial, European/North American plant communities. The dominant lycophytes of the late Carboniferous gave way to previously marginal plants (e.g. conifers) adapted to drier habitats. The inner circle represents the wettest environments, the middle band represents the non-swamp habitats that were progressively affected by seasonal dryness into the Permian, and the outer band represents the uplands that were rarely wet. (DeMichele and Aronson, 1992)

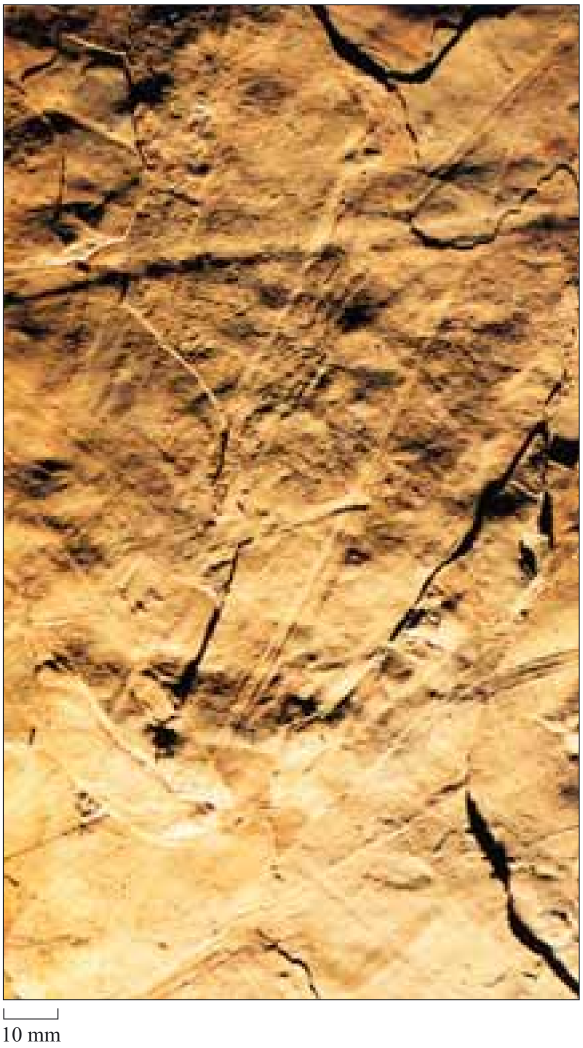
the end of the Permian, when conditions finally became more arid and – in contrast to Europe and North America – China, Australia and South Africa have major Permian coal reserves.

Elsewhere, extensive forests had developed in high southern latitudes during the early Permian. These were dominated mainly by the **glossopterids** (deciduous trees with distinctive tongue-shaped leaves). These leaves formed great fossilised mats where they were shed and buried annually in the swamps (Figure 7.8). Glossopterids have a particular historical claim to fame in that they played a major role in the original reconstruction of Pangea by Alfred Wegener, the German geologist who proposed the theory of continental drift, early in the 20th century. He noted that they were found in several areas across the present southern continents and so used them to help show the assembly of those continents in the past. The vegetation must have been abundant, since the dead remains accumulated as thick peat deposits (providing commercially mined coal reserves in Australia, for instance). From earlier discussions about the extensive southern ice sheets, it may therefore seem strange that such thick peat deposits should have accumulated shortly after the ice retreated from this area. In contrast to the warm, humid conditions at low latitudes in the icehouse world, these peats formed in cool, swampy bogs at high latitudes in the newly developing greenhouse world. (Section 7.5 will return to the question of how such productivity could have occurred at high latitudes by examining similar forests that grew some 100 Ma later in the even more extreme greenhouse world of the Cretaceous.)

7.4 A synthesis for the icehouse

Intense glacial conditions typified the late Carboniferous and early Permian, but why did they occur and persist? The role of plants seems to have been crucial. The timing of the maximum spread of Carboniferous coal-forming swamps coincided with minimum estimated CO_2 levels and maximum glaciation. The impact of land plants, however, was inextricably linked with other factors. For example, the relative reduction of mid-ocean ridge systems may have resulted in a sea-level fall, providing extensive lowlands for the coal-forming swamps. Moreover, the reduced volcanic activity may have produced less CO_2 to counteract the effects of the biotic sequestering and the accumulation of polar ice might itself have ensured further falls in global sea level, resulting in yet more exposure of continental shelf area. In addition, movement of part of the land mass over the South Pole may also have played a role in the observed cooling. Finally, the formation of Pangea itself as a result of major collisional processes, causing continental uplift, would have subsequently increased weathering rates. The copious sediment shed from these mountains would also have contributed to the preservation of coal by continually burying the swamp peats in vast delta systems. Together, these factors established a sustained net drain on atmospheric CO_2, so reducing temperatures and maintaining icehouse conditions.

These conditions were followed by deglaciation towards the end of the early Permian, resulting in only a few small ice caps remaining on the highlands of southern Africa. Cool, humid conditions prevailed over the rest of the southern part of the land mass, enabling the growth of glossopterids and the formation of high-latitude coal deposits. There was a subsequent loss of even these remaining ice caps, with the further development of globally warm conditions in the late Permian. The movement of Pangea away from the South Pole, so as to straddle the Equator in the Triassic, may have given rise to the development of an extremely strong monsoonal system, with pressure systems and precipitation zones swinging seasonally from hemisphere to hemisphere. Warming would have been enhanced by exposure and oxidation of some of the organic carbon sequestered during the late Carboniferous and early Permian. Indeed, the loss of most coal-swamp vegetation may have provided another positive feedback to the warming, since there would have been less capacity for CO_2 removal from the atmosphere. It seems that tectonically driven influences on climate now overwhelmed any cooling and related change due to CO_2 reduction by biotic sequestering. The result was a greenhouse world that lasted for some 250 Ma. Some of the factors that allowed for the development of a greenhouse world during the Cretaceous will form the focus of attention in the next section.



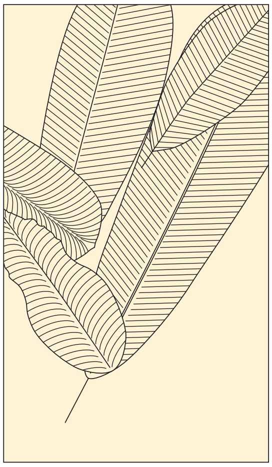


Figure 7.8 Numerous *Glossopteris* leaves preserved in layers of fine-grained sediment. The positions of the leaves are shown in the key.

7.5 The Cretaceous greenhouse world

Figure 7.9 shows the palaeogeographic arrangement of continents for the mid-Cretaceous, along with the distribution of some climatically sensitive deposits. The widespread occurrence of coals at high palaeolatitudes (>60°) demonstrates that temperatures were high enough there for plant life to flourish and that large volumes of glacial ice (prevalent during the early Permian) were now absent. At low palaeolatitudes (<30°), the extent of evaporites (especially in the Northern Hemisphere) shows that large areas were predominantly arid, with evaporation exceeding precipitation. Contrast this with the extensive tropical rainforests of today in the Amazon Basin, Africa and South-East Asia. Although some coals (a sign of active plant growth and, therefore, water) formed at mid- to low palaeolatitudes (<60°) in the Cretaceous, they did so on a limited scale and only close to ocean margins.

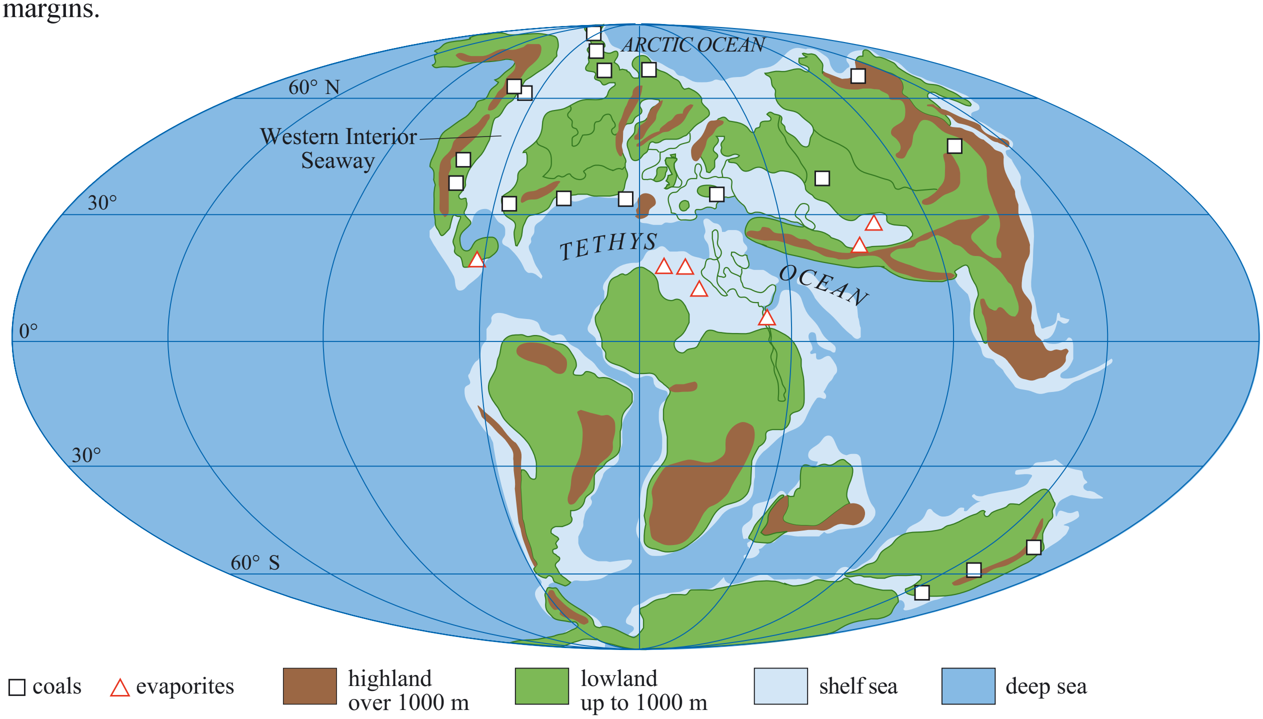


Figure 7.9 Mid-Cretaceous palaeogeography (around 95 Ma) and climatically sensitive deposits. (Parrish et al., 1982)

Another noticeable feature of the map is that the individual land masses are smaller in extent than those of today: there are no corresponding areas of land as large as the modern Eurasia or North America, for example. The reason for this is twofold: firstly, referring back to the map showing the latest Permian palaeogeography (Figure 7.1b) reveals that the Cretaceous world was a product of the rifting apart of the large supercontinent Pangea; secondly, Cretaceous sea levels were, at times, a few hundred metres higher than at present, so that large areas of the continents were covered by shallow seas.

Question 7.4

From what you now know about the differences between the Cretaceous Earth and the Permo-Carboniferous icehouse Earth, suggest two reasons why sea levels should have been relatively higher in the Cretaceous.

One of these shallow continental interior seas formed during the Cretaceous was the Western Interior Seaway in North America, which at various times during the Cretaceous connected the Tethys Ocean with the Arctic Ocean. These shallow seas were important to the world climate in that:

- they were a source of moisture in what would otherwise have been dry land areas
- they warmed and cooled more slowly than the surrounding land (because of the high heat capacity of water) and, therefore, affected heat distribution
- they acted as conduits for heat as water currents flowed from one ocean to another.

7.6 Polar climate

7.6.1 The case of Alaska

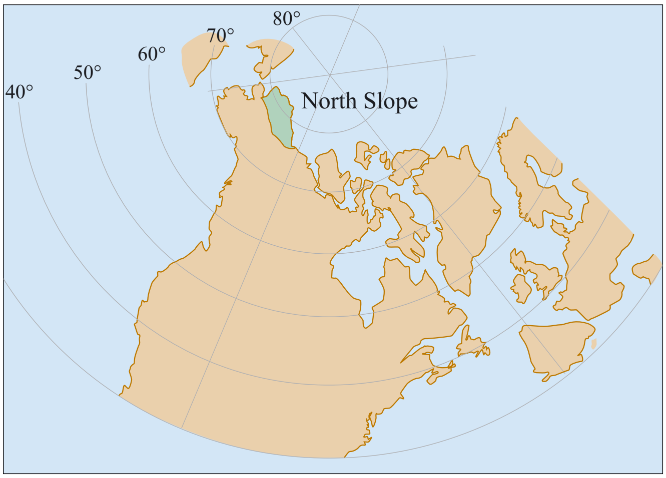


Figure 7.10 Mid-Cretaceous position of Alaska.

Climate change is most strongly expressed at the poles so, for this reason, it is appropriate to begin to look at the greenhouse world of the Cretaceous by studying the evidence for its polar climates, looking in particular at the High Arctic.

One of the best known Cretaceous sedimentary sequences in the Arctic is that of northern Alaska. Today, the northernmost point in Alaska is Point Barrow (71.23° N); Figure 7.10 indicates the position of northern Alaska (the North Slope) during the mid-Cretaceous.

The obliquity of the Earth is measured as the departure of the axis of rotation from the vertical, where the 'vertical' is defined as being perpendicular to the Earth's orbital plane around the Sun. At the latitude of Point Barrow today, continuous winter darkness (i.e. darkness longer than 24 h) does not occur, but there are about 2 months of twilight. For a period of almost 4 months the period of light during the day changes; during the summer there is a period of about 2.5 months with continual light.

The Cretaceous rocks found in Northern Alaska are extremely rich in coal. In fact, current estimates suggest that there are 2.75×10^{12} tonnes of coal lying under northern Alaska, which represents about one-third of the total US coal reserves of all ages combined (including those of the Carboniferous). By any measure, this near-polar environment was an extremely effective long-term carbon sequestering and storage system during the Cretaceous.

Observation of tree stumps preserved in life-position rooted in fossil soils indicates that the coal-forming vegetation during this time was in the form of forests rather than tundra. Their existence poses two questions: first, why was this forest ecosystem so effective at capturing carbon; and second, how was the carbon so effectively buried?

It is easier to answer the second question first. Rocks of mid- to late Cretaceous age were laid down in northern Alaska as a series of deltaic sediments that built out northwards into a trough to the north of the newly uplifted Brooks Range Mountains. Though the details are unresolved, the mountain range appears to have been generated by local plate collision. Uplift was most rapid during the last part of the early Cretaceous, but continued through into the late Cretaceous. Erosion of these mountains during the mid- to late Cretaceous supplied the deltaic sediments.

Plants colonised the delta floodplains skirting the mountains and, as the sediments containing the organic matter subsided (due to weighting and gravity), more sediments were deposited on top of them and more forests grew. Such a process, typical of many long-lived deltas, provided an ideal setting not only for the preservation of fossils, but also for burying peat.

7.6.2 The Arctic forests

There are peats forming in northern Alaska today, but there are no forests. Since northern Alaska was further north of its present position in the Cretaceous, the conclusion is that climatic conditions were not the same in the Cretaceous as they are now. Conditions must have been more favourable in the Cretaceous to have allowed the growth of forests at these latitudes – but did they grow?

■ What alternative explanation might there be for Cretaceous polar forests if climate conditions then were the same as now?

■ The tolerances of plants might have changed. For example, the plants might have had a different biochemistry that allowed enzymes to function more efficiently at lower temperatures.

This is unlikely, however, because it would be expected that plants with such specialised adaptations would have survived subsequently, particularly during the Quaternary glacial events, and still to be in evidence today. The fact that such plants are not present, particularly in today's cool climate, suggests they never existed.

So, if conditions (rather than the fundamental requirements for plant growth) were different, how can these conditions be deduced? To do this, it is necessary to examine the rocks and try to decode the information they contain; not only must the fossils be examined, but also the sedimentary context in which they are found.

Plant fossils have been known from the Arctic for a very long time. Some finds of apparently warmth-loving plants at high latitudes can be eliminated from further consideration because they are found on tectonic plates that were at lower latitudes when the plants were alive, but which subsequently drifted to their near-polar settings of today. This still leaves the problem of northern Alaska, the palaeolatitude of which during the Cretaceous is well constrained (to within 5°). A wealth of fossils can be found there, but the fact that they represent trees is incompatible with present conditions at the latitudes where they grew.

7.6.3 The cycad conundrum

Among the more problematical finds in North Alaska are those that are thought to be fossil **cycads**. These plants, which only occur today at low latitudes where frosts are absent or infrequent, are represented most commonly in the Cretaceous fossil record of Alaska by the leaf form, *Nilssonia* (Figure 7.11).

Figure 7.11 *Nilssonia* frond.

Modern cycads typically have the appearance of a squat palm tree: they have a trunk composed mostly of tissue rather like that in an apple or potato and very little wood. At the top of the trunk is a crown of leathery evergreen fronds. The sensitivity of the modern cycad to frost and its evergreen characteristics have posed severe problems for interpreting Arctic palaeoclimates. For a start, if the biology of Cretaceous cycads was the same as that of the modern cycads, then the polar regions must have been much warmer than today. It is difficult to see how such conditions could have been sustained with long periods of winter darkness.

Even more problematic, however, is the fact that modern cycads retain their leaves all the year round: they are evergreen. In addition to photosynthesising, plants must respire to release the energy stored in their food reserves. The rate at which metabolic processes (including respiration) proceeds increases with temperature. The optimum temperature range varies with the type of plant, but in general most species function best between 5 °C and about 40 °C. Below 5 °C, metabolic rates of all living things are very slow, whereas above 40 °C some processes are inhibited or prevented as enzymes are damaged. Thus, the balance of photosynthesis and respiration is both light dependent and temperature dependent. In climates where temperatures never (or only very rarely) drop to near freezing, respiration rates are relatively high. In cold climates, especially in winter, respiration rates are very low, so respiration in the leaves does not use up much food. Plants in cold, dark situations, such as experienced today during winters at high latitudes, can survive even though the darkness prevents the production of food by photosynthesis. This is because they do not exhaust their food store by having a low rate of respiration.

Assuming that in the late Cretaceous the Earth's obliquity was the same as at present (Section 7.6.1), and given that the palaeolatitude of the centre of the North Slope was approximately 80° N, it follows that the *Nilssonia* plants would have experienced continuous winter darkness for some three months, and that in the spring and autumn there would have been a period of two weeks of twilight. If the *Nilssonia* plants were indeed evergreen, then maintaining the leaves through a long, dark but relatively warm winter would have caused an intolerably high respiratory drain on the plant, particularly for young plants and seedlings.

It is not surprising that some scientists have suggested that if the Arctic cycads were evergreen, then they must have received winter light. This would enable them to manufacture food to replace some or all of that consumed by leaf respiration. To achieve this more even distribution of light all the year round at the poles, the obliquity of the Earth would have had to have been considerably less than the present 23.4°, with obliquity possibly as low as 5°. This reduction is, of course, outside the range produced by the Earth's regular orbital variations and would have required a special mechanism to have produced this change.

Are there any additional factors that need to be taken into account before becoming concerned about the apparent anomaly of evergreen plants growing in northern Alaska in the Cretaceous? One factor that has been overlooked so far is the question of whether we can be sure that the palaeomagnetic pole used to determine the palaeolatitudinal positions of the continental plates was the same, or nearly the same, as the Earth's rotational pole. It is the position and inclination of the rotational pole or axis that determines the light regime. To answer this question, the symmetry of distribution of climatically sensitive deposits can be examined. These sediments should be symmetrical about the rotational pole because the rotation of the Earth controls atmospheric dynamics and, therefore, climate. If the position of the sediment-determined rotational pole agrees with that determined palaeomagnetically, then it can be assumed that the rotational and magnetic poles were essentially the same.

In the latest Cretaceous, when northern Alaska was at palaeomagnetic 85° N, the rotational pole appears to have been within 4° of the palaeomagnetic pole, i.e. less than the expected error for palaeomagnetic positioning. It may be concluded, therefore, that the rotational and magnetic poles were effectively the same at that time, and that the palaeomagnetically determined palaeolatitude can be assumed to have been more or less the same as the true palaeolatitude in relation to the rotational pole. Therefore, it has to be presumed that these cycads did indeed experience prolonged winter darkness.

So, has the biology of these plants been correctly interpreted? Modern cycads exhibit what is known as a relict distribution, i.e. they are restricted to relatively few sites that are geographically isolated, with individual genera occurring at several of these separated sites. The more widespread distribution and greater taxonomic diversity of cycads in the Mesozoic implies that their present distribution must represent merely a relict of the former dominance of the group as a whole. This poses two questions:

1. Were the environmental conditions that suit cycads more widespread in the Mesozoic (i.e. was global climate more uniformly warm)?
2. Have the remaining relict forms adapted to a narrower range of conditions than that tolerated by Cretaceous forms?

To answer these questions, it is necessary to go back to the fossils and examine them without being prejudiced by the biology of the modern relicts. In 1975, two Japanese palaeobotanists, Tatsuaki Kimura and Shinji Sekido, described a Cretaceous cycad quite unlike any that are alive today; they called this plant *Nilssoniocladus* because it bore *Nilssonia* leaves branching from side shoots (Figure 7.12). It is this unique cycad that is found across North Alaska in the Cretaceous.

Unlike typical modern cycads, which have a squat, palm-like appearance with a thick trunk, *Nilssoniocladus* had a thin vine-like stem. Arranged along this stem were side shoots that bore numerous scars where leaves had been attached. This observation suggests that *Nilssoniocladus* was a

Figure 7.12 A reconstruction of part of the *Nilssoniocladus* plant that grew throughout the mid- and late Cretaceous of the Arctic. The fronds are about 20 cm long.

deciduous cycad (i.e. one that shed its leaves seasonally throughout its life). Moreover, the plant apparently not only shed its leaves seasonally, but did so in a synchronous fashion (i.e. leaves were shed at the same time, leaving the plant devoid of all leaves for significant periods in its life). Evidence for this comes from the observation that *Nilssonia* leaves are often found as leaf mats and that individual leaves have not simply broken off the main plant, but have distinct bases that are specialised for leaf separation. Moreover, the leaves are usually found intact and therefore must have been shed intact, without damage or rotting. Leaves of different sizes are also found on single bedding planes, indicating that they all fell off the plant at the same time. As a result of this powerful evidence that *Nilssoniocladus* was deciduous, it can now be inferred that it was the biology of the Cretaceous cycads that was different and that modern cycads do indeed represent a relict subset of a group that previously had a wider range of environmental tolerances.

Notice here that a combination of sedimentological evidence, observations on leaf characteristics (size, shape and whether they display signs of decay) and shoot architecture is being used. The study of sedimentological and biological evidence relating to explanations of fossilisation phenomena is known as **taphonomy** (from the Greek *taphos*, a tomb) and is of critical importance in palaeoenvironmental research.

7.6.4 A new perspective

What are the implications of this new understanding of Mesozoic cycads? Firstly, it is dangerous to extrapolate uncritically the biology and climatic tolerances of modern plants back in time. Secondly, if the cycads were deciduous, then the paradox caused by winter darkness ceases to be a problem (at least for the cycads), but was such a deciduous nature a general characteristic of Cretaceous vegetation of northern Alaska?

Similar evidence for deciduous features has been found in many other plant groups. For example, the angiosperms first appear in the middle part of the Cretaceous and have large leaves that look very much like those of modern plane trees (Figure 7.13). These are informally termed platanoid leaves and are typical of deciduous angiosperms: they tend to be simply constructed, in that they have a thin texture. This contrasts with longer lived, thicker leaves produced by evergreens, such as rhododendron or holly. Moreover, platanoid leaves have relatively thin cuticles because they do not have to limit water loss during the winter, when the root zone might be frozen. They also have an expanded base to their stalk, which is a feature of seasonally shed leaves.

Many platanoid leaves are large, being more than 10 cm in breadth; the size range is also large – varying from small to large. In spite of their large size and the coarseness of the sediment, these fossil leaves are invariably complete within the rock. As with the interpretation of leaf mats, this strongly suggests that they were shed intact and were all buried together before any of them had had time to decay.

Figure 7.13 Cretaceous leaf in sandstone (×0.5).

So far, representatives of angiosperms and cycads have been considered, but these groups represent only a small fraction of the polar land vegetation. The most ubiquitous plants appear to have been deciduous conifers similar to modern redwoods, together with ginkgos, or 'maidenhair' trees.

The options of 'deciduousness' or 'evergreenness' are restricted to long-lived woody taxa; herbaceous plants do not normally shed their leaves. What did the herbaceous plants do during the winter darkness?

Much depends on whether the plants were annuals or perennials. Annuals grow from seed each year, reproduce and then die in the autumn; overwintering is therefore in the form of seeds. Perennial herbaceous plants adopt a different strategy: they die back to basal food storage organs such as rhizomes (a modern example is the iris), corms (e.g. crocus) or bulbs (e.g. tulips and onions). In the Cretaceous, there is no evidence for corms or bulbs, but many ground-cover plants had rhizomes, as evidenced by the remnants of rhizomes found in fossil soils. Many are characteristic of modern *Equisetum* (horsetails or scouring rushes), and are assigned to the fossil form *Equisetites*, whereas others represent ferns. In some instances, it is evident that ferns formed the ground cover because they are found preserved in situ, buried beneath volcanic ash-falls overlying fossil soils. In the winter, the above-ground parts of *Equisetites* and associated ferns, which formed two main ground-cover plants, would have died back to their rhizomes and become dormant (fossil evidence suggests that grasslands had not yet evolved).

Fossil evidence shows that the near-polar forests also supported a diverse fauna, including large herds of plant-eating dinosaurs, including the duck-billed *Edmontosaurus* and the horned ceratopsians, which were preyed upon by meat-eating dinosaurs such as *Tyrannosaurus*.

Wildfires were also common in the polar forests (as evidenced by abundant fossil charcoal) and must have released some plant carbon back into the atmosphere as CO_2, while yet more would have been oxidised through bacterial action, or converted into methane under reducing conditions in boggy areas. Other remnants of the vegetation would have been transported as partly rotted microscopic particles into sediments, where they have survived as particulate material or as organic molecules.

From the kinds of evidence discussed above, it is possible to build up a picture of the northern Alaskan Cretaceous forests as one consisting of plants that were either deciduous or died back to underground organs during the winter months. As such, there is no need to postulate year-round light, or day–night cycles.

There is further direct evidence that the polar light regime was like that of today. In addition to fossil leaves, the Cretaceous sediments of northern Alaska yield abundant fossil wood that has well-preserved internal structures. At some sites in northern Alaska, tree stumps are found rooted in fossil soils, indicating that trees did indeed grow under near-polar conditions. When sections of the fossil logs are studied under the microscope, fine preservation of the structure, down to the subcellular level, may often be seen. Interpretation of these preserved structures, however, is not straightforward, as a given pattern of ring features may be the result of genetic factors rather than environmental constraints. If a number of different taxa display the same pattern, it is probable that this pattern was environmentally produced, either through direct influence on growth or through selection for certain genetically produced characteristics that confer specific advantages in the prevailing environmental regime.

The pattern observed in many of the northern Alaskan woods of mid-Cretaceous age is distinctive. The earlywood produced in the spring is clearly visible as xylem cells with large internal cavities through which water flowed. The cell walls of the earlywood cells are thin. The latewood cells have thicker walls and smaller cavities, forming the dark bands in the wood. The uniformity of the mid-Cretaceous earlywood shows that growth conditions varied little throughout the growing season. This principally means that drought (or waterlogging) and chill rarely occurred. It also means that other events that could diminish growth, such as severe insect attack, were also of no great consequence. Towards the end of the Cretaceous, however, environmental conditions changed markedly.

Growth rings found in some fossils show interruptions during the summer growing season. These interruptions can be caused by any factor that reduces the tree's photosynthetic activity. For example, they might be caused by: sudden cold snaps that depress the rate of photosynthesis; by drought, which causes the stomata to close as a water conservation measure, thereby stopping the supply of CO_2 to the photosynthetic process; or by trauma, such as massive insect damage. Such rings are called **false rings** and are a measure of environmental variations that exceed the tolerance of that particular plant. Many of the latest Cretaceous woods are characterised by such frequent false rings. Often, false rings and true (annual) rings are difficult to differentiate, and this in turn makes measuring ring thicknesses difficult. In general these later trees have narrower rings, but because the amount of latewood is about the same as that in the mid-Cretaceous specimens, the ratio of earlywood to latewood diminishes. This implies that growth conditions throughout the latest Cretaceous summer were less temperate than those in the mid-Cretaceous.

Simultaneous examination of the sediments associated with different late Cretaceous fossils reveals that drought indicators, including preserved mud cracks, are lacking, although the frequency of charcoal in the latest Cretaceous sediments is higher than in the earlier beds, implying that vegetation was drier and so more predisposed to combustion. In the absence of direct evidence for insect damage (e.g. chewed leaves or borings in the wood), the most likely explanation for the variation in summer growth of late Cretaceous vegetation was temperature fluctuation: there were periodic cold snaps. This might imply that the average summer temperatures were lower in the latest Cretaceous, such that temporary falls in temperature from the lower average value were sufficiently cold to limit photosynthetic activity.

7.6.5 Taking stock

Using qualitative sedimentological and palaeobotanical evidence only, the following points have been established:

1. The obliquity of the Earth's rotational axis was essentially the same in the late Cretaceous as it is now.
2. The rotational pole was essentially in the same location as the magnetic pole.
3. The polar light regime was similar to that of today.

4 The Arctic climate supported forests up to at least 85° N.

5 The overall polar climate must have been warmer than now.

6 There was sufficient rainfall to support abundant plant growth.

7 The vegetation must have dried sufficiently to burn from time to time.

8 The Arctic forests were deciduous.

9 Some plants had substantially different climatic adaptations when compared with their modern relatives.

By now, quite a detailed picture of the Cretaceous Arctic has been established. There is substantial evidence to show that in many respects, the high southern latitude (Antarctic) vegetation and climate mirrored that of the Arctic.

7.7 Low-latitude vegetation and climate

7.7.1 Water supply

This section investigates the other end of the Equator-to-Pole temperature gradient that powers the climate system: the low latitudes. Returning to Figure 7.9 for a moment, you may recall that one feature of the Cretaceous low latitudes was the extensive area of arid climates characterised by evaporites. To form, evaporites need a high evaporation rate, as well as a supply of water carrying dissolved minerals, so that continued salt precipitation takes place. The presence of evaporites over large continental areas, therefore, implies that those areas were not constantly dry but must have had some water supply on a frequent basis. If this were so, then some evidence for vegetation might be expected. Fortunately, this is exactly what is seen, and, as before, the plants tell a great deal about the environment.

In Cretaceous sediments deposited between palaeolatitudes 40° N and 40° S, it is common to find large quantities of the fossil pollen type *Classopollis*. This is a very easily recognised pollen form that is known to have been produced by a family of extinct conifers known as the Cheirolepidiaceae (Figure 7.14). The pollen is found in the cones of these plants, for which fossils of both foliage and wood have also been identified. Examples of cheirolepidiaceous foliage and wood can be found in many early Cretaceous sediments in southern England (which was then at ~36° N), with the sediments deposited at the margins of a seaway that connected with the Tethys Ocean. For example, on the Isle of Portland, tree stumps, logs, foliage and pollen are found associated with sediments of earliest Cretaceous age containing **halite** (salt) **pseudomorphs**. This and other evidence suggests the plants grew under considerable evaporative stress, where rainfall was, at best, highly seasonal. There is also a strong seasonal signal in the growth rings of the wood.

The Cheirolepidiaceae were not the only plants adapted to this harsh environment. There were also some ferns with very thick cuticles and specialised stomata, designed to combat water loss. Additionally, parts of the fern fronds are often found as charred remains, indicating the vegetation was frequently burnt and must, therefore, have been dry for this to happen.

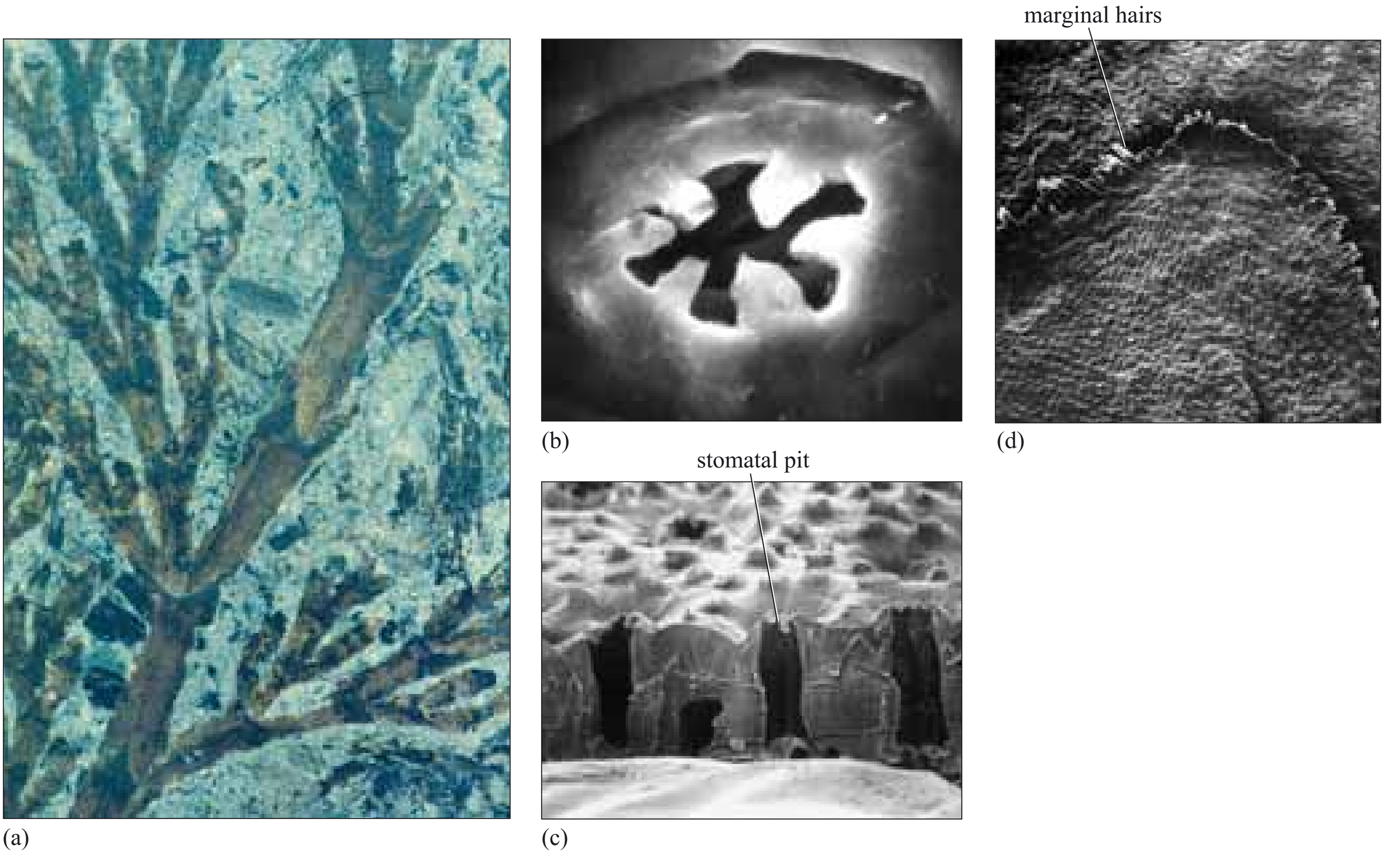


Figure 7.14 (a) *Frenelopsis ramosissima* shoot showing the typical segmented structure seen in many members of the extinct Cheirolepidiaceae (×13). (b) Scanning electron micrograph of a single stoma of *Pseudofrenelopsis* (×2600). (c) Vertical section through the cuticle of *Pseudofrenelopsis* showing the deep stomatal pits (×310). (d) Leaf of *Pseudofrenelopsis* showing marginal hairs behind which is the groove at the junction with the next shoot segment (×80).

7.7.2 Qualitative and quantitative inferences

The low-latitude plants around the margin of the Tethys Ocean and Tethyan margin plants were architecturally very different from those growing in the polar regions, and these differences reveal a great deal about the varying climates of those regions, and in particular the temperature, evaporative stress and frequency of rainfall. It is also possible to determine that the main sites of land-based plant productivity were at high and not low latitudes, and that the equivalent of today's tropical rainforests did not exist to any great extent during the Cretaceous. These observations are of critical importance in understanding what might happen to the future climate in general, and agriculture in particular, should the Earth return to its warm (greenhouse) conditions. Even more can be discerned when these observations are combined with those of sediments; however, as all of this information is qualitative, it is not possible to quantify what the exact temperature was, nor how much rainfall there was. Alternative methods of obtaining quantitative palaeoclimate data are therefore required.

7.8 Climate reconstructions

7.8.1 Plants as thermometers

So far in this chapter, the evidence that suggests the late Cretaceous polar light regime was more or less as it is now, has been reviewed. Apart from deducing that the overall temperature regime was warmer than now, although not necessarily very warm as some frosts were likely, it has not been possible to quantify the temperature regime so far. This section will consider some of the ways in which atmospheric Cretaceous polar temperatures can be determined using techniques that can be applied anywhere that suitable plant fossils are preserved.

To commence, it will be assumed that the range of temperature within which growth could have occurred is much the same as it is today, i.e. somewhere between 5 °C and 40 °C. This is a rather large temperature range and is little help in trying to understand the dynamics of polar (and global) climate. As such, some additional criteria must be considered. In relation to this, palaeobotanists have long recognised that land plants are excellent climate indicators, and, broadly speaking, two approaches are commonly adopted:

- nearest living relative technique
- physiognomy.

7.8.2 The problem with relatives

The first technique is based on the climatic tolerances of nearest living relatives (NLRs) and is known as the **NLR technique**. This assumes that ancient plants and plant communities lived under similar conditions to those of their nearest living relatives. The success of the technique, which is widely used in Quaternary studies, depends on the correct identification of the fossil and, of course, limited evolutionary change. Where the fossils are in the form of reproductive structures, such as pollen or seeds, NLR techniques are particularly useful because the taxonomy of living plants is based mostly on their reproductive characteristics; correct identification, however, is less difficult than it is when working with vegetative organs, such as leaves. For *pre-Quaternary* fossils that may represent extinct taxa with very different environmental tolerances to their living relatives, and for vegetation for which there are no living counterparts, such as the greenhouse polar forests, a different approach has to be adopted. As such, the NLR technique is not suitable to investigate Cretaceous flora as climate indicators.

7.8.3 Following form

The second method for using plants as climate indicators is based on the architecture, or **physiognomy**, of the plant or community, and is applied when the fossils are in the form of vegetative organs, particularly leaves. As plants cannot move around once they have taken root, they must be well adapted to their local environment or they will die, either because an environmental tolerance is exceeded or because they are outcompeted by better-adapted plants. Either way, there is a selective premium on being as efficient as possible in the local circumstances with respect to water conservation, gas exchange and light interception. In the course of evolution, most plants have become honed for successful exploitation of particular environmental niches, and many display specially adapted physiognomies. One extreme example is seen in desert plants, which have a low surface area to volume ratio so as to conserve water, low leaf-area indices and thick cuticles.

■ List some examples of plants adapted to desert environment.

■ Cacti and their 'Old World' counterparts, euphorbias, are but two that illustrate these traits well.

Rainforests, by contrast, are characterised by plants with large leaf-area indices, forming a vertical succession of layers within the forest.

As a result of physiognomic adaptations to environment being so consistent, quantitative comparisons for determining pre-Quaternary climates can be made, within certain limits. One of the most successful applications of this approach was devised as long ago as 1915, when two American botanists, Bailey and Sinnott, noted that the leaves of modern woody broadleaved flowering plants (such as alder, willow and figs) tended to have smooth (entire) leaf margins in warm climates, but toothed, jagged, margins in cool climates (Figure 7.15). Jack Wolfe, another American palaeobotanist, developed this methodology further in the late 1970s and, by using modern species growing in drought-free environments in South-East Asia, plotted the mean annual temperature (Figure 7.16) against the percentage of species with entire margined leaves (see Figure 7.13).


(a) (b)

Figure 7.15 Leaf margin types. (a) A variety of tropical rainforest species all displaying smooth (entire) leaf margins. Some also show an extended leaf apex ('drip tip') for shedding water. Drip tips are characteristic of plants growing under very wet conditions. (b) A typical temperate tree bearing leaves with toothed margins.

This technique of **leaf margin analysis** can be applied to the Alaskan fossils. It is known that, in mid-Cretaceous time, northern Alaska rarely experienced drought because there are numerous thick coal seams; and, although charcoal is present, it is scarce. In addition, tree rings show that growth was uniform throughout the summers; therefore water was not limiting. The sediments have also yielded a large number of leaf fossils and so far 67 different species of woody broadleaf angiosperms have been distinguished, of which 22 species have entire leaf margins preserved. Referring to Figure 7.16, this indicates that the mean annual temperature of mid-Cretaceous northern Alaska was similar to that of the southern British Isles today. However, bearing in mind the polar light regime, it is likely that the mean annual *range* of temperature in the mid-Cretaceous was much greater.

A number of assumptions have been made using leaf margin analysis in this instance. First, there is an assumption that there is no change in slope of the graph (Figure 7.16) over time, i.e. that the slope determined for the plants of today is applicable to the mid-Cretaceous, which was very early in angiosperm evolution. Secondly, there is an assumption that the relationship between margin characteristics and temperature was not affected in any way by the polar light regime. As there is no obvious break in Figure 7.16 in the slope of the relationship for modern-day plants above or below latitude 66° N (the likely position of the Arctic Circle then), it can be presumed that the polar light regime has little effect.

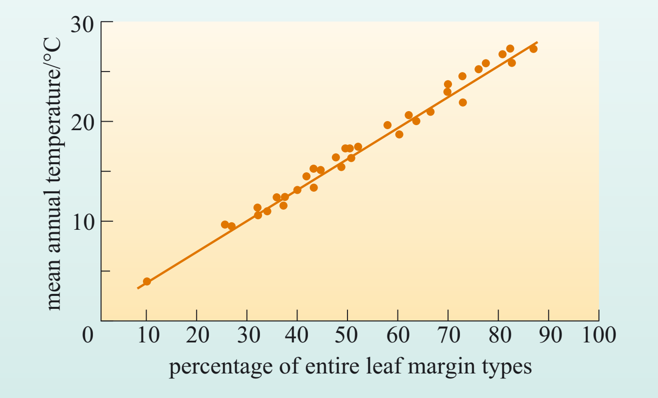


Figure 7.16 Plot of mean annual temperature against the percentage of entire leaf margin types. This graph was constructed using plants in drought-free environments in South-East Asia. (USGS Printing Office)

Physiognomic analysis can be applied to different vegetation types. Instead of relying on the response of one group of plants (the woody broadleaves) to climatic variables, all taxa, including gymnosperms, can be involved. This is an advantageous approach to use because when a broad spectrum of taxa is used, it is unlikely that they will all relate by chance to the climate in the same way, making this technique particularly robust.

A discussion of how ancient vegetation can be reconstructed accurately from dispersed fossilised remains is beyond the scope of this book, however it is suffice to say that a considerable amount of detective work is required to link leaves, wood, and reproductive structures into complete plants of known form, ecological setting, community association and abundance. This detective work combines detailed observation of plant form with occurrences in a wide range of sediments, in much the same way as that described earlier when examining the leaf-shedding habits of the plants of the polar forests.

Figure 7.17 depicts a reconstruction of the mid-Cretaceous forests of northern Alaska, predominantly composed of conifers. The most dominant plant was the deciduous conifer, which is related to the bald cypress and dawn redwood; however, other taxa such as river-margin angiosperms and ginkgos were also prevalent, with ferns and horsetails commonly forming ground-cover plants. The mid-Cretaceous vegetation was not a pure conifer forest then, but one mixed with other components of a broadleaved nature.

Figure 7.17 Reconstruction of northern Alaskan forests of the mid-Cretaceous.

7.9 Geographical framework

7.9.1 The marine environment

The previous sections concentrated largely upon the Cretaceous vegetation at high latitudes, as this reflected most strikingly the contrast with today's climate. In the marine realm, however, the main differences between then and now were most apparent in low to mid-latitudes associated with the Tethys Ocean, which separated the northern and southern continents (Figure 7.18), as well as in the equatorial Pacific.

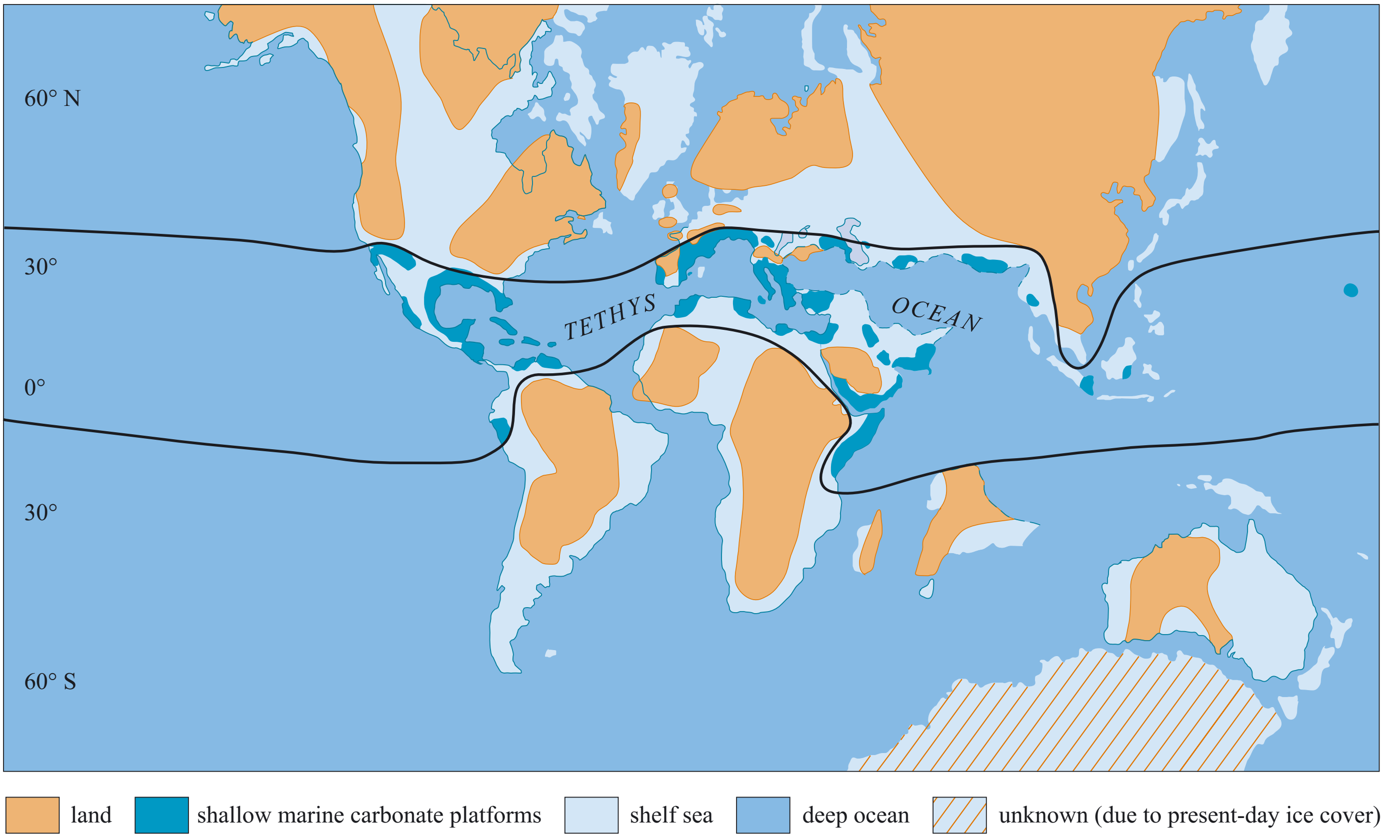


Figure 7.18 The geography of earlier Late Cretaceous, showing the zone of major carbonate platforms formed in and around the Tethys Ocean. The distribution of land and sea in Antarctica is not well known because of the present-day ice cover. (Sohl, 1987)

■ Study the palaeogeographic map in Figure 7.18, noting, in particular, those parts of the continents shown between the bold lines on the figure (i.e. between ~10° N and ~30° N). Which covered a relatively greater area – shallow sea or land?

□ Within this palaeolatitudinal belt (which included the Tethys Ocean), shallow sea covered by far the larger proportion of the area than was covered by continental crust. Indeed, some continental extensions from the North African margin are shown to have formed isolated broad shallow marine platforms, straddling the central part of the ocean.

Elsewhere, seaways spread across the continental interiors, a consequence of the exceptional rise in global sea level during the Cretaceous Period.

Geological evidence reveals that topographical relief in the land areas bordering the shallow shelf seas was generally subdued. The main zones of uplift generated by plate tectonic activity around the Tethys Ocean were limited to volcanic island arcs, associated with the subduction of oceanic crust. These lay predominantly along the northern Tethyan margin, where they formed chains of islands and submerged ridges similar to the Sunda Archipelago of South-East Asia today. One of the few mountain ranges that was present in the Cretaceous was situated away from the Tethys Ocean at higher latitudes in northern Alaska (the Brooks Range).

The climate along the Tethyan belt (i.e. the ocean and its surrounding areas) was predominantly arid, though some uplifted areas appear to have generated local monsoonal systems, with seasonal humidity.

Question 7.5

Taking into consideration the topography and climate of the lands bordering the Tethyan belt, what would you expect the dominant composition of the sediment accumulating in the shallow shelf seas to have been?

Limestone formed in this way is indeed the most characteristic sedimentary rock type left by the shallow seas around the Cretaceous Tethys. Vast tracts now form imposing mountains and plateaux, uplifted by subsequent tectonic activity, extending from Mexico to the Middle East, and on the Tethyan suture zone of the Himalaya into South-East Asia.

The Cretaceous world thus stood in marked contrast to that of the present day. Today's shelf seas in corresponding latitudes are narrower and mainly limited to the margins of continents. In many instances, mountain ranges have shed copious quantities of physically eroded land-derived sediments into them, with these sediments both inhibiting the growth of many carbonate-sediment-producing organisms (e.g. corals and calcareous algae) and swamping any shell debris that is produced. Such conditions reflect both today's relatively lower global sea level and the extensive mountain building that has occurred in low and mid-latitudes since the Cretaceous. Consequently, shallow tropical carbonate provinces are now much less widespread than those of the Cretaceous.

7.9.2 Tethyan carbonate platforms

Limestones are a crucial component of the carbon cycle and, hence, of the climate system. The limestones formed around the margins of the Cretaceous Tethys are, therefore, worth a closer look, first to see how they came to be so extensive and, secondly, in order to estimate their quantitative contribution to carbon burial during this period.

Characteristically, the Cretaceous Tethyan limestones accumulated so as to form broad, shallow, submarine plateaux, termed **carbonate platforms**, the outer margins of which sloped away into neighbouring basins. The depth of the basins varied greatly, according to tectonic setting (i.e. tectonic regime of a region), but within most areas of continental crust, it usually ranged from only some tens to a hundred or more metres.

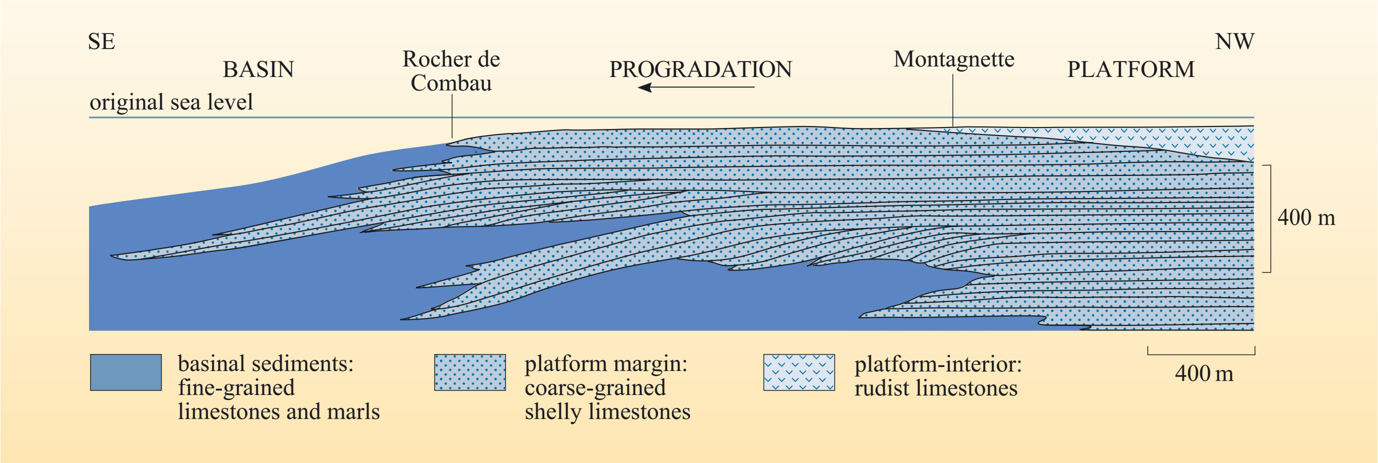


Figure 7.19 Diagrammatic section across the platform to basin transition of the Vercors Platform in eastern France, showing the geometry of the constituent beds.

In recent years, very detailed studies have been carried out on the geometry and constitution of the beds composing such platforms, with the aim of reconstructing how the platforms grew. Figure 7.19 is a vertical section across the edge of one such platform – the Vercors Platform in eastern France, dating from the early Cretaceous. The platform shows a pattern seen very frequently in Cretaceous Tethyan carbonate platforms: sets of inclined beds of relatively coarse sediments (mainly shell debris), derived from the top of the platform, project obliquely down like overlapping tongues into the finer sediments of the basin. This indicates that the platform margin gradually built out laterally into the basin (progradation), as the coarser sediment spilt down its flanks. The transport of material off the top of the platform was a consequence of more shell debris being produced than could be accommodated in the shallow waters covering the platform; in other words, there was an overproduction of sediment by the platform 'carbonate factory', which was swept off by waves, tides or storm currents onto its flanks. Between periods of progradation, occasional subsidence of the platform due to a rise in sea level allowed basinal sediments to build up the flanks again until progradation resumed. These **regressive** episodes yielded the thin wedges of finer material that separate the progradational tongues.

There was, inevitably, much variation on this basic depositional theme, as a result of differences in the rates of deepening (due either to subsidence or eustasy) and in the multitude of factors affecting sediment production and transport on the platforms. For example, where contemporaneous faulting at the platform margin accentuated the depth of the neighbouring basin, the sediment spilling off the platform had a larger space to fill, so marginal slopes became steeper and outward growth less marked. On the other hand, the platforms themselves were sometimes 'drowned' when their carbonate factories failed to keep pace with rising sea levels because of adverse water conditions, e.g. storm action and/or too rapid deepening.

Nevertheless, for much of their development, the platforms tended to build up and outwards in fits and starts, as space to accommodate the sediment produced was provided by successive deepening events. At this point, it would be justified in asking why there were so much repeated deepening, and why there were not as many episodes of emergence, leading to weathering and dissolution of the limestones. This leads to a crucial distinction between the Cretaceous greenhouse world, in which these platforms developed, and today's icehouse world.

Although some evidence (e.g. marine dropstones, which are stones picked up by glacial ice sheets and then dropped at some distant location when the ice sheets melt) has been proposed to suggest that a few minor glacial advances caused sea level to fall in the early Cretaceous, this evidence is in dispute, with some critics claiming the boulders could have been rafted on floating tree trunks. Any brief glaciation that there might have been was minor and never on a scale to compare with those of the Quaternary.

By contrast, glacially driven sea-level change has been instrumental in shaping current tropical carbonate platforms, giving them a geometry unlike that of the Cretaceous platforms. Many modern platforms are rimmed by sturdy coral reefs, which reach up to sea level and form prominent barriers to incoming ocean waves. It would be tempting to suppose that this modern barrier reef topography was entirely created by the vigorous upward growth of the coral reef itself at the platform margin. In many cases, however, the reef has been installed on a pre-existing topography that already had a raised margin. How might that have got there? The **glacio-eustasy** mentioned above provides the answer to this question. Commonly, reefs grow upon older carbonate platforms, which would have been emergent during the last glacio-eustatic fall. Dissolutional weathering of these older platforms often left behind projecting edifices around their edges, rather like castle walls, periodically cut across by gullies. When these weathered platforms became submerged once again, these prominences provided the hard foundations for the re-establishment of reefs around the margins.

The Cretaceous world lacked such glacio-eustatic fluctuations of sea level, at least on any comparable scale. Hence, significant emergence and weathering of the carbonate platforms was infrequent, except where local tectonic activity intervened. Instead, the platforms tended to experience only successive minor deepening events brought about through a combination of the overall eustatic rise of the period, and regional subsidence of the crust. Between these sporadic deepening events, carbonate sediment overproduction led to the cycles of progradation discussed above.

How did this characteristic pattern of growth of the Cretaceous platforms affect the organisms that dwelt on them, and ultimately created the platforms? The common lack of inherited topographical relief sculpted by emergence and weathering, and the frequent fluxes of carbonate sediment across the prograding margins meant that there was little opportunity for the stable establishment of barrier reefs. The platforms thus lacked the sturdy protective rims created by barrier reefs today, which take the brunt of incoming waves from the open sea and limit the flux of water and sediment across the platform margins. Instead, the outer parts of the Cretaceous platforms tended to be dominated by migrating banks or sheets of current-swept shell sand and debris, which graded into expanses of muddier lime sediments in the platform interiors. These broad sediment surfaces supported myriads of bottom-dwelling shelly organisms, the growth and death of which returned more sediment to the system. Foremost among the larger skeletal sediment-producers, particularly in the late Cretaceous, were some oddly shaped gregarious bivalves that lived in the Cretaceous called **rudists** (Figure 7.20). These grew within or lying upon the loose sediment as vast 'meadows' of

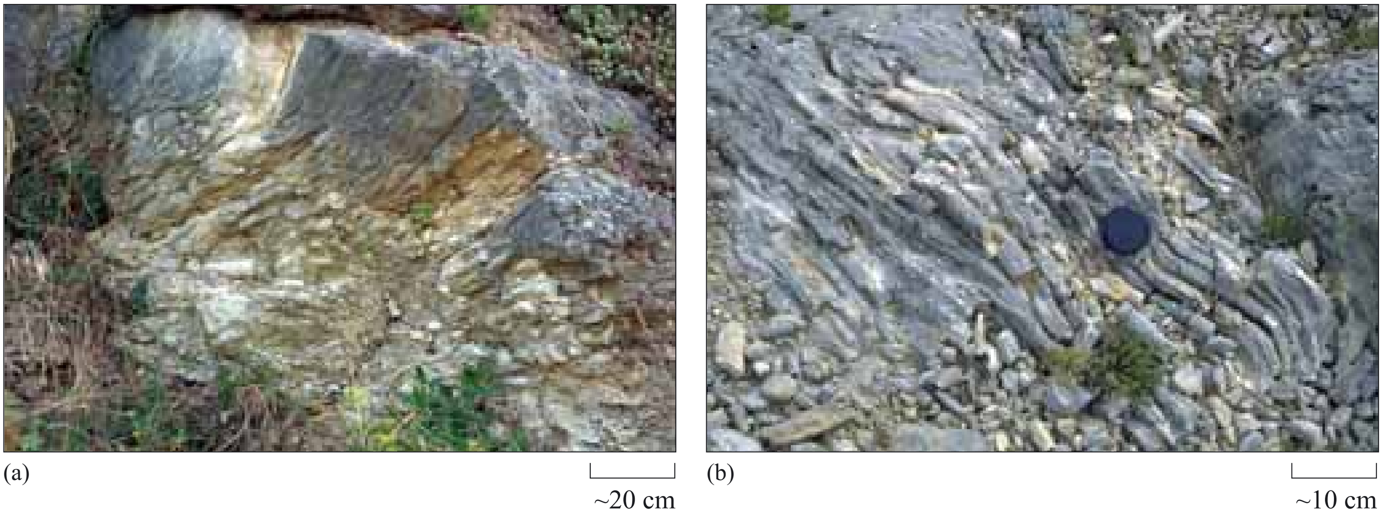


Figure 7.20 Clusters of tubular rudist bivalve shells, preserved mostly in life position, implanted in the sediment in which they grew, from the Upper Cretaceous of (a) Provence, southeast France and (b) the Spanish Pyrenees.

clustered shells, rather like oyster beds today. Frequent disruption of these congregations, usually by storm currents, together with breakage and perforation of the shells by burrowing and boring organisms, helped to turn them into shell sand and mud. The upward and outward growth of the platforms was thus self-sustaining, as shell debris was harvested over huge areas and spread both inwards and out onto the marginal slopes.

Sometimes these rudist-dominated formations are referred to in textbooks as ‘rudist reefs’; but, as the description above shows, this is quite a misleading term as far as the anatomy and growth of the carbonate platforms were concerned. Rather, the rudists were essentially bottom sediment dwellers, forming shelly ‘meadows’ and associated carpets of redistributed debris.

7.9.3 Quantifying the growth of the platforms

This section will consider some quantitative aspects of these Cretaceous Tethyan carbonate platforms, the areal extent of which naturally varied through the Cretaceous, with long periods of expansion punctuated by brief episodes of decline, when carbonate production was temporarily reduced or even halted on many platforms due to adverse conditions. During periods of adverse conditions, large tracts of the platforms subsided. This in turn necessitated regrowth by progradation from shallower areas once conditions improved. A major study by a team of French geologists has investigated various quantitative aspects of the history of a number of carbonate platforms across France. They found that one of the main phases of global platform growth was approximately halfway through the Cretaceous, between about 94 and 92 Ma (contemporaneous with some of the northern Alaskan forests). The Tethyan carbonate platforms at that time have been estimated to have covered a total area of some 9.68×10^6 km^2 (an area approximately equivalent to that of China or Europe). Individual platform thicknesses, of course, varied according to the amount of accommodation space available due to subsidence, itself dependent on the local to regional tectonic setting. Growth rates calculated for several examples of this age from around the

Middle East and the Mediterranean, however, commonly range between 10 and 100 m Ma^{-1}, with most closer to the lower end of the range. A value of 30 m Ma^{-1} is therefore a reasonable estimate of the average vertical rate of accumulation for the purposes of calculating burial rates, and it is important to note that at this time, the Tethyan carbonate platforms *alone* were burying carbon (in the form of carbonate) at nearly half the total rate for *all* marine carbonate sediments today.

7.9.4 Other sinks for carbon

These Tethyan platforms were by no means the only sites of carbonate deposition in the Cretaceous seas. Neighbouring basins on subsiding areas of continental crust around the Tethys Ocean, frequently accumulated fine-grained carbonate sediment, or mixtures of carbonate mud and clay (marl), with the volumes involved also considerable, although less easily quantified.

At mid-latitudes, vast areas of the continents were blanketed by deposits of **chalk**, a distinctively fine-grained limestone. The white cliffs of Dover are probably the best-known example of such deposits, but similar thicknesses of chalk of the late Cretaceous may be traced across much of northern France and the Low Countries, into Germany, Poland and Russia. Similar deposits are also present across large tracts of the American Midwest, as well as in Western Australia. Chalk is composed mainly of the minute skeletal plates of some planktonic unicellular algae called coccolithophores (Figure 7.21), accompanied by the remains of other calcareous planktonic forms, such as foraminiferans (protists), and remains of various bottom-dwelling organisms. Although calcareous-shelled plankton first evolved some time earlier (at least by the late Triassic), their abundance increased dramatically in the late Cretaceous, yielding the extensive thick chalk deposits mentioned above.

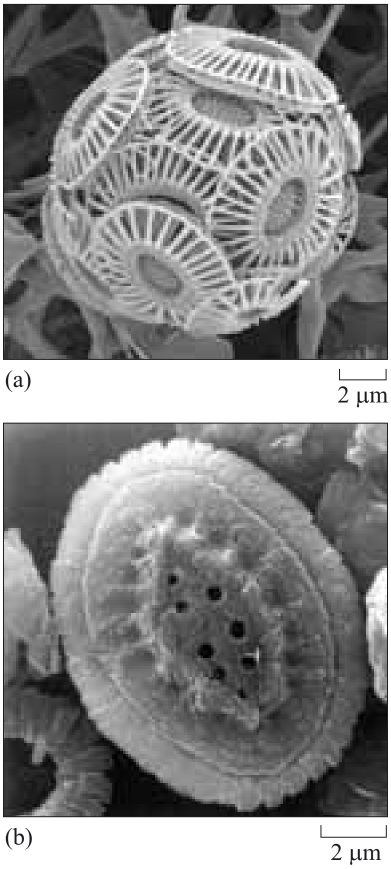


Figure 7.21 Scanning electron photomicrographs of coccoliths of the late Cretaceous: (a) a complete cell coating (coccosphere) of coccolith plates; (b) an isolated coccolith from a different species.

At a crude approximation, the European chalks alone have been estimated to have buried carbon at a rate equivalent to the Tethyan carbonate platforms (i.e. 30 m Ma^{-1}). Still more carbonate was deposited in the oceanic realm. What is clear, therefore, is that carbon was being buried in Cretaceous limestones at a rate significantly greater than that of today. Exactly by how much is not yet known because precise estimates have still to be calculated. In addition, no compensating decline in other carbon sinks has been readily detected and instead they too seem to have increased their rates of sequestration.

In addition to the prolific burial of coal on land in high latitudes throughout the Cretaceous, huge amounts of organic carbon were also buried under the sea due to a combination of factors. In contrast to the cold saline bottom waters of today’s oceans, the Cretaceous oceans tended to acquire deep reservoirs of warm saline water produced by intense evaporation at the surface (especially in the arid low latitudes). Whereas today’s cold bottom waters are relatively well oxygenated, their warm counterparts in the Cretaceous were much less so due to a variety of reasons, one being simply the declining solubility of gases as water temperature rises. From time to time, extensive water masses within the Cretaceous oceans became anoxic, allowing abundant organic material to be deposited without being oxidised on the way, and therefore to accumulate in the bottom sediments. Moreover, the complex geometry of the Tethys Ocean and its surrounding seas created numerous basins with relatively restricted flow, the bottom waters of which were particularly prone to stagnation and anoxia. Indeed, many of the giant oil fields of the Arabian Peninsula contain oil from Cretaceous source rocks that accumulated in such basinal areas within the continent, and which migrated to and became trapped in shallow marine platform limestones that flanked the basins. A detailed analysis of $\delta^{13}C_{carb}$ values in the English Chalk has shown a strong positive shift in values within Upper Cretaceous strata corresponding to the end of the mid-Cretaceous episode of carbonate platform building (see Box 5.1 for a discussion of carbon isotope measurements) and a similar change in Italian sequences of the same age suggests a widespread influence from briefly enhanced rates of organic carbon burial.

From the values of $\delta^{13}C_{carb}$ for the Cretaceous, it has been estimated that the rate of marine burial of organic carbon may at times have reached up to three times its present value. The timing of these episodes of organic burial in relation to the growth of the carbonate platforms is by no means simple, and is still not well resolved; there may have been a degree of counter-balancing, with one increasing as the other declined. It is however evident that, at times, both organic burial and carbonate platform growth were occurring synchronously, though in different regions.

Notwithstanding the need to resolve details of timing still to be worked out, it is already clear that the overall rate of burial of carbon in the Cretaceous greatly exceeded that of today. Where all the extra carbon may have come from poses an interesting problem. Such a high rate of burial of carbon could not possibly have been sustained throughout the period from the Earth's surface reservoirs of carbon alone, without compensation from elsewhere. The atmospheric reservoir (taking today's figure of 0.76×10^{15} kg of carbon) would have been exhausted in a matter of thousands of years; clearly it was not, as the loss of this greenhouse gas would have caused a drop in global temperature, in contrast to the notably warm climatic conditions of the period. Likewise, given the rates of carbon sequestration, the total carbon reservoir in the soil and oceans would only have lasted some tens of thousands of years; that too was not detectably depleted, as there is no shortage of fossil evidence for the healthy continuation of life through the Cretaceous. Hence, another source of extra carbon must be sought that could sustain the excessive supply overtime throughout the Cretaceous.

7.10 A surfeit of carbon: the key to the Cretaceous greenhouse

7.10.1 *De profundis*

The only remaining large-scale source of carbon available is volcanic outgassing of CO_2. During the Cretaceous, there is widespread evidence in the western Pacific, in particular, for massive volcanism associated with a mantle superplume. Unlike rift volcanism, the volcanoes associated with this intraplate source would have reached sea level, where their gases would have been released directly into the atmosphere. The volcanic activity in the Pacific was spread over a long time interval, largely between about 125 and 80 Ma, with a major initial phase in the first 15 Ma followed by a later phase peaking during the last 10 Ma. Carbonate platforms developed extensively, though with episodic drowning, throughout this interval in question. The anomalously high sea levels of the time, particularly of the late Cretaceous, can also be linked with the widespread thermal doming of the ocean floor associated with the volcanism.

7.10.2 The greenhouse atmosphere

If there is a plausible explanation for the hyperactivity of the Cretaceous global carbon cycle, as well as the elevated sea levels of the period, in the form of the 'Pacific superplume', then one vital piece of the jigsaw remains to be put in place: what effect did the enhanced flux of carbon have on atmospheric levels of CO_2 and hence on climate? This is a tricky question because it cannot be assumed that a simple connection exists between the rate of through-flow of carbon in the atmosphere and its level in that temporary reservoir. Yet, it is this temporary reservoir that would have exerted an influence on climate through its greenhouse effect. For example, think of the analogy of running water from a tap into a bucket that has some holes in the bottom. Given a sufficient rate of supply, the water in the bucket is going to fill up to a certain level at which the head of water in the bucket causes the rate of outflow to match that of the inflow. At this point the water level will remain balanced (i.e. in equilibrium). If the rate of inflow is increased, the level in the bucket will rise to a higher level, but increase the size of the holes as well and the rate of outflow will increase, causing the water to drop back to a lower level again if the same rate of inflow is maintained. The rate of through-flow would therefore have increased without necessarily raising the actual water level. The fluctuations in level in this analogy suggest a possible model for the Cretaceous carbon cycle.

In the Cretaceous world, volcanoes may be considered as equivalent to the tap in the above analogy, ultimately supplying the carbon; changes in volcanic activity would have caused fluctuations in the rate of supply. Continuing the analogy, the Tethyan carbonate platforms may be regarded as one of the larger 'holes' for the outflow of carbon, and as seen in Section 3.3, the carbon would have been deposited as calcium carbonate produced by increased rates of weathering, with the calcium carbonate deposited as a by-product of weathering. The overall surface area of the platforms therefore corresponds to the size of the 'hole'. As described above, the areal extent of the platforms did fluctuate quite markedly with time, with short episodes of widespread platform drowning, punctuated by longer periods of re-establishment and progradational expansion. This pattern implies a degree of necessary lag between any increases in carbon supply (from volcanic CO_2 emissions) and compensatory expansion of the platforms.

What about the reverse, i.e. a decrease in volcanic emissions? Reversing the argument above, it could be expected that CO_2 levels in the atmosphere would drop as carbon was still being deposited. The ensuing climatic cooling (with associated effects) is therefore likely to have been detrimental to the growth of the carbonate-precipitating organisms, allowing atmospheric levels of CO_2 to start climbing. Oxygen isotopic studies suggest that some of the major episodes of platform extinctions were associated with climatic cooling. When volcanic emissions rose again, there would have been undercompensation from the platforms, and a new cycle of platform growth would have ensued.

Thus, the lag between volcanic emissions and platform growth (a mismatch between the rates of change of the fluxes supplying and burying carbon) could have led to increased levels of atmospheric CO_2 throughout much of the Cretaceous. Such increased levels would certainly have contributed to climatic warming. The ecosystems that arose in response (such as the Tethyan carbonate platform communities and the polar forests discussed in this chapter) reflect the collective adaptive responses of organisms to the conditions that ensued. They have no equivalents in today's icehouse world, which has its own, equally distinctive, ecosystems.

7.11 Conclusions

Both the greenhouse world of the Cretaceous and the icehouse world of the Permo-Carboniferous reflect the complex process of continuous re-equilibration between the feedbacks of evolving life and the changing Earth. Conditions at the Earth's surface have clearly fluctuated, primarily in response to changes within the Earth itself (e.g. controlling palaeogeographical organisation and superplume activity), but also as a consequence of evolutionary innovations with major environmental impacts (largely upon atmospheric composition, but also upon weathering rates and sedimentation). Other influences have included changes in solar radiation. Overall, no consistent stable state is evident, with each age finding its own unique balance of interacting influences.

Summary of Chapter 7

1. The Carboniferous icehouse world comprised one major continent – Pangea, part of which lay over the South Pole, creating a 'cap world' configuration with extensive ice sheets in high southern latitudes. The dominant type of plants and animals present at this time were different from today, although the distribution of Carboniferous vegetation was similar, with plant productivity highest in low latitudes. Extensive CO_2 sequestering and coal formation occurred in these equatorial regions.
2. Other factors, such as extensive mountain building, relatively fewer mid-ocean ridges, marine regression, and even lowered levels of solar radiation, contributed to the onset and persistence of globally cool conditions during the Carboniferous, either directly or by reducing atmospheric CO_2 levels.
3. The relative importance of different factors described above, along with the interplay and feedbacks between different processes, must be considered in relation to global cooling. For example, marine regressions occurred in the late Carboniferous and latest Permian, but resulted in two different effects. The first enabled vegetation to expand and colonise newly exposed land, enabling further CO_2 sequestering and cooling, whereas the second led to weathering of previously buried coal, release of CO_2 and enhanced global warming. This can be explained by changes in the relative importance and role of other factors, such as the development of a monsoonal system and changes in the kinds of plants able to colonise these environments.

4 Interpretations are further complicated by uncertainties concerning the timing of events and processes. A complex interplay of interactions and feedbacks is suspected to have been responsible for the icehouse–greenhouse transition.

5 In the Cretaceous, the Equator-to-Pole temperature gradient was much smaller than at present, with the difference largely due to much warmer poles.

6 Low latitudes were seasonally arid and, compared with today, there were few areas where rainforest could develop. The low-latitude plants of this period also typically display special adaptations to conserve water.

7 The polar light regime during the Cretaceous was similar to that of the present, with prolonged periods of winter darkness.

8 The Arctic was devoid of permanent ice and supported luxuriant forests dominated by deciduous conifers, with ferns, ginkgos, cycads and some angiosperms also present. These forests were effective carbon-sequestering systems.

9 In high latitudes delta floodplain accumulations of peat were buried as a result of subsidence and sediment shedding from nearby mountains (e.g. Alaska).

10 Palaeoclimatic determinations cannot be based reliably on relict species such as the cycads, whose modern representatives reflect a small extent of past biological diversity and climatic tolerances. More time-stable techniques based on physiognomy need to be used.

11 Flooding of the continents during the mid-Cretaceous provided broad shallow seas around the equatorial Tethys Ocean, flanked by predominantly arid lands of low relief. These seas proved favourable sites for the development of extensive carbonate platforms.

12 Cretaceous carbonate platforms differ in structure from present-day tropical platforms because of the effects on the latter of significant glacio-eustatic fluctuations. Unlike today's platforms, the Cretaceous examples typically lacked marginal reefs, with their outer zones dominated by migrating banks of current-swept shell sand and debris. The prolific growth of shelly organisms on these surfaces fuelled the massive carbonate sediment production of the platforms.

13 The rate of burial of carbon in the form of carbonate on the Tethyan platforms alone, at times equalled approximately half that in all carbonate sediments (of deep, and shallow, water origin) today. In addition to these platform carbonates, further carbon was also sequestered in the Tethyan basins and mid-latitude chalks. Given the high rates of burial of organic carbon throughout the Cretaceous as well, it has been estimate that carbon was being buried at a significantly higher rate than it is today.

14 The only likely source for this excess carbon in the Cretaceous is increased volcanism associated with the 'Pacific superplume'. Rising levels of CO_2 in the Cretaceous atmosphere can be attributed to increases in volcanic emissions and compensatory growth in the carbonate platforms. Episodic extinction and drowning of the carbonate platforms may have been associated with climatic cooling, brought about by temporary net excesses of CO_2 drawdown.

15 The icehouse and greenhouse case studies highlighted in this chapter reflect the complex process of continuous re-equilibration between the feedbacks of evolving life and the changing Earth, a process that is continuing today.

Learning outcomes for Chapter 7

You should now be able to demonstrate a knowledge and understanding of:

7.1 How a combination of physical, geological, palaeontological and isotopic evidence can be used to determine how and why the Earth's climate has varied over geological time, between the extremes of ice-house and greenhouse conditions.

7.2 The complex processes and interactions that result in the transition between ice-house and greenhouse conditions, as well as an appreciation that the same feedback mechanisms can result in vastly different outcomes in relation to the direction of global climate change (e.g. marine transgressions during the Late Carboniferous and Late Permian periods).

7.3 Why changes in physiognomy rather than the nearest living relative technique, is a more reliable method of determining palaeoclimatic conditions in pre-Quaternary sequences, and how this in turn has been used to investigate global climatic conditions during the Cretaceous greenhouse.

7.4 The processes that permitted the formation of extensive carbonate sequences during the Cretaceous, as well as how and why these differ structurally to modern-day carbonate reefs.

7.5 The roles of, and interplay between, plume-related volcanism and carbonate platform formation in altering atmospheric CO_2 levels, which in turn resulted in climatic warming during the Cretaceous.

Chapter 8

End of book summary

Returning to the general theme of this book: what is the fundamental nature of the relationship between evolving life and the Earth – benign partnership, or a chaotic system lurching from one temporary state of balance to another?

8.1 Possible worlds

There are several possible answers to this question. At one extreme, one might postulate that the role of life had been purely passive, with no significant effect on conditions at the Earth's surface: organisms have merely adapted to changes dictated by the Earth's physical and chemical state. At the other extreme, the Earth, together with the life it supports, might be seen as a kind of 'superorganism' that has evolved a tightly coupled system of feedbacks ensuring that 'the Earth's surface environment is, and has been, regulated at a state tolerable for the biota'; this is the 'Gaia hypothesis' of James Lovelock (Box 2.4). Between these two extremes is the view that, while life has significantly altered conditions at the Earth's surface relative to what a lifeless Earth would have been like, the feedbacks concerned are not tightly coupled in any manner akin to the homeostatic mechanisms of an individual organism: at most, they may contribute, along with the Earth's abiotic processes, to temporary equilibria. Nevertheless, these equilibria are not stable over the long term, being subject to alteration due to changes in the balance of feedbacks both from the Earth and from evolving life itself, including the effects of sporadic major environmental perturbations.

Before reading further, you may wish to ponder these three possibilities in the light of what you have learned so far, to see which you consider the most plausible view. Consider, first, whether or not the presence of life has had any significant effect on conditions at the Earth's surface. If so, consider whether or not such influences have consistently tended to regulate conditions in a state 'tolerable for the biota'.

8.2 Review of the options

The first option – life as a purely passive passenger on Earth's voyage through time – can probably be discounted as the scale of life's impact on the Earth has been repeatedly stressed throughout this book. That leaves the nature of such feedbacks between life and the Earth to be considered – is the interaction Gaian, or is life merely a contributor to complex, but essentially chaotic, biogeochemical cycles?

Consider, first, the expectations of the theory of evolution by natural selection. This theory emphasises selection at the level of the individual, not at the level of entire systems, let alone the global biosphere.

If natural selection theory thus provides no grounds for the Gaia hypothesis, what, then, of the empirical evidence? Does the geological record support the proposition that ‘the Earth’s surface environment is, and has been, regulated at a state tolerable for the biota’? Might such self-regulation have come about by means other than evolution by natural selection? The first problem in tackling this question is the woolliness of the proposition itself. Which ‘biota’ is being talked about? You have seen that the Earth’s biota has changed quite considerably over time. If you had been able to question, for example, the anaerobic denizens of the Archean oceans, to whom today’s levels of molecular oxygen would have been toxic, or the high-latitude forests of the Cretaceous Period, whose domains are now icy wastes, on the issue, their responses would not have been wholeheartedly supportive of the Gaia hypothesis. Nor, apparently, were these life-forms the unfortunate victims of mass extinctions, which might be blamed on extraneous perturbations: their environments simply changed beyond their limits of tolerance and they were eventually written out of the drama (or, in the case of the anaerobic microbes, literally went underground, or into the guts of animals including humankind, where their descendants continue to thrive in anoxic regimes). Obviously, then, the reference to the biota in the proposition is not intended to be comprehensive: presumably *any* manifestation of life is intended.

The observation that life in general appears to have persisted at least from early Archean times is trivial, in this respect, as it is merely consistent with, but does not necessarily confirm, the Gaian hypothesis: it does not disprove the alternative model that life has managed to continue participating in a chaotic system that lurches between temporarily equilibrating states. It could simply be the case that the ‘lurching’ has not, so far, transgressed the limits of tolerance of all life forms: some form of life has always been able to survive, furnishing successive ages with appropriately adapted organisms. In other words, there has always been somewhere, so far, where DNA has proved robust.

So, does the geological record suggest any *predominant* tendency towards the establishment and stabilisation of optimal conditions? Demonstration of the mere existence of some feedbacks having this effect would not be enough to settle the issue, as some such effects could be expected in the chaotic model – by chance alone. The Gaian model explicitly proposes a coherent integration of feedbacks, together yielding homeostatic self-regulation. A suitable test, therefore, is to see whether such a pattern has been predominant over geological time. If it has not – with the feedbacks being sometimes stabilising, sometimes not so – then the Gaia hypothesis should be rejected.

Consider, for example, the various feedbacks involved in regulating Permo-Carboniferous atmospheric composition and hence climates, which were discussed in Chapter 7. Do these appear to have consistently stabilised a particular set of conditions? Or were their effects variable – sometimes maintaining a given state, and sometimes helping to install a different regime?

Again, in the Cretaceous, the extensive carbonate platform biota, as well as the high-latitude land flora, did not enjoy uninterrupted exploitation of the enhanced supply of atmospheric CO_2 and the associated warm climatic conditions. It seems that they were poorly suited to respond to hiccups in the supply, as they continued to draw down carbon at excessive rates, and so perhaps contributed to episodic crises involving climatic cooling and eventual drowning of the platforms themselves. Thus, far from consistently stabilising optimal conditions for the incumbent biota, the Cretaceous Earth–life system became implicated in important environmental fluctuations, which were attended by extinctions on a variety of scales. The same story emerges for any geological period when investigated in sufficient detail.

Of the two models that have been considered, that of a complex, essentially chaotic, system seems to be the more plausible. The Gaia hypothesis is supported neither by evolutionary theory nor by the empirical evidence of the geological record.

However, it is worth pondering how the fluctuations in conditions remained within the limits of tolerance of living organisms, and why present-day conditions seem to be so well suited to the living biota. It is, in fact, easier to answer the second question first, as it is really a trick question, but tackling it helps a little way towards answering the first, and it also raises the crucial issue of rates of change.

While the ‘rapid’ fluxes of biogeochemical cycles that are largely mediated by ecological interactions may balance out over the short term, slower geological and evolutionary processes alter such equilibrium states over longer timescales. Atmospheric oxygen is a case in point, the nice mutual adjustment of major sources and sinks (e.g. photosynthesis and respiration) over the timescales of human observation providing a telling contrast to the dramatic long-term changes of the past. So long as these slower changes do not outstrip the limits of tolerance conferred on individuals by available genes, evolution can deliver suitably adapted organisms. Thus, to marvel at the appropriateness of conditions for life is simply to put the cart before the horse: it is the evolutionary responsiveness of organisms that has ensured the fit. With a little bit of adaptation, today’s problem can even become tomorrow’s manna. This is known as the ‘helpful stress effect’. In recent times, rats have provided a good example of such a change of status in their evolution of resistance to the pesticide Warfarin. Warfarin is poisonous to normal rats because it suppresses blood-clotting (leading to fatal bleeding) and interferes with the uptake of vitamin K. Soon after its introduction, rats resistant to the pesticide began to appear and to replace the ordinary Warfarin-sensitive strains. However, the frequency of the resistant forms rapidly declines when use of the pesticide is stopped. Thus Warfarin-resistance evidently bears a cost to fitness under normal circumstances (probably related to an increased vitamin K requirement), such that the Warfarin-resistant strains positively depend on the presence of the pesticide in order to survive.

Stark testimony to the importance of this principle in the history of life is provided by instances where rates of environmental change have evidently outstripped the capacity for evolutionary response of organisms: the results have been dramatic – extinction, and in cases where such perturbations were widespread and pervasive in their effects, mass extinction. Thus the *rate* of an environmental change, perhaps rather more than its nature, is crucial to its effect: be it slow enough, and it provides new opportunities for adaptation; be it too fast, and it becomes a catastrophe, leaving a trail of extinctions in its wake. Emissions of CO_2 associated with major volcanic episodes seem to illustrate the contrast between these two effects. Brief but massive eruptions of flood basalts may well have been implicated in some mass extinctions. Yet those associated with the postulated Pacific superplume of the Cretaceous, which were erupted on an even greater volumetric scale, but over a longer period, helped to create the conditions in which the spectacular carbonate platform ecosystems and high-latitude forest ecosystems of the period thrived.

The other question raised above was: how did the fluctuations in conditions remain within the limits of tolerance of living organisms? To some extent, the progressive evolutionary tracking of changing conditions discussed above can help to explain this. The limits of tolerance have themselves shifted in some respects. Had the physical and chemical conditions of today's world been miraculously switched on in, say, the Archean or the early Proterozoic, the effect on life then would certainly have been devastating, perhaps even fatal. Nevertheless, that is certainly not the whole story: the limits within which mean global surface temperatures appear to have remained, for example, are impressively modest. It is a curious but characteristic feature of complex systems, involving myriads of feedbacks between component parts, that they tend to settle within relatively narrow limits of physical and chemical states. The numerical modelling of such behaviour involves a difficult branch of mathematics – chaos theory – that is beyond the scope of this book. An important point to note, however, is that such sets of conditions ('strange attractors', as they are known) are far from inviolable. As you have already seen, they lack the protection of co-adapted homeostatic mechanisms characteristic of individual organisms. They are indeed quite sensitive to initial conditions, and unpredictable shifts to new states can result from small but critical changes in the components of the system. Possibly, then, mean global temperature may have been broadly constrained in this manner, though evidently it fluctuated between the contrasting greenhouse and icehouse modes. Perhaps, moreover, we have just been lucky, in that the early removal of carbon from the Earth, with the formation of the Moon, followed by the sustained drawdown of CO_2 from the atmosphere, removed the risk of a runaway greenhouse effect as the Sun warmed. There is no satisfactory answer to this question at present.

8.3 Conclusion

In summary, it is clear that evolving life has profoundly influenced conditions at the Earth's surface over time. Yet it is equally apparent that the feedbacks between Earth and life have interacted over the long term in a chaotic, undirected, manner, lacking the kind of tightly coupled self-regulation that may be admired in individual organisms. Life on Earth is a risky game, then, but with so many players around, there have always been sufficient winners to keep it going, so far. Some puzzlingly 'benign' aspects nevertheless still stand out, such as the relative stability of mean global surface temperatures. It is still too soon to say whether this can be put down to luck, or to some, as yet poorly understood, system of global stabilisation.

Question 5.1

Condensation of moisture to form rain releases latent heat originally taken up from the ocean as latent heat of evaporation. Thus, air that is rising because it has been warmed by the underlying continent (Figure 1.29b) has an extra heat source, and rises more vigorously, intensifying the low pressure over the region and drawing in moist air from the south even more strongly.

Question 5.2

(a) There have been a number of large fluctuations in the relative abundance of *G. bulloides*, but the first main change occurred between about 9 Ma and 7.5 Ma, when the relative abundance increased rapidly from <1% to >50%. In more recent times the proportion has fluctuated, but has never been reduced to less than what it was at 8.5 Ma (with the exception of the extreme low at about 5.5 Ma).

(b) The increase in the relative abundance of *G. bulloides* at 7.5–9 Ma could well indicate an increase in upwelling of nutrient-rich water. As shown in Figure 5.10b, at the present day, upwelling and high levels of primary productivity occur during the southwest monsoon. Therefore it is reasonable to interpret Figure 5.11b as an indication of a strengthening of the winds of the southwest monsoon at 8–9 Ma.

Question 5.3

(a) (i) The total flux of dissolved material from the rivers listed in Table 5.1 is:

$$\frac{679\times10^{6}\ \text{t y}^{-1}}{2130\times10^{6}\ \text{t y}^{-1}}\times100 = 31.9\%\ \text{of the global total (to 3 sig. figs).}$$

(ii) The total flux of suspended material from the rivers listed in Table 5.1 is 3518×10^{6} t y^{-1}, which is:

$$\frac{3518\times10^{6}\times\text{t y}^{-1}}{20\,000\times10^{6}\times\text{t y}^{-1}}\times100 = 17.6\%\ \text{of the global total (to 3 sig. figs).}$$

(b) Approximately 30% of the global dissolved products of weathering and ~18% of the global suspended material is derived from just 5% of the available land area by the rivers in Table 5.1. This suggests unusually high weathering rates in the Tibet/Himalaya region.

Question 5.4

According to Figure 5.13, there was a period of relatively fast cooling starting at about 80 Ma, followed by a second period with a high rate of cooling starting at ~50 Ma, then a sharper increase in the rate of cooling commencing at about 15 Ma, and a final even sharper decline starting at about 5 Ma.

(a) In relation to the GEOLAB model, Figure 4.10 indicates that the rate of production of oceanic crust gradually decreased between 110 Ma and 80 Ma, and then decreased more sharply over the next 1 Ma. After that, it remained roughly constant. This general decline in ocean crust production over the course of the past 110 Ma or so is consistent with the GEOCARB model. In addition, the model is also supported by the sharp temperature drop at ~85–70 Ma, with the decrease in ocean-floor production occurring over roughly the same period. According to Figure 4.10, however, the rate of production of ocean floor since 50 Ma has been fairly stable, and so the decrease in temperature over the past 50 Ma cannot be accounted for on the basis of the GEOCARB model.

(b) The Himalaya and the Tibetan Plateau began to rise some time after 50 Ma, but presumably the high rates of weathering would have been established some time after this, when the topography had become high and steep. The phase of global cooling over the past 50 Ma, therefore, is consistent with the mountain-forcing model.

Question 5.5

(a) If the flux of organic carbon from the continents increased significantly, then the average δ^{13}C value of marine sediments would decrease.

(b) The largest increase in the flux of organic carbon to the ocean will be indicated by the largest decrease in δ^{13}C in marine carbonates, which according to Figure 5.16 occurred at about 58–56 Ma. (You can assume that the δ^{13}C plot in Figure 5.16 is determined mainly by the flux of organic carbon from *land* because that from marine primary and secondary production is very small by comparison.)

Question 6.1

A mini-glaciation.

Question 6.2

The most obvious example is that of the human population explosion, itself a consequence of a decrease in the individual death rate (i.e. increased survivorship of individuals), due to social and medical advances. Alternatively, if you are a gardener, you may have thought of the unwelcome rise in aphids each summer: this is unleashed by the onset of rapid asexual reproduction, easily outstripping the death rate of individuals, as they feed on new plant growth.

Question 6.3

Following on from that in the late Ordovician, comparable sharp falls in diversity occurred in the:

- late Devonian
- late Permian
- late Triassic
- late Cretaceous.

At first glance, it might seem that the late Triassic extinction was not on a par with the others. However, the relative drop in diversity was still considerable, given the depleted numbers of families that remained after the particularly severe late Permian extinction.

Question 6.4

After each mass extinction, the diversity of organisms increased relatively rapidly. Such a consistent response accords well with the hypothesis discussed in relation to the Cambrian Explosion, i.e. that of unrestrained evolutionary radiations filling vacated habitats.

Question 6.5

Following the trends proposed, it is possible that rates of origination could decline and extinction rates increase until they eventually matched one another, as diversity simultaneously rose. As a result of this balanced budget of origination and extinction, diversity would stay at the same level (or at least hover around it, allowing for small random fluctuation).

Question 6.6

No. Each successive fauna appears to have been proportionately less drastically affected by mass extinction than its predecessor. This is most clearly seen in the case of the mass extinction at the end of the Permian. At this time, family diversity in Palaeozoic fauna plummeted (the Cambrian fauna being already of negligible diversity at this time), whereas the modern fauna were much less profoundly affected. (This is also apparent on Figure 6.9.) In terms of reduction in numbers, the late Ordovician extinction almost halved the diversity of the Cambrian fauna, compared with the loss of under a third of the families in the Palaeozoic fauna. Thus, each mass extinction (particularly that at the end of the Permian) left a biased set of animal groups among the survivors.

The reasons for such differential survival are not well understood and may not just reflect differences in the fitness of individuals in their perturbed environments, according to the normal principles of natural selection. It is also possible that certain properties of whole groups, such as their geographical distribution, may have enhanced survival and/or extinction potentials. For example, there is some evidence that genera containing species distributed across different regions stood a better chance of surviving a mass extinction than those limited to a single area. This form of hierarchical filtering can be readily explained by the environmental perturbations affecting different regions unequally (Box 6.2).

Question 6.7

As the calcareous plankton died and sank to the sea floor, they would have added to the carbonate sedimentation found further offshore and in deeper water, continuing the trend noted earlier for the Cambrian radiations.

This offshore deposition enhanced the carbonate contribution to the carbon cycle, representative of a time when these planktonic groups underwent major radiation.

Question 6.8

It can be supposed that sufficient CO_2 to meet photosynthetic requirements (limited by other factors) could have entered the plants through relatively few stomata. If water were the limiting factor for photosynthesis, then having only a few stomata would have been advantageous because it would have reduced water loss to the atmosphere.

As plants colonise the land, rising percentage levels of carbon were transferred from the atmosphere and fixed in the soil, with increasing amounts ending up buried in sediments. Land plants, therefore, added a new component to the biological removal of CO_2, which prior to their evolution had only taken place in the marine environment.

With atmospheric CO_2 decreasing, it, rather than water, eventually became the limiting factor of photosynthesis, and plants therefore had to adapt by increasing their stomatal numbers. The presence of stomata, and the fact that cuticles and waxes are not totally impervious to water inevitably led to greater water loss from plants back to the atmosphere; to compensate, more water had to be supplied to the leaf. This, in turn, led to natural selection of a more efficient root system and better vascularisation within plants. Thus, with increasing branching systems and leafy photosynthetic areas, there is a corresponding increase in vascular complexity in late Devonian plants. Alongside this, the diameters of the water transport cells also increased in many taxa (Figure 6.21). Early ferns provide some good examples of the developments described above (Figure 6.22).

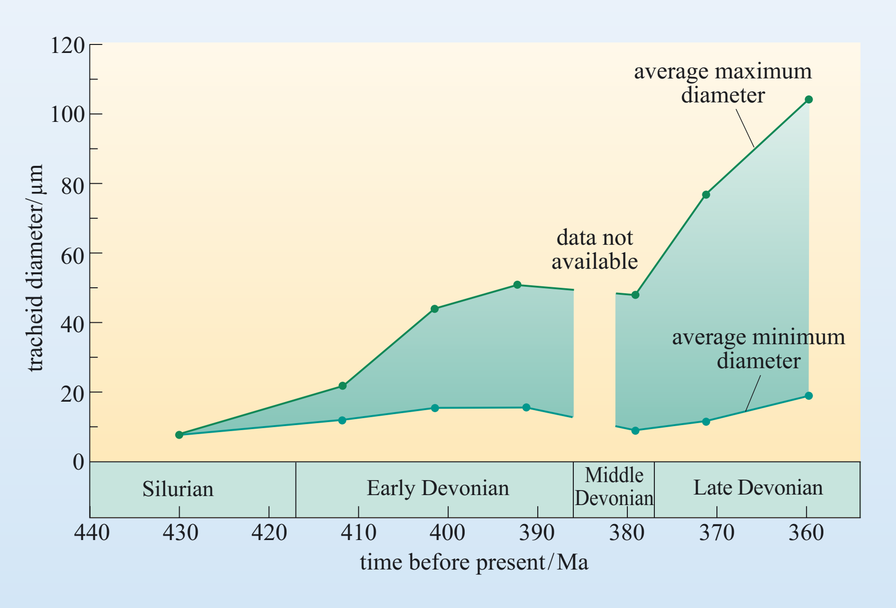
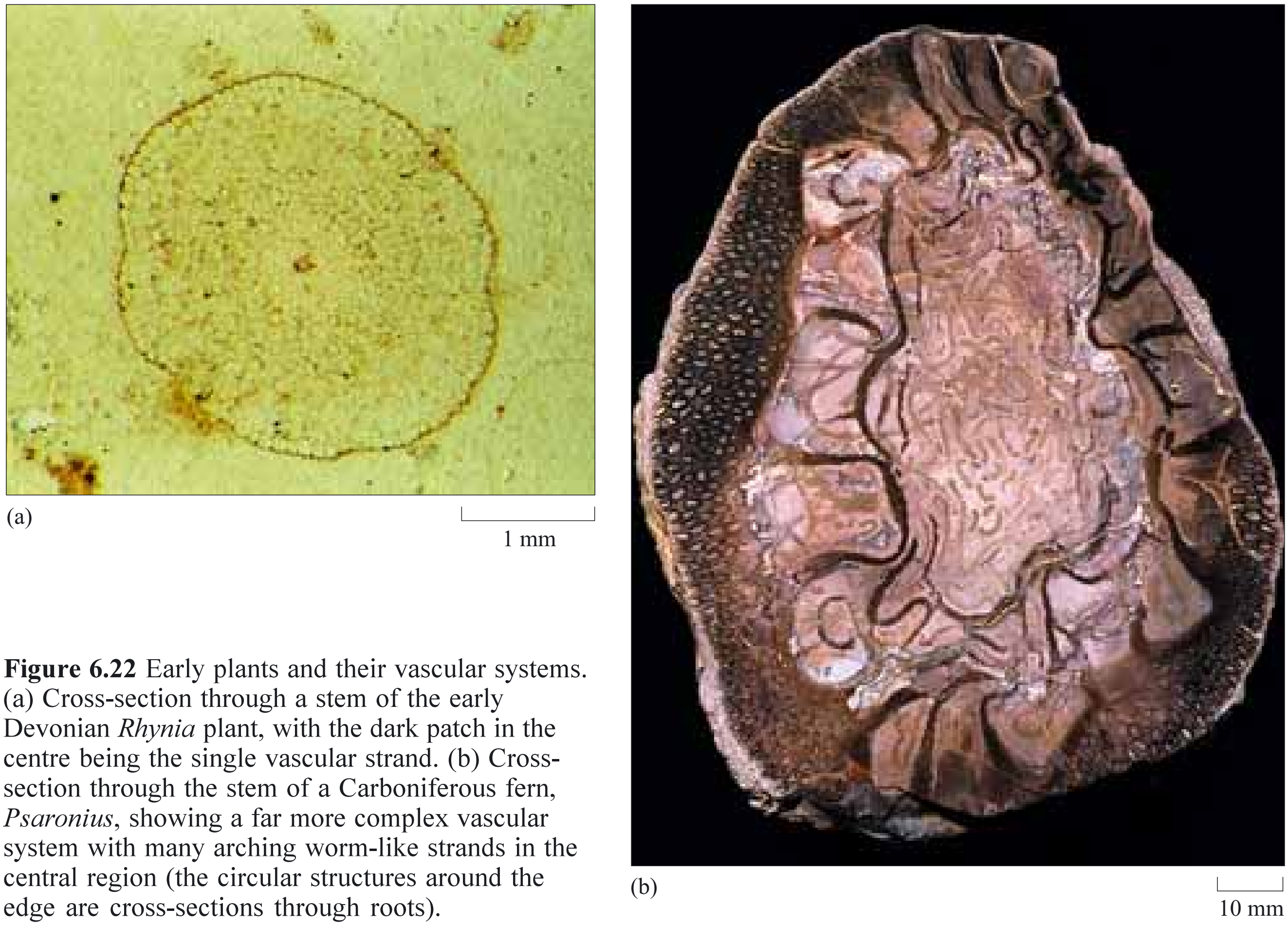


Figure 6.21 Changes in water transport cell diameter in land plants over time.



(a)

(b)

Figure 6.22 Early plants and their vascular systems. (a) Cross-section through a stem of the early Devonian *Rhynia* plant, with the dark patch in the centre being the single vascular strand. (b) Cross-section through the stem of a Carboniferous fern, *Psaronius*, showing a far more complex vascular system with many arching worm-like strands in the central region (the circular structures around the edge are cross-sections through roots).

Question 7.1

In contrast to today, Figure 7.1 shows there was one enormous supercontinent (Pangea), which incorporated all bar some of the Asian microcontinents and which extended from the South Pole to high northern latitudes.

Question 7.2

Referring to Section 3.3.2, the two main reactions considered involve the weathering of calcium carbonate ($CaCO_3$) and silicate ($NaAlSi_3O_8$) rocks (Equations 3.7a and b). The first reaction takes in one molecule of CO_2 for each molecule of $CaCO_3$ weathered, but because the precipitation of carbonate releases it again, there is no net drawdown of CO_2:

$$CaCO_3 + CO_2 + H_2O \underset{\text{carbonate precipitation}}{\overset{\text{carbonate dissolution}}{\rightleftarrows}} Ca^{2+} + 2HCO_3^-$$

The second reaction – silicate weathering, removes two molecules of CO_2 from the atmosphere for every silicate molecule weathered:

$$\underbrace{CaSiO_3}_{\text{silicate rock}} + \underbrace{2CO_2 + 3H_2O}_{\text{from rainwater}} \rightarrow \underbrace{Ca^{2+} + 2HCO_3^{-} + H_4SiO_4}_{\text{stream/river water}}$$

As the precipitation of carbonate releases one molecule of CO_2 into the atmosphere (see the carbonate precipitation reaction above), a net drawdown of CO_2 from the atmosphere occurs when silicate rocks are weathered.

Question 7.3

Such mountain building would have resulted in an increase in the amount of rock available to be eroded. This in turn would have led to more CO_2 being sequestered from the atmosphere as rock silicates were weathered, ultimately ending in the oceans as $CaCO_3$.

Question 7.4

First, the rifting and break-up of Pangea would have created several new mid-oceanic ridge systems by Cretaceous times, the combined volume of which would have displaced corresponding amounts of water from the ocean basins. Second, the water that in late Carboniferous to early Permian times was tied up in the south polar continental ice sheet would have returned to the oceans in the Cretaceous.

Question 7.5

The subdued relief, together with the aridity of the hinterland, would have meant that supplies of land-derived sands and muds carried by streams and rivers would have been temporarily and spatially limited, associated only with localised zones of uplift. By contrast, the breakdown of calcareous shells produced by the myriads of organisms thriving in the broad expanses of warm shallow sea (the 'shallow water carbonate factory') would have generated copious amounts of carbonate sediments, which would eventually form limestone. Higher temperatures leading to the thermal expansion of water also contribute to higher sea level.

Appendix A

The elements

Atomic number, *Z*	Name	Chemical symbol
1	hydrogen	H
2	helium	He
3	lithium	Li
4	beryllium	Be
5	boron	B
6	carbon	C
7	nitrogen	N
8	oxygen	O
9	fluorine	F
10	neon	Ne
11	sodium	Na
12	magnesium	Mg
13	aluminium	Al
14	silicon	Si
15	phosphorus	P
16	sulfur	S
17	chlorine	Cl
18	argon	Ar
19	potassium	K
20	calcium	Ca
21	scandium	Sc
22	titanium	Ti
23	vanadium	V
24	chromium	Cr
25	manganese	Mn
26	iron	Fe
27	cobalt	Co
28	nickel	Ni
29	copper	Cu
30	zinc	Zn
31	gallium	Ga
32	germanium	Ge
33	arsenic	As
34	selenium	Se
35	bromine	Br
36	krypton	Kr
37	rubidium	Rb
38	strontium	Sr
39	yttrium	Y
40	zirconium	Zr
41	niobium	Nb
42	molybdenum	Mo
43	technetium	Tc[a]
44	ruthenium	Ru
45	rhodium	Rh
46	palladium	Pd
47	silver	Ag
48	cadmium	Cd
49	indium	In
50	tin	Sn
51	antimony	Sb
52	tellurium	Te
53	iodine	I
54	xenon	Xe
55	caesium	Cs
56	barium	Ba
57	lanthanum	La
58	cerium	Ce
59	praseodymium	Pr
60	neodymium	Nd
61	promethium	Pm[a]
62	samarium	Sm
63	europium	Eu
65	terbium	Tb
66	dysprosium	Dy
67	holmium	Ho
68	erbium	Er
69	thulium	Tm
70	ytterbium	Yb
71	lutetium	Lu
72	hafnium	Hf
73	tantalum	Ta
74	tungsten	W
75	rhenium	Re
76	osmium	Os
77	iridium	Ir
78	platinum	Pt
79	gold	Au
80	mercury	Hg
81	thallium	Tl
82	lead	Pb
83	bismuth	Bi
84	polonium	Po[a]
85	astatine	At[a]
86	radon	Rn[a]
87	francium	Fr[a]
88	radium	Ra[a]
89	actinium	Ac[a]
90	thorium	Th[a]
91	protoactinium	Pa[a]
92	uranium	U[a]

[a] No stable isotopes.

Appendix B

SI fundamental and derived units

Table B1 SI fundamental and derived units.

Quantity	**Unit**	**Abbreviation**	**Equivalent units**
mass	kilogram	kg	
length	metre	m	
time	second	s	
temperature	kelvin	K	
angle	radian	rad	
area	square metre	m^2	
volume	cubic metre	m^3	
speed, velocity	metre per second	$m\ s^{-1}$	
acceleration	metre per second squared	$m\ s^{-2}$	
density	kilogram per cubic metre	$kg\ m^{-3}$	
frequency	hertz	Hz	(cycles) s^{-1}
force	newton	N	$kg\ m\ s^{-2}$
pressure	pascal	Pa	$kg\ m^{-1}\ s^{-2}$, $N\ m^{-2}$
energy	joule	J	$kg\ m^2\ s^{-2}$
power	watt	W	$kg\ m^2\ s^{-3}$, $J\ s^{-1}$
specific heat capacity	joule per kilogram kelvin	$J\ kg^{-1}\ K^{-1}$	$m^2\ s^{-2}\ K^{-1}$
thermal conductivity	watt per metre kelvin	$W\ m^{-1}\ K^{-1}$	$m\ kg\ s^{-3}\ K^{-1}$

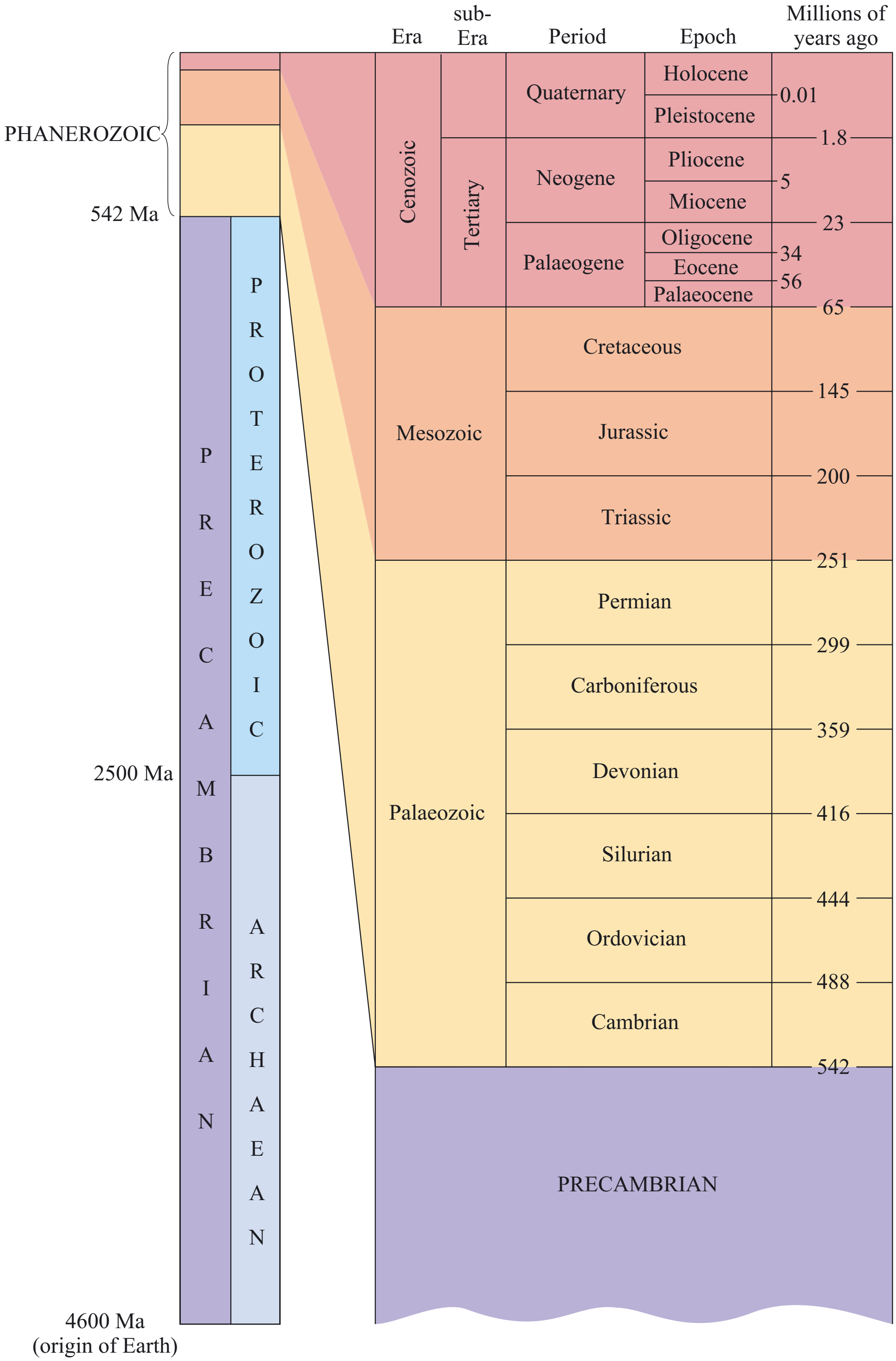
The Greek alphabet

Table C1 The Greek alphabet.

Name	Lower case	Upper case	Name	Lower case	Upper case
Alpha	α	A	Nu (new)	ν	N
Beta (bee-ta)	β	B	Xi (cs-eye)	ξ	Ξ
Gamma	γ	Γ	Omicron	ο	O
Delta	δ	Δ	Pi (pie)	π	Π
Epsilon	ε	E	Rho (roe)	ρ	P
Zeta (zee-ta)	ζ	Z	Sigma	σ	Σ
Eta (ee-ta)	η	H	Tau (torr)	τ	T
Theta (thee-ta; ‘th’ as in theatre)	θ	Θ	Upsilon	υ	Y
Iota (eye-owe-ta)	ι	I	Phi (fie)	ϕ	Φ
Kappa	κ	K	Chi (kie)	χ	X
Lambda (lam-da)	λ	Λ	Psi (ps-eye)	ψ	Ψ
Mu (mew)	μ	M	Omega (owe-me-ga)	ω	Ω

Appendix D

Additional figures



Note that time intervals are not drawn to scale. You may see other versions of this timescale with minor differences, as the subdivisions and radiometric age dates are subject to revision.

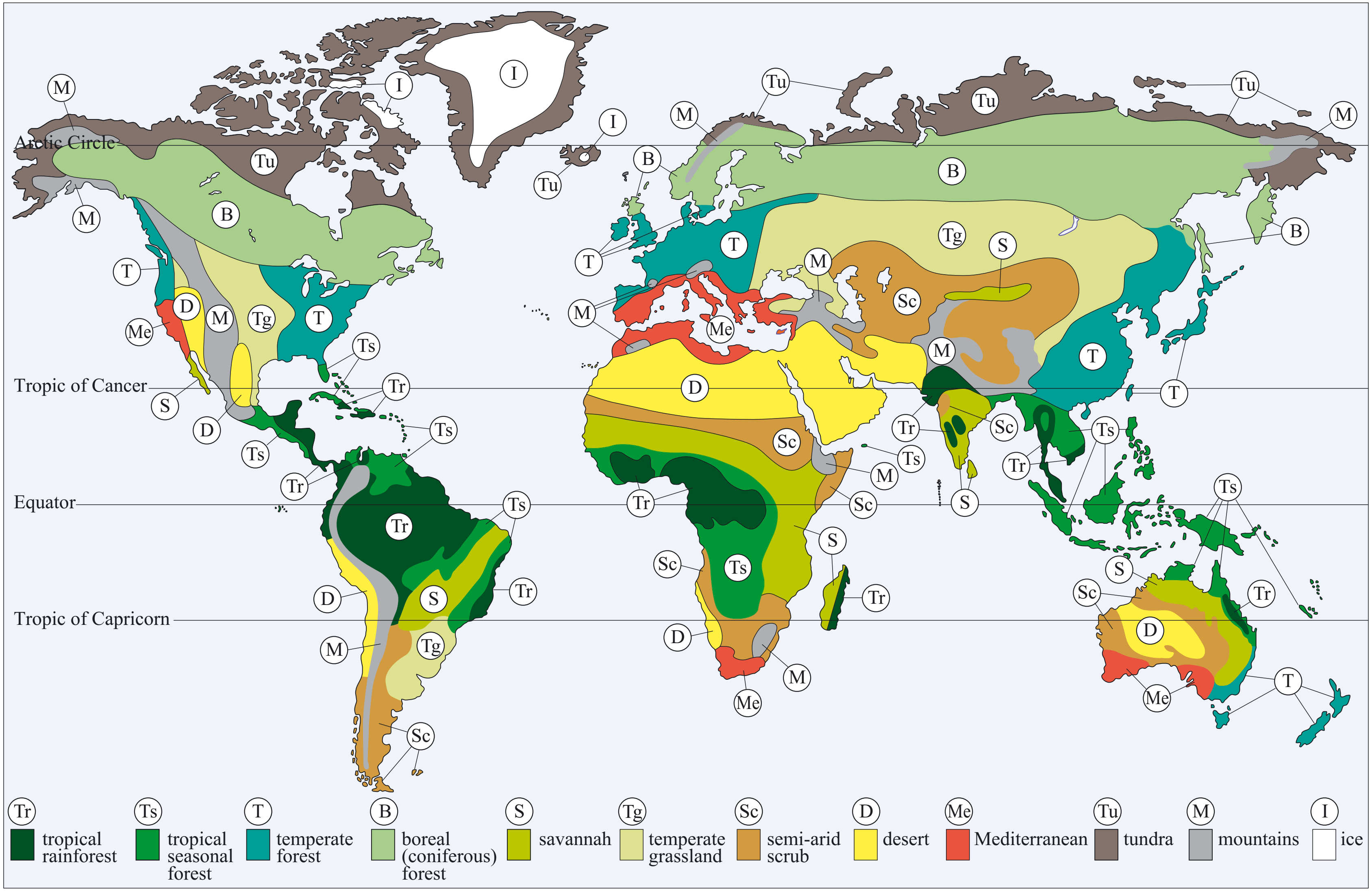


Figure 3.4 Geographical distribution of the major natural regional ecological communities or biomes.

Further reading

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Acknowledgements

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