Chapter 4: Patterns in time

Aims of the chapter

In this chapter, we will briefly review the evolution of the flora and fauna of the earth and the role that plate tectonics, climate and sea level played in their evolution. We shall then go on to:

- review the evidence for the climatic changes that characterised the late Cenozoic era, and especially during the Quaternary
- outline the impact of this climatic variability on the present-day composition and distribution of the global flora and fauna, with exemplification from Europe and the Americas.

We will conclude with a brief discussion of the impact of *Homo sapiens* on global flora and fauna over the last 12,000 years.

Learning objectives

By the end of this chapter and the relevant reading, you should be able to:

- describe the advent, evolution and kinds of life on earth
- relate life on earth to the abiotic climate and geological controls
- describe the major functional groups of plant and animal life and when they first appeared
- describe the major radiations of reptiles, mammals, gymnosperms, angiosperms and grasses
- relate these radiations to Phanerozoic tectonic plate positions, especially the Great America Biotic Interchange
- account for the major extinctions in the biological record
- describe the biological impact of Pleistocene glaciations on the latitudinal distribution of global biomes
- discuss the evidence for Quaternary environmental and biological change.

Essential reading

Lomolino, M.K., B. Riddle and J.H. Brown *Biogeography*. (Sunderland, Mass.: Sinauer Associates, 2005) third revised edition [ISBN 0878930620]. Chapters 8, 9, 10, 11, 12.

Recommended reading

Allen, J.R.M. et al. ‘Rapid environmental changes in southern Europe during the last glacial period,’ *Nature* 400 1999, pp. 740–3.

Benton, M.J., and B.C. Emerson ‘How did life become so diverse? The dynamics of diversification according to the fossil record and molecular phylogenetics’ *Palaeontology* 50(1) 2007, pp. 23-40. Pdf from http://palaeo.gly.bris.ac.uk/Benton/reprints/2007diversification.pdf

Birks, H.J.B. ‘Late Quaternary biotic change in terrestrial and lacustrine environments, with particular reference to north-west Europe’, in Berglund, B.E. (ed.) *Handbook of Holocene palaeoecology and palaeohydrology*. (Chichester: John Wiley, 1989), pp. 3–66.

Cerling et al. 'Carbon dioxide starvation, the development of C4 ecosystems, and mammalian evolution'. *Phil. Trans. R. Soc. Lond*. 353 1998, pp. 159–171 www.journals.royalsoc.ac.uk/content/53dtkenk19tjrged/fulltext.pdf

Cheddadi, R., J.-L de Beaulieu, J. Jouzel, V. Andrieu-Ponel, J.M. Laurent, M. Reille, D. Raynaud and A. Bar-Hen 'Similarity of vegetation dynamics during interglacial periods', *Proceedings of the National Academy of Sciences USA* 102 2005, pp. 13939–13943. www.pnas.org/cgi/reprint/102/39/13939

Cheddadi, R. et al. 'Imprints of glacial refugia in the modern genetic diversity of Pinus sylvestris', *Global Ecology and Biogeography* 15 2006, pp. 271–282.

Cox, C.B. and P.D. Moore *Biogeography: An ecological and evolutionary approach*. (Oxford: Blackwell, 2005) seventh edition [ISBN 1405118989].

EPICA community members 'Eight glacial cycles from an Antarctic ice core', *Nature* 429(6992) 2004, pp. 623–626. Pdf from: www.antarctica.ac.uk/BAS_Science/programmes2000-2005/SAGES/nature02599.pdf

Forster, P. 'Ice ages and the mitochondrial DNA chronology of human dispersals: a review', *Philosophical Transactions of the Royal Society of London* B 359 2004, pp. 255–264. A review of the evolution and dispersal over 200,000 years. Highly recommended reading. Free online pdf from www.journals.royalsoc.ac.uk/content/102022

Hewitt, G. 'The genetic legacy of the Quaternary ice ages.' *Nature* 405 2000, pp. 907–913.

Jansen, E. et al. 2007: 'Palaeoclimate,' in S. Solomon, S et al. (eds) *Climate change 2007: The physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (Cambridge, United Kingdom and New York, NY: Cambridge University Press, 2007), pp. 433–497. [ISBN 9780521705967]. Pdf from http://ipcc-wg1.ucar.edu/wg1/wg1-report.html

Lister, A.M. The impact of Quaternary Ice Ages on mammalian evolution. *Philosophical Transactions of the Royal Society* B 359 2004, pp. 221–241. www.journals.royalsoc.ac.uk/content/tpv2e71eg4txbuly/fulltext.pdf

Mann, M.E. 'Climate over the past two millennia', *Annual Reviews of Earth and Planetary Science* 35 2007, pp. 111–136. Pdf from http://holocene.meteo.psu.edu/Mann/index.html under 'articles'.

Miller et al. The Phanerozoic record of global sea-level change, *Science* 310(5752) 2005, pp. 1293–1298.

Paillard, D. 'Glacial cycles: Towards a new paradigm', *Reviews of Geophysics* 39 2001, pp. 326–346. www.geog.ox.ac.uk/~mnew/teaching/Online_Articles/paillard_rev_geophys_2001.pdf

Petit, J.R. et al. 'Climate and atmospheric history of the past 420,000 years from Vostok ice core, Antarctica', *Nature*, 399(6735) 2000, pp. 429–436.

Prentice, I.C., D. Jolly, and BIOME 6000 participants, 'Mid-Holocene and glacial-maximum vegetation geography of the northern continents and Africa', *Journal of Biogeography* 27(3), 2000, pp. 507–519. www.bridge.bris.ac.uk/projects/BIOME_6000/75_Prentice_et_al.pdf

Sage, R.F. 'The evolution of C4 photosynthesis', *New Phytologist* 161 2004, pp. 341–370. Pdf from www.newphytologist.org/tansley.htm

Stringer, C. 'Modern human origins: progress and prospects', *Philosophical Transactions of the Royal Society of London* B 357 2002, pp. 656–579. A key paper, online at www.journals.royalsoc.ac.uk/content/bwye9unlp8t5du1r/fulltext.pdf

Tzedakis, P.C. et al. 'The duration of forest stages in southern Europe and interglacial climate variability', *Science* 306 2004, pp. 2231–2235.

Willis, K.J. and K.J. Niklas 'The role of Quaternary environmental change in plant macroevolution: the exception or the rule', *Philosophical Transactions* *of the Royal Society* B 359 2004, pp. 159–172. Pdf from www.journals.royalsoc.ac.uk/content/102022

Zachos, J., M. Pagani, L. Sloan, E. Thomas and K. Billups ‘Trends, rhythms, and aberrations in global climate 65 Ma to present’, *Science* 292(5517) 2001, pp. 686–693. Note: this issue of Science has seven other papers on palaeoclimatology that are relevant to this chapter.

Further reading

An extensive and detailed list of further reading is provided on the University of London External Programme web site in the EMFSS student area, following the link for ‘Further unit subject guides’.

Internet resources

A preliminary version of *An Atlas of the Ice Age Earth* is obtainable by clicking on the region maps (page 2): Europe, Eurasia. Africa and Australasia. Each map comes with a full text explanations: for example, clicking the European map gives access to *Europe during the last 150,000 years*, which again has plenty of explanatory maps of vegetation distribution. An extensive bibliography is attached. Other links give papers on rainforests. www.esd.ornl.gov/projects/gen/rainfo.html and on the Pliocene www.esd.ornl.gov/projects/qen/pliocene.html

Benton, M.J. The Fossil Record 2.
The Fossil Record 2 database, located at the University of East London. A wonderful site, which allows you to plot the geological patterns of family diversity for different habitats and all the major families of the five kingdoms. At the time of writing, 7,186 families are recorded.
www.fossilrecord.net

BIOME 6000 vegetation reconstructions
www.ngdc.noaa.gov/paleo/biome6000.html
World Data Center for Paleoclimatology site gives surface reconstructions for 6,000 B.P. See also www.bgc-jena.mpg.de/bgc_prentice/projects/biome6000/biomes6000.html and http://stommel.tamu.edu/~baum/paleoveg.html for 27,000 B.P. maps.

Fossilrecord.net.
The Date-a Clade service for the molecular tree of life is excellent, www.fossilrecord.net/dateaclade/index.html. Clicking on the nodes of the cladograms gives snapshot information on the lineage of the group of animals shown.

Globalwarming.com.
This site contains downloadable graphic of world climate, CO_2, sea-level changes and slides, most of which can be freely downloaded. Excellent links to the sources, with some brief discussions.
www.globalwarmingart.com

ICWG (Ice Core Working Group)
Ice core contributions to global change research: past successes and future directions.
www.nicl-smo.sr.unh.edu/icwg/icwghtml.html

NOAA Climate Timeline Information Tool.
This an interactive presentation of climate signals from 1 day to beyond 100,000 years: www.ngdc.noaa.gov/paleo/ctl/overview.html
The section ‘Resources beyond 100,000 years’ deals with plate tectonics and climate: www.ngdc.noaa.gov/paleo/ctl/resourcebeyond.html

NOAA Paleoclimatology Program
www.ncdc.noaa.gov/paleo/paleo.html.
This site has some very useful online slides covering ice ages, tree rings, ice cores, coral reefs and fossil soils.
www.ncdc.noaa.gov/paleo/slides/slideset/index.html

North American Pollen Atlas Maps and Diagrams has interactive distribution maps and climatograms for Williams et al. (2006)
www.ncdc.noaa.gov/paleo/pollen/atlas/atlas.html

Pollen Viewer, WDC for Climatology.
This is an interactive viewer for selection and automatic plotting of isopollen maps in 1,000 year time steps from the maximum of the last glaciation in North America 18,000 years ago. Start with ‘palaeogeography with Ice Sheets.’
www.ncdc.noaa.gov/paleo/pollen/viewer/webviewer.html

Scotese, C.R. *Paleomap Project.*
This is the definitive site for plate tectonic reconstructions, with animations of plate movements and the assembly of Pangaea, and earth history. It also has graphs of average global temperature climate history from the Permian to the present. The Caribbean reconstruction is particularly informative regarding the American Biotic Interchange. The plate tectonic animations at the University of California’s Museum of Palaeontology based on Scotese’s animations are at www.ucmp.berkeley.edu/geology/tectonics.html.
www.scotese.com/Default.htm

Smithsonian Institute Human Evolution.
An interactive phylogenic tree of human origins with photographic illustrations of the fossils. The site Human Origins describes in detail the fieldwork campaigns if you follow the links at
www.mnh.si.edu/anthro/humanorigins/aop/aop1.html
www.mnh.si.edu/anthro/humanorigins/ha/a_tree.html

The Paleogeographic Atlas Project, University of Chicago (2000), Ziegler, F.
This site contains animations of plate tectonic evolutions and climate evolution. Wonderful and informative site.
http://pgap.uchicago.edu
USGS *This dynamic earth: the story of plate tectonics*.
Can either be viewed online as a sequence of animations, or downloaded as a pdf at http://pubs.usgs.gov/gip/dynamic/dynamic.html

World Data Centre (WDC) for Paleoclimatology.
Excellent overview of the various data sources for investigating palaeoclimate.
www.ncdc.noaa.gov/paleo/paleo.html

Introduction

We saw in Chapter 3 that the present-day patterns of families and genera are partially explicable using the evidence from plate tectonics. In particular, we noted that the present terrestrial continental configuration only came into existence during the mid-Cenozoic era – that is, about 25–30 million years ago. The last major period of the late Cenozoic – the Quaternary (and its associated glaciations) – finally moulded the distribution of flora and fauna worldwide to that which we see today.

The fossil record of flora and fauna

The record of life on earth is preserved in the sedimentary record as fossil remains, the study of which is palaeontology and palaeobiology. During the eighteenth and nineteenth centuries, methods of dating sedimentary rock using fossils were developed by Cuvier, Smith and Lyell. These records of the relative age of sediments based on their fossil content were used by Charles Darwin in 1859 in his *Origin of the species* to argue that life on earth had evolved through natural selection over the age of the earth, which in 1859 was estimated by Lord Kelvin to be about 100 million years.

The current estimate of the age of the earth at 4.56 billion years. The result of these endeavours was the development of the **geological timescale**[1] – one of the major scientific achievements of the last 200 years (Table 4.1).

Period or eon	Period/epoch	Time, millions of years ago	Geological events	Climatic events/extinctions	Biogeographic events
Archean		3.8–2.5 billion		• Reducing atmosphere	• First bacteria • Developments of Stromatolites
Proterozoic		2.5–0.544 billion	• Appearance of stable continents	• Oxygen begins to form • Banded iron formations • Glaciations	• Eukaryotic forms evolve 2.1 billion years ago, multicellular algae 1.8 billion years ago • First marine animals at 700 million years
Paleozoic	Cambrian	543–490	• Major continental fragments	• Early Cambrian extinction	• Multicellular marine life explosion-shelled invertebrates (trilobites)
			• Iapetus ocean separates America from other continents	• Oxygen levels close to present	• First fish • Microbial mats on land?
	Ordovician	490–443	• 2 major continental fragments: Gondwanaland and Euramerica	• Gondwanan Ice • Ordovician extinction	• Nautiloids, corals, graptolites appear • Trilobite peak • Non- vascular plants-lichens-bryophytes-fungi expand • Detrivors dominant
	Silurian	443–417		• Narrowing of Iapetus Ocean	• First land plants evolve from freshwater algae • First land arthropods (scorpions/spiders) • First ammonoids
	Devonian	417–354	• Iapetus Ocean closes • Caledonian Orogeny Urals, Appalachians	• Mid/late Devonian extinction	• Aquatic freshwater plants • Vascular plants-roots (ferns, horsetails) • Herbivory common • Gymnosperms appear 360 million years
	Carboniferous	354–290	• Pangaea forms • No barriers • Widespread marine transgression	• Tropical climate • Cooling • Glaciation, extinctions	• Major plants groups diversify • Insect herbivory • Plants include pteridosperms, ferns, lycopods, conifers, cordaites, sphenopsids • Reptiles appear
	Permian	290–248	• Pangaea nearly fully formed	• Major extinction at end • Permian Warming	• Regional differentiation of floras – Gigantopteris and Glossopteris • Ginkgoes • Cycadophytes • Conifers and pteridophytes dominate floras.
Mesozoic	Triassic	248–206	• Pangaea starts to break up in Late Triassic	• Major extinction ends Triassic Tropical	• Faunas cosmopolitan • First dinosaurs • Reptiles dominant • Ancestors of mammals.
	Jurassic	206–144	• Pangaea fragments into Laurasia and Gondwanaland, which breaks to form Africa, S. America, Australia and Indo-Madagascar.	• Tropical • Extinction event	• Birds evolve from reptiles • Vegetation mix of cycads, gymnosperms and herbaceous pteriophytes • Conifers most diverse group • Herbivorous insects common • Beetles appear • Herbivorous sauropods – Stegosaurs ecological dominants
	Cretaceous	144–65	• Pangaea continues to fragment • Laurasia subdivided by pro-Atlantic • Circumtropical Tethys sea	• Warm • Major extinction event	• First angiosperms important in tropics • Conifers, cycads, cycadeoids similar to Jurassic • In late C. angiosperms undergo explosive diversification • Lepidoptera, ants, termites, aphids, gall-wasps first appear
Cenozoic	Paleocene	65–54.8	• Laurasia reunited as circumpolar landmass • Southern continents widely separated	• Sub-tropical climate dominant, although overall cooling continues	• Mammals rapidly become dominant • Marsupials evolve in S America and radiate to Australia via Antarctica • Angiosperms dominate terrestrial ecosystems
	Eocene	54.8–33.7	• Eurasia and N. America separated by Atlantic • Africa joins Laurasia	• Climate cools and dries in tropical regions	• Co-evolutionary radiation between biotically dispersed angiosperms and fruit/seed eating mammals
	Oligocene	33.7–23.8	• India with Asia-Himalayas starting		
	Miocene	23.8–5.3	• Alps formed in Europe by northward movemen of Africa • Australia moves towards south-east Asia	• Global cooling continues	• First grasses appear • Modern placentals in Laurasia, marsupials in Australia, S. America • Savanna biomes form.

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[1] *See the UCMP site for an interactive version of this (www.ucmp.berkeley.edu/exhibit/exhibits.html).*

	Pliocene	5.3–1.8	• Land-bridge between N and S America forms • Wallaces's line formed in south-east Asia	• Global cooling, and sea levels start to fall • Tropics wetter/ warmer than present	• Mammal exchange between North and South America • Rise of primates • Savannas become established • Hominid ancestors in savanna woodlands, Africa
	Pleistocene	1.8–0.01	• Continents in present configuration • Bering land-bridge open during quaternary low sea-levels	• Onset of Quaternary glaciations with Milankovich cycles	• Major equatorial migration of biomes in glacial advances • Homo sapiens evolves from Neanderthals/Cro-Magnon
	Holocene	0.01–present	• No changes	• Holocene warming • Sea-level rises 230 m • Extinction event? • Anthropogenic warming • CO2 highest since early Tertiary	• All biomes/ecosystems disturbed by humans • Major deforestation • Anthropogenic increase in CO2 • Major losses of species/biodiversity • Major biogeochemical cycles disturbed • Spread of agroecosystems

Table 4.1 Patterns in time: Major events in the evolution of the continental crust, the global climate, animals, plant, extinctions and ice-ages and global sea level. Ages are based on the 1999 Geologic Timescale (http://mologic.org/temp/gsatimescl.pdf)

Plate tectonics and biogeography

In 1910, Alfred Wegener was one of the first scientists to use the evidence presented by fossils, geology and topography (marine and terrestrial) to hypothesise that during the Late Carboniferous period there was a single supercontinent – Pangaea (Greek, 'all earth') – which fragmented; the individual continental fragments drifting to their present positions.[2] The biological consequence of this **theory of plate tectonics** has been profound, and it is described Lomolino et al. (2005), and by Cox and Moore (2005). The details of the changing plate positions are given in Table 4.1.

Learning activity

At this stage, you should run one of the plate tectonic simulation programs listed above. The simulations easiest to use are those provided by Scotese's Paleomap Project web site.

Use the simulations provided by this program to investigate the following:

- the formation of Pangaea (spelled 'Pangea' on the web site)
- the break-up of Pangaea
- the evolution the Caribbean and joining of North and South America
- the movement of India/Madagascar
- climate history of the different epoch/periods
- palaeoclimate changes associated with plate movement over time.

The other site worth investigating is that of the University of Chicago's Paleogeographic Atlas Project (http://pgap.uchicago.edu), which shows how fossil evidence can be used to reconstruct past climates in the Jurassic and Permian periods.

The evolution of terrestrial life – plants and animals – which started in the Cambrian and Ordovician, was associated with the formation of Pangaea about 350 Ma, and its subsequent fragmentation after the Triassic, 248 Ma.

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[2] *See the USGS site* This dynamic earth *at http://pubs.usgs.gov/gip/dynamic/dynamic.html and The Paleogeographic Atlas Project, University of Chicago. This site contains animations of plate tectonic evolutions and climate evolution. http://pgap.uchicago.edu). Wonderful and informative site.*

Global climate over time

The major trends of climate over the earth's surface since the Cambrian are reviewed at the Paleomap Project's web site, and Zachos et al. (2001).[3] The general patterns observed are as follows.

Over Phanerozoic time, latitudinal gradients of climate have generally had two modes:

- A **cold climate mode**, in which the latitudinal temperature gradient was such that there was polar ice and the equatorial regions were cooler and drier – the present Holocene is an example, as are the Carboniferous–Permian periods. Average global temperature was about 12°C and sea levels were lower.
- A **warm climate mode**, in which the latitudinal temperature gradient was such that there was no polar ice and the equatorial regions were warmer and more humid – the Jurassic and Cretaceous periods are examples. Average global temperature was about 20°C and sea levels were higher.

Greatest marine inundations occurred in the Ordovician–Silurian and Cretaceous periods; sea level was lowest in the Precambrian, Permo-Triassic and Quaternary periods.[4]

Glaciations when the continental plates moved over or nearer to the poles were associated with reduced or fluctuating sea levels. These major glaciations occurred in the Precambrian, Cambrian, Late Ordovician (in the Sahara), Carboniferous–Permian (Gondwana continents) and Quaternary periods and they also relate to changes in atmospheric CO_2 levels (see Figure 4.1).

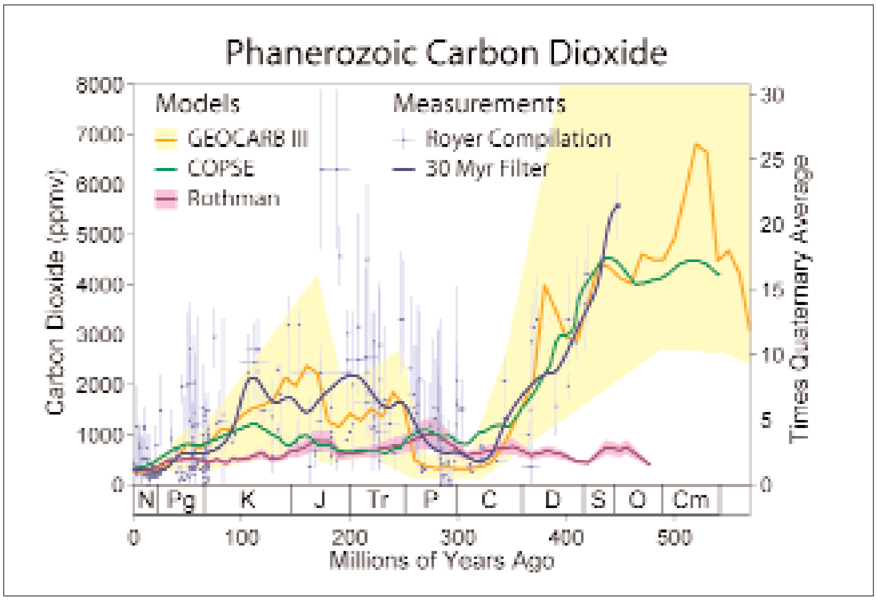

Figure 4.1 Long-term changes in atmospheric CO_2

www.globalwarmingart.com/wiki/Image:Phanerozoic_Carbon_Dioxide_png

Learning activity

Compare the temperature record of the Phanerozoic with the CO_2 record over the same period, using the references and sources cited.

How do these records relate to the changes in eustatic sea-level reported for the same period by Miller et al. (2005)?

Now consider the opportunity that flora and fauna had/have for dispersal over the last 65 m.y., in relation to barriers or land-bridges. Does any pattern emerge? Hint: look at

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[3] *See www.Globalwarmingart.com/wiki This site contains downloadable graphics of world climate over the last 65 My, CO_2, sea-level changes, most of which can be freely downloaded. Excellent links to the sources, with some brief discussions.*

[4] *See the graphic of sea-level change at www.globalwarmingart.com/wiki/Image:Phanerozoic_Sea_Level_png over the last 540 My, and the paper by Miller et al. (2005). The Phanerozoic record of global sea-level change,* Science *310, pp. 1293–1298.*

the Paleomap simulation of plate tectonics for the last 40 my in south-east Asia and Central America.

The combination of tectonic changes, CO_2 changes and the associated long-term climatic changes briefly reviewed above have produced a generalised model of two Phanerozoic supercycles (see Figure 4.2).[5]

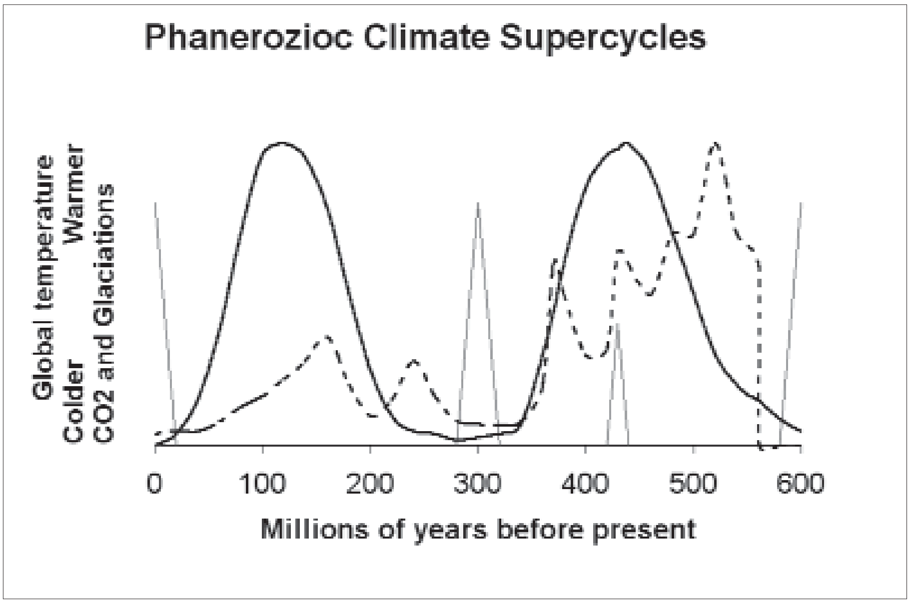

Figure 4.2 Phanerozoic supercycles

What this discussion shows is that nearly all of the indicators listed above are correlated, although the pattern of sea levels is not so clear. The subject of Pleistocene (Quaternary) environmental change will be discussed later in this chapter.

Learning activity

At this stage, it would be useful if you were to investigate the ways in which global climate has changed over the last 500 m.y. using the sources given and Scotese's Paleomap Project web site, which has palaeoclimate reconstructions.

Questions that you might consider are:

- What relations exist between global temperature and atmospheric CO_2?
- How does the distribution of land and sea affect continental aridity, and what effects might this have on evolution?
- What were the major vicariance events (barriers, land bridges, etc.) over this period of time?
- What effect does climate change (temperature) have on sea levels over this period of time?

Important geological–biogeographical events were:

- the joining of the Eurasian and African plates in the Early Miocene period, which permitted the migration of mammals, including early hominids, into Eurasia
- Other important biogeographical events were the isolation of South America, which resulted in the isolation of the flora and fauna, and the movement of Australia away from Antarctica northwards on its 50 million years' drift towards south-east Asia.[6] The collision of the Australian plate with the Indonesian plate between 15 m.y. and 3 m.y. and the creation of the biotic discontinuity called Wallace's Line.

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[5] *But see the more detailed illustration at www.globalwarmingart.com/wiki/Image: Phanerozoic_Climate_Change_Rev_png and the accompanying notes and references.*

[6] *See Lomolino et al. (2005), Chapters 9 and 10.*

- The joining of North America and South America about 3.5 million years ago, which provided a filter dispersal route between the two continents.[7] This resulted in what has been called 'the Great American biotic interchange', which saw more genera move south than northwards. For example, only three southern species – porcupine, opossum and armadillo – are now found in North America.[8]

Patterns of animal and plant diversification

You should have already studied Table 4.1, which shows that there have been several distinctive phases of expansion and diversification of life forms on earth. There are excellent discussions of these changes in the text by Willis and McElwain (2002), and the paper by Benton and Emerson (2007).[9] The major biological changes that have taken place to the terrestrial flora and fauna are outlined below:

- **'Slime World'** 3.8 to 0.54 billion years (b.y.) of the emergence of **prokaryotes** – anaerobic (without free oxygen) **bacteria** at about 3.8 b.y and **cyanobacteria** (blue-green algae) at about 3.5 b.y. The latter formed **stromatolites** – calcareous mats covered on the outside by photosynthesising cyanobacteria, with anaerobic bacteria below – which can be found, for example, alive and well in western Australia at Shark Bay. **Eukaryotic** organisms – primarily algae – evolved in the oceans, and **protists** – single-celled organisms in the oceans – evolved about 1 b.y. Soft-bodied organisms, such as 'jellyfish' (medusoids) and primitive arthropods – animals with joined legs – are found from about 670 m.y.
- **Plants on land**.[10] The most recent findings – part of the 'Deep Green' Floral Genome Project – show that green, land plants evolved from freshwater green algae before evolutionary divergence about 470 million years ago into two phyla: the **Streptophyta** (green plants, including related green algae known as charophytes) and the **Chlorophyta** (the rest of the green algae). The first land plants were spore-producing **liverworts and mosses**. The emergence of green, land plants allowed arthropods to follow. **Vascular plants** – for example, *Cooksonia* – and true seed plants had evolved by the end of the Devonian. The earliest forests included tree-like lycopods (an ancestor of the club mosses) and the ancestors of gymnosperms *Archaeopteris*.
- The first seed plants – *pteridosperms* or seed ferns, which are now extinct – occurred at the end of the Devonian period. **Gymnosperms** made their first appearance and began to dominate the drier areas away from the floodplains.[11] By the end of the Permian period, conifers had become widespread, and in Gondwanaland, the flora was dominated by the pteridosperms *Glossopteris* and *Gangamopteris*. In the Jurassic period, there was a rapid evolution of the flora, with the appearance of true ferns, cycads, cycadeoids, Ginko and horsetails (*Equisetites*), along with new conifers and pteridosperms. It is estimated that 80 per cent of the plant species at this time were gymnosperms (Willis and McElwain, 2002).
- The early Cretaceous period saw the evolution of the first flowering plants – the **angiosperms** – and their rapid radiation and taxonomic diversification in the Late Cretaceous, especially in tropical regions. High-latitude Late Cretaceous floras tended to be dominated by conifers and ferns.

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[7] *See the excellent discussion in Lomolino et al. (2005), Chapters 9 and 10.*

[8] *See the Biographic note on Wallace at http://evolution.berkeley.edu/evolibrary/article/_0/history_16 and at http://en.wikipedia.org/wiki/Alfred_Russel_Wallace. Wallace independently arrived at the theory of evolution at the same time at Charles Darwin 1858 in his paper 'On the tendency of varieties to depart indefinitely from the original type' (www.zoo.uib.no/classics/varieties.html)*

[9] *Available online at http://palaeo.gly.bris.ac.uk/Benton/reprints/2007diversification.pdf*

[10] *The best account of this is the text by Willis and McElwain (2002) – see www.oup.com/uk/plantevol where you can view PowerPoint presentations of biomes evolution over the last 470 Ma.*

[11] *See History of Palaeozoic Forests site (www.uni-muenster.de/GeoPalaeontologie/Paleao/Palbot/ewald.html).*

- The major evolutionary radiations after the Cretaceous were further diversification of the angiosperms. This culminated in the Eocene period, when tropical multistratal forests occurred as far north as 30ºN and subtropical vegetation to 60ºN was typified by the Eocene London Clay flora.
- The evolution and radiation of grasses in the late Eocene period, probably associated with the increasing seasonality, cooling and drying of mid-latitude regions.[12]
- Global cooling continued and was associated with a gradual expansion of C3 and C4 grassland-dominated ecosystems (Sage, 2004), open woodland and deserts. Evergreen forest species were gradually replaced by broad-leaved deciduous trees in temperate forests, and palaeotropical evergreen forests were restricted to equatorial regions. Herbaceous dicotyledons and monocotyledons evolved and diversified.
- Animals on land. Initially, terrestrial life was dominated by arthropods – animals with jointed legs, such as insects, scorpions, spiders – all detritus feeders. During the late Carboniferous–early Permian periods, terrestrial tetrapods (four-footed vertebrates) made their appearance as amphibians; they were predominately insectivores and carnivores. Reptiles appeared and became widespread in the Permian period. Major species and family extinctions of animals occurred during this period. In the Jurassic period, the first dinosaurs appeared, becoming dominant on the land and spreading to the air (pterosaurs) by the end of the Jurassic period.
- The start of the break-up of Pangaea produced pronounced differences in tetrapod faunas, with herbivorous sauropods becoming dominant in the southern hemisphere. There was a decrease in diversity in the northern hemisphere, as hadrosaurid ornithopods increased their circumpolar distribution. Toothed birds (*Archaeopteryx*) evolved from reptiles. Flies appeared, along with gall-wasps, termites, ants and bees. Small mammals made their first appearance. Finally, the earliest placentals evolved in the Late Cretaceous north of the Tethys Sea – marsupials and probably the monotremes evolved in the America–Antarctica–Australia continental land mass. A mass extinction event at the end of the Cretaceous wiped out the dinosaurs.
- Throughout the Palaeogene period, global temperatures gradually fell.[13] The rapid diversification of the angiosperms lead to their dominance of terrestrial ecosystems, along with the co-evolution of fruit- and seed-eating mammals and pollinating insects, such as moths and butterflies.
- A huge rise in mammal placental diversity in the Palaeocene–Holocene period. Bird diversity increased.
- The expansion of savannah-like open woodlands and warm temperate forests provided a suitable habitat for the evolution of early hominids. You should remember that the Sahara was probably covered in semi-arid vegetation up to about 1. 8 million years ago.[14] The origin and expansions of early hominids from Africa is discussed in detail by Stringer (2002) and Forster (2004).

This brief overview of the various biological radiations needs to be viewed in conjunction with the climatic, tectonic and eustatic sea-level changes already mentioned above. What is evident is that many of the patterns of families and genera discussed in the previous chapter are accountable in terms of these combined environmental variables.

[12] *See the recent review of the rise of C4 grasses by R.F. Sage 'The evolution of C4 photosynthesis',* New Phytologist *161 2004, pp. 341–370, and the article by Cerling et al. 'Carbon dioxide starvation, the development of C4 ecosystems, and mammalian evolution',* Phil. Trans. R. Soc. Lond. *353 1998, pp. 159–171.*

[13] *See the illustration and notes at www.globalwarmingart.com/wiki/Image:65_Myr_Climate_Change_Rev_png*

[14] *See Johnathan Adams web site link to the Pliocene.*

Learning activity

Open the FossilRecord.net link at www.fossilrecord.net/dateaclade/index.html, and interactively review the evolution of:

- mammals
- insects
- primates.

You will note that the major radiations take place in the Late Palaeozoic, Mesozoic and Cenozoic. Relate these radiations to plate tectonics and Phanerozoic climate change.

Patterns of extinction

Benton and Emerson (2007) have recently showed that the fossil record of all the organisms in the Fossil Record 2 database demonstrate an exponential increase since the Precambrian period.

Benton and Emerson showed that Sepkoski's five major mass extinctions in the marine fossil record – the Ordovician–Silurian, the Late Devonian, the end-Permian, the Triassic–Jurassic and the Cretaceous–Tertiary (K/T) – also extended to the terrestrial faunal record. They also recognised and confirmed that extinctions also took place in the Early Cambrian and Late Carboniferous. The most significant extinction event was the end-Permian event, in which 60.9 per cent of all life, 62.9 per cent of marine organisms and 42.6 per cent of terrestrial organisms died out. The Cretaceous–Tertiary extinction only accounted for a maximum of about 13 per cent of all organisms.[15]

There is a good discussions of these various hypotheses by MacLeod (2003).[16] It is noteworthy that the extinctions so widespread in the faunal record do not appear in the global floral record – a point worth thinking about.

Quaternary environmental change[17]

After the long cooling that took place during the Cenozoic period, the Quaternary period (1.8 m.y. to the present) has, so far, been marked by a sequence of northern and southern hemispheric glaciations, the last finishing about 12,000 years ago. During these glacial episodes, much of Europe, North America and Central Asia (one-third of the land surface) was covered by ice sheets up to 3 kilometres thick. The present Antarctic ice sheet is the nearest extant example. You will recall that the previous major global glaciations occurred in the Permo–Carboniferous period (about 300 m.y.), in the Late Ordovician period (about 450 m.y.), in the Late Proterozoic period (between 800 and 670 m.y.) and in the Early Proterozoic period (about 2.3 b.y.).

Geological, geomorphological and ocean sediments evidence shows that cool periods and glaciations have occurred throughout the Quaternary period:

- **Glacials**, which are extensive periods of cold associated with the spread of ice sheets and glaciers. The last British glacial, the Devensian (Wurm, Weichelian), is the equivalent to the Wisconsin[18] in North America. Sea levels are lowered during glacials. Glaciations occupy 80 per cent of the Quaternary period, and vary in duration between 75,000 to 300,000 years. During these glaciations, much of the northern hemisphere land surfaces were ice covered, with extensive permafrost as far south as 40^o N (Hewitt, 2000).

[15] *See the paper by MacLeod (2003) on Extinctions.*

[16] *Listen to the video recording of Dr MacLeod regarding the geological record and extinctions.*

[17] *See the NOAA Paleoclimatology Time-line link at www.ngdc.noaa.gov/paleo/ctl for a 'Powers of 10' review of Quaternary climatic graphics.*

[18] *See http://en.wikipedia.org/wiki/Wisconsin_glaciation for a discussion.*

- **Interglacials**, or warmer, non-glacial periods (such as the present Holocene), in which mid-latitudinal forests expanded poleward. Sea levels are high in interglacials. Typical interglacials were of short duration, typically 10,000–30,000 years, and only occupy 20 per cent of Quaternary time. At these times thermophilic (heat-loving) species migrated from the various glacial refugia, as discussed below. Climate at these times was essentially similar to that of the present.

Learning activity

Use the NOAA Paleoclimatology link to explore the extend of the Last Glacial Maximum and its melting at www.ncdc.noaa.gov/cgi-bin/paleo/peltice.pl and its thickness at www.ncdc.noaa.gov/cgi-bin/paleo/pelttopo.pl

Quaternary cycles of climatic change

Since Louis Agassiz first recognised the evidence of glaciation in 1837, and the four glaciations in Europe – the Guntz, Mindel, Riss and Wurm – were subsequently identified by Geikie and Penck and Bruckner, various theories have been put forward about the causes of glaciations. The current view is based on the **Milankovitch astronomical theory**.[19] This theory predicted that three major cycles of climatic forcing have periodicities of 100,000 years, 42,000 years and 21,000 years, associated with cycles of eccentricity, cycles of obliquity, and the precession of the equinoxes in the sun–earth system.

The marine isotope record of benthic foraminifer shells has confirmed that there were at least seven cold periods. During glaciations the seawater and foraminifer shells contains more ^{18}O than during interglacial times.[20] The first accurate chronology of the Late Pleistocene climate, based on the pioneering research of N.J. Shackleton, was provided by Pacific ocean deep-sea cores and was subdivided into '**marine isotope stages**' – odd numbers for warm episodes, even numbers for glacial stages. Spectral analysis of these and other cores (see SPECMAP[21]) provided the first confirmation of the dominance of the 100,000-year cycle and its link to both Milankovitch theory and CO_2 (Shackleton, 2000). Over the 2.6 Ma (million years) of the 5.3 Ma marine oxygen isotope record, there are 104 marine isotope stages, with alternating warm (odd numbers) and major cold periods (even numbers) at roughly 100,000-year intervals during the first 800,000 years. The paper by Didier Paillard (2001) provides an excellent review of the various hypotheses and the latest thinking on the causes of glacial cycle, and it should be read.

The ice-core record

Ice cores obtained from the Antarctic and Greenland over the last 15 years provide an uninterrupted record of climatic and environmental changes over the last 740,000 years (Petit et al., 2000; ICWG web site; EPICA community members, 2004). In particular, they provide evidence of past:

- temperature via the deuterium content of the ice
- CO_2 and CH_4 (methane) and N_2O (nitrous oxide)
- ^{18}O isotope, which reflects changes in global ice volume
- dust and dust chemistry (sodium and calcium, which reflect both volcanic activity and interglacial and interpluvial periods)
- biomass burning

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[19] *See http://earthobservatory.nasa.gov/Library/Giants/Milankovitch/milankovitch_2.html and http://en.wikipedia.org/wiki/Milankovitch_cycles for fuller details*

[20] *'Cold climates, warm climates: How can we tell past temperatures?' See www.giss.nasa.gov/research/intro/schmidt.01 and www.giss.nasa.gov/research/ briefs/schmidt_01/*

[21] *SPECMAP information can be found at www.ncdc.noaa.gov/paleo/paleo.html*

- anthropogenic impacts on atmospheric chemistry: sulphate (SO_4), nitrate (NO_3) and chloride (Cl), which are all indicators of fossil fuel burning and acid deposition
- changes in atmospheric circulation patterns.

The Vostok and Greenland ice cores have provided proof that atmospheric CO_2 and CH_4 are strongly involved in glaciations – glacial periods always have lower levels of these gases and interglacial have higher levels. The IPCC (2007) climate change report has an excellent review of the palaeoclimate data for the Quaternary (Jansen et al., 2007).[22]

The Vostok core shows four climate cycles, corresponding to the marine isotope record. The last four interglacials occurred at isotope stages 5e, 7e, 9c and 11 and usually lasted for periods of 10,000–15,000 years. During each interglacial, sea levels rose by up to 130 metres. The Antarctic Dome C results now extend the record to eight glacial cycles, although the four glacials before 430,000 years have a lower amplitude and much longer interglacial periods. The reasons for this change are not yet fully understood.

Holocene climate change

The Pleistocene period terminated with a rapid warming (the Late Glacial or Allerod Interstadial in Europe), interrupted by a short sharp cold stadial – the Loch Lomond readvance in the UK and Younger Dryas in Scandinavia. The pattern of climate change in the last 10,000 years (the Holocene) has been marked by rapid warming (by 4–5ºC) to the Holocene temperature optimum between 4,000 and 7,000 years before present (B.P.),[23] when temperatures were about 1ºC warmer than at present. Sea levels rose by up to 122 metres. Between 4,000 and 2,000 years B.P., the climate cooled, and it then warmed to the little optimum, AD 750–1300 (Jansen et al., 2007). The following period, AD 1450–1890, was marked by global cooling – the 'little ice age' – until the warming trend resumed in the 1900s. Good discussions of these climatic changes can be found in Jansen et al. (2007).

Quaternary biotic change

In biogeography, we are not so much interested in glaciations per se, but rather the effect of the associated climatic changes and pedological changes on the biota of the earth. During the onset of the Pleistocene, the flora and fauna of temperate regions such as North America and northern Europe were dominated by genera such as Sequoia, Tsuga, Carya and Nyssa, which formed part of the circumboreal flora of the northern hemisphere.

An international research programme, called BIOME 6000,[24] has used extensive palaeovegetation data (primarily pollen and plant macrofossils) along with climate modelling to reconstruct past vegetation/biome distributions at the following times in the past, for both northern and southern hemispheres:

- the Holocene climatic optimum at 6,000 years B.P.
- the last glacial maximum of the Weichselian at 27,000 years B.P.[25]
- palaeoclimate–vegetation simulations for 21,000, 16,000, 14,000, 11,000 and 6,000 years ago.

[22] *The IPCC Report chapter is accessible online at http://ipcc-wg1.ucar.edu/wg1/Report/ AR4WG1_Ch06-v2.pdf*

[23] *B.P. means 'before 1957'.*

[24] *The World Data Center (WDC) maintains the Biome6000 records for palaeoclimate at www.ncdc.noaa.gov/paleo/biome6000.html and www.ncdc.noaa.gov/paleo/biome6000_figures.html*

[25] *See Biome6000 web sites.*

Learning activity

Access the BIOME6000 site at www.ncdc.noaa.gov/paleo/biome6000_figures.html and download the biome reconstructions for 0, 6,000, and 18,000 years B.P.

Compare the changing distributions of the temperate forest and boreal forest northern limits at full glacial (18,000 years B.P.) and post-glacial optimum (6,000 years B.P.). How far did the vegetation biome boundaries move on each continent?

The *Global atlas of palaeovegetation* reconstructions by Adams (1997) and Adams and Faure (1997)[26] use a combination of plant fossils, faunal evidence and palaeopedological evidence published in the literature to give reconstructions for all regions of the world between 150,000 years ago – that is the Eemian interglacial warm Isotope Stage 5e – and the present. This material is essential reading, but don't forget to follow the citations to the literature. Print out the maps and compare the changing biomes over a full glacial cycle.

Flora of glacial periods in western Europe

The flora of glacial periods in western Europe has been reviewed by, for example, Adams (1997), who showed that, in general, they were dominated by Arctic and alpine elements, such as dwarf willows, Arctic birch, *Dryas octapetala*, lichens and mosses. This vegetation is similar to that found in present-day tundra, which we will consider in a later chapter. Globally, polar deserts, semi-deserts, tundra and evergreen warm/mixed forests reached their maximum extent.

Glacial refugia during the glaciations

During the glacial advances, species underwent repeated cycles of habitat fragmentation, isolation, local extinction and migration, as vegetation changed from forested to non-forested (Allen et al., 1999; Willis and Niklas, 2004). Within Europe, remnants of the formerly extensive forest species were isolated in the northern Mediterranean peninsulas of Spain, Italy and Greece. Since the Late Tertiary, the number of tree (arboreal) taxa of north-western Europe underwent a progressive reduction from 49 to 16 at the start of the Holocene (Willis and Niklas, 2004). The current European widespread genera have a greater tolerance of winter temperatures and cold growing seasons than the extinct genera.

Case study of taxa migration in Europe: *Pinus sylvestris* (Scots pine)

Cheddadi et al. (2005) reconstructed the migration routes and location of glacial refugia for *Pinus sylvestris* in north-western Europe. During the last glacial maximum (LGM), *P. sylvestris* was restricted to three sites – Iberian(A) and Italian (B) peninsulas, and parts of Hungary and the Alps (C). Mitochondrial DNA was used to identify three different haplotypes; haplotypes from C dominate the present-day remaining distribution. This shows how modern genetic diversity has been changed by Quaternary glaciations.

(N.B. Haplotypes are defined as a set of alleles of closely linked loci on a chromosome that tend to be inherited together.)

Flora of interglacial periods in western Europe

Each interglacial period, including the present one, is marked by a rise in temperature (3–6°C) to an optimum, followed by a fall as the ice sheets expand again. Usually, extreme dryness occurs at the opening of an interglacial, so that the tropical-dry savanna, cool grass/shrub and tropical forest biomes are at their maximum extent at these times, and they contract

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[26] *Adams, J.M. and H. Faure. (eds) Review and atlas of palaeovegetation: Preliminary land ecosystem maps since the Last glacial maximum. (1997) (www.esd.ornl.gov/ern/qen/adams1.html). Superb review and maps.*

as the interglacial progresses. Palynological evidence from a wide range of sites in Europe has shown that there is a distinctive cycle of vegetation change, which passes through four phases:

I **Cryotocratic phase**: in which the climate is cold, soils are immature and base-rich, vegetation is open Arctic–alpine, and permafrost and solifluction are common. As the temperature warms, this passes into the:

II **Protocratic phase**: in which the base-rich, mull soils deepen, and the vegetation passes from park-tundra to light-demanding woodland genera and grassland dominated by *Betula, Populus, Salix* and *Corylus*. This is followed by the:

III **Mesocratic phase**: which has deep, mature, brown forest, moderately acid, mull soils. Climax-closed, deciduous forests are dominated by *Quercus, Ulmus, Tilia* and *Corylus*. As the temperature starts to fall the:

IV **Telocratic or oligocratic phase** starts, rainfall increases and soils become increasingly leached to low nutrient status mor acid podsols and acid brown earths. Coniferous forests dominated by *Picea, Abies* and *Fagus* and blanket bog and peats expand. As cooling continues, boreal genera, such as *Pinus* and *Betula*, expand, along with heathland/moorland dominated by Ericaceous genera.

The basic pattern of these phases of change have been confirmed for both Europe (e.g. Cheddadi et al., 2005; Tzedakis et al., 2004) and North America. Pollen isochrone maps for north-western Europe have been published by for example Birks (1989). You should study these maps and papers very carefully, as they show that the rate of northward migration depends on the tree species involved.

Learning activity

1. Use the Adams web sites, the published palaeovegetation maps, and the Pollen Viewer WWW to discover the pattern of vegetation change in Europe, North America, Africa, Asia and South America during the Quaternary.

   What do these palynological studies tell us about the rate of vegetation advance northwards of post-glacial Europe and North America?
2. Use the NOAA Paleoclimate link at www.ngdc.noaa.gov/paleo/ctl/clisci100kb.html to download the pollen diagram for Lago Grande di Monticchio, Italy, 1–100,000 B.P. Read Allen et el. (1999) and comment on the changes in biomes and pollen types between the glacial and interglacial (Eemian and Holocene) periods.
3. Use the Interactive Pollen Viewer at www.ncdc.noaa.gov/paleo/pollen/viewer/webviewer.html to view pollen maps of North American. American plant taxa distributional changes since the last glacial maximum (LGM). How do the North American taxa changes differ from the European ones?

Expansion of humans and their ancestors[27]

The earliest hominids – including *Australopithecus afarensis* (‘Lucy’) – had their origins in East Africa in the Late Tertiary and Early Pleistocene (5.3 to 1.6 million years ago), and they were the ancestors of *Homo habilis, Homo erectus* and *Homo neanderthalensis*, who lived in the period 1.6–0.25 million years ago.

The first archaic human species – *Homo sapiens sapiens* – were found in Africa 175,000 years ago and Cro-Magnon man was found in West Asia

[27] *See the Smithsonian Institute Human Evolution web site for detailed phylogenies and illustrations.*

100,000–90,000 years ago (Stringer, 2002). True humans – *Homo sapiens* – probably made their appearance about 52,000 years ago.[28] It has been argued that the evolution and spread of hominids around the globe was due to the environmental impacts of the Quaternary glaciations, with the expansion of savanna grasslands and lowering of sea level being the major factors.

The best evidence for the last hominid migration out of Africa 80–60 k.y. ago is based on recent work on maternally inherited mitochondria DNA (Forster, 2004). The maps of Forster (2004) show the movement after 60 k.y. was eastward, and then divergent; one branch going north-east to central Asia, the other following the coastline of the Indian Ocean eastwards through Indo-China to Papua New Guinea and Australia by about 50 k.y. The earliest North American migrants came over the Bering land bridge (Beringia) into Alaska around 20 k.y. ago, and eventually reached South America by about 15 k.y. The rest of North America and Eurasia was inhabited when the Devensian Ice finally retreated about 12 k.y. ago. The final migration was into Micronesia and Polynesia about 2 k.y. ago.

Associated with the expansion of hominids after 60 k.y. are major megafaunal extinctions that saw the elimination of most birds and large mammals weighing greater than 5 kg and other ecological changes, with a repeatable pattern – e.g. in both Australia and the Americas. Two hypotheses – the 'overkill hypothesis' of Paul Martin[29] and the 'climate-change hypothesis' – are still hotly contested.

The major difference between vegetation change in the present interglacial – the Holocene or Flandrian – and earlier interglacials is the impact of *Homo sapiens*. Although Upper Palaeolithic and Mesolithic (10,000–5,700 years B.P.) human vegetation impacts were small, the activities of Neolithic farmers (5,700–4,000 years B.P.) is indicated by increases in grass pollen and weed pollen associated with forest clearance, such as plantains (*Plantago lanceolata*), dock (*Rumex*) and nettle (*Urtica*), and a dramatic decrease in the elm (*Ulmus*) pollen – the so-called 'elm decline'. Considerable controversy exists over the cause of this decline, but the most recent research suggests that elm disease, rather than Neolithic clearance, was the major cause. During the Bronze Age (4,000–2,700 years B.P.) and Iron Age (2,700–2,000 years B.P.), forest clearance continued and animal cultivation became important.

A reminder of your learning outcomes

In this chapter, we have covered an enormous amount of material, and by the end of this chapter and the relevant reading, you should be able to:

- describe the advent, evolution and kinds of life on earth
- relate life on earth to the abiotic climate and geological controls
- describe the major functional groups of plant and animal life and when they first appeared
- describe the major radiations of reptiles, mammals, gymnosperms, angiosperms and grasses
- relate these radiations to Phanerozoic tectonic plate positions, especially the Great America Biotic Interchange
- account for the major extinctions in the biological record
- describe the biological impact of Pleistocene glaciations on the latitudinal distribution of global biomes
- discuss the evidence for Quaternary environmental and biological change.

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[28] *See the Smithsonian Institution Human Origins Program 'dedicated to understanding the biological and cultural foundations of human life'. www.mnh.si.edu/anthro/humanorigins*

[29] *See the review in American Scientist at www.americanscientist.org/template/BookReviewTypeDetail/assetid/50748*

Sample examination questions

1. 'Plate tectonics, perhaps more than any other phenomena, has had profound effects on the biogeographical patterns of both terrestrial and marine biotas'. Discuss.
2. 'Most of the global turnover of species [genera and families] has been gradual, rather than catastrophic.' Discuss with examples.
3. 'Our understanding of Quaternary environmental change has been irreversibly changed as a result of deep-ocean sediment and ice-core research.' Discuss.
4. Critically review the kinds of evidence that can be used to reconstruct past vegetation at the local and biome scale.
5. Account for the impact of *Homo sapiens* on terrestrial ecosystems before AD 0.

Notes