Figure 1.1 People love to collect fossils. Many professional paleontologists got into the field because of the buzz of finding something beautiful that came from a plant or animal that died millions of years ago. Fossils such as these tiny fishes from the Eocene of Wyoming (a),
may amaze us by their abundance, or like the lacewing fly in amber (b), by the exquisite detail of their preservation. (Courtesy of Sten Lennart Jakobsen.)
Figure 1.2 Important figures in the history of science: (a) Sir Francis Bacon (1561–1626), who established the methods of induction in science; and (b) Karl Popper (1902–1994), who explained that scientists adopt the hypothetico-deductive method.
Figure 1.3 Reconstructed skeleton of the oviraptorid *Ingenia* sitting over its nest, protecting its eggs. This is a Bay State Fossils Replica.
Figure 1.4 Some of the earliest reconstructions of fossil mammals. These outline sketches were drawn by C. L. Laurillard in the 1820s and 1830s, under the direction of Georges Cuvier. The image shows two species each of *Anoplotherium* and *Palaeotherium*, based on specimens Cuvier had reconstructed from the Tertiary deposits of the Paris Basin. (Modified from Cuvier 1834–1836.)
Figure 1.5 The sabertooth *Smilodon* as seen in *Walking with Beasts* (2001). The animals were reconstructed from excellent skeletons preserved at Rancho La Brea in Los Angeles, and the hair and behavior were based on studies of the fossils and comparisons with modern large cats. (Courtesy of Tim Haines, image © BBC 2001.)
Figure 1.6 Lying stones: two of the remarkable "fossils" described by Professor Beringer of Wurzburg in 1726: he believed these specimens represented real animals of ancient times that had crystallized into the rocks by the action of sunlight.
Figure 1.7 Nicolaus Steno's (1667) classic demonstration that fossils represent the remains of ancient animals. He showed the head of a dissected shark together with two fossil teeth, previously called glossopetrae, or tongue stones. The fossils are exactly like the modern shark's teeth.
Figure 1.8 Proof of extinction: Cuvier's comparison of (a) the lower jaw of a mammoth and (b) a modern Indian elephant. (Courtesy of Eric Buffetaut.)
Figure 1.9 The first dinosaur craze in England in the 1850s was fueled by new discoveries and dramatic new reconstructions of the ancient inhabitants of that country. This picture, inspired by
Sir Richard Owen, is based on his view that dinosaurs were almost mammal-like. (Courtesy of Eric Buffetaut.)
Figure 1.10 Statistical study of the Permian brachiopod *Dielasma*. Two measurements, sagittal length (L) and maximum width (W) were made on all specimens. The size–frequency distributions (a, b) indicate an enormous number of small shells, and far fewer large ones, thus suggesting high juvenile mortality. When the two shape measurements are compared (c), the plot shows a straight line ($y = 0.819x + 0.262$); on a previous logarithmic plot, the slope (α) did not differ significantly from unity, so an isometric relationship is assumed, and the raw data have been replotted.
Figure 1.11 Composition of a Middle Jurassic vertebrate fauna from England. The proportions of the major groups of vertebrates in the fauna are shown as a pie chart (a). The sample can be divided into categories also of bone types (b) and taphonomic classes (c), which reflect the amount of transport. Dimensions of theropod dinosaur teeth show two frequency polygons
(d) that are statistically significantly different (*t*-test), and hence indicate two separate forms.
Figure 1.12 Finding the most complete titanosaur, *Rapetosaurus*, in Madagascar: (a) Kristi Curry Rogers (front right) with colleagues excavating the giant skeleton; (b) after preparation in the lab, the whole skeleton can be laid out – this is a juvenile sauropod, so not as large as some of its relatives. (Courtesy of Kristi Curry Rogers.)

Figure 2.1 (a) Steno's series of diagrams illustrating the deposition of strata, their erosion and subsequent collapse (25, 24 and 23) followed by deposition of further successions (22, 21 and 20). These diagrams demonstrate not only superposition but also the concept of unconformity. (b) Giovanni Arduino's primary, secondary and tertiary systems, first described from the Apennines of northern Italy in 1760. These divisions were built on the basis of Steno's Law of Superposition of Strata. (c) Idealized sketch of William Smith's geological traverse from London to Wales; this traverse formed the template for the first geological map of England and Wales. Data assembled during this horse-back survey were instrumental in the formulation of the Law of Correlation by Fossils. (a, from Steno 1669; c, based on Sheppard, T. 1917. *Proc. Yorks. Geol. Soc.* **19**.)
Figure 2.2 The main types of biozone, the operational units of a biostratigraphy. (Based on Holland 1986.)
Figure 2.3 Behavior of ideal zone and facies fossils through a hypothetical global stratigraphic section.
Figure 2.4 (a) Hypothetical and minimalist graphic correlation based on the stratigraphic distribution of the five apparent chronospecies of the Silurian brachiopod *Eocoelia*, in ascending order: *E. hemisphaerica*, *E. intermedia*, *E. curtisi*, *E. sulcata* and *E. angelini*; the first four range through the middle and upper Llandovery whereas the last is characteristic of the lower Wenlock. The ranges of these species are given from two artificial sections with the first appearances of each species plotted on both sections as x and y coordinates. The straight line fitted to the points allows a precise correlation between each part of the two sections. In this simple example all the points fit on a straight line; in practice a regression must be fitted to the

scatter of data points.
(b) Seriation of biostratigraphic data. The five *Eocoelia* species were collected from five horizons in a stratigraphic section; the data were collected and plotted randomly as a range chart. Seriation seeks to establish any structure, usually gradients, within the matrix by maximizing entries in the leading diagonal. The seriated matrix reveals the stratigraphic succession of *Eocoelia* species that is widely used for the correlation of Lower Silurian strata. Most seriations are based on much larger and more complex data matrices where any non-random structure, if present, is initially far from obvious.
Figure 2.4 (*Continued*) (c) The RASC method predicts the solution most likely to occur in the next section based on previous data. Three sections (1–3) are presented and, based on a majority vote, the RASC solution is constructed; since the first two sections are similar they win over the third slightly different section. This is different to the maximum range solution that may be constructed by other methods. (c, based on Hammer & Harper 2005.)
Figure 2.5 Approximate stratigraphic ranges through time of the main biostratigraphically useful invertebrate fossils groups. (Replotted from various sources.)
Figure 2.6 Key concepts in the definition of stratotypes and parastratotypes applicable to all stratigraphic units. The base of stage X is defined at an appropriate and suitable type section, coincident with the base of biozone Y, which can be used to correlate the base of the stage. The type section is usually conserved and further collecting across the boundary interval is restricted to the parastratotype section. The base of the stage is indicated as XXX. (Based on Temple, J.T. 1988. *J Geol. Soc. Lond.* **145**.)
Figure 2.7 Stratigraphic case study: description and definition of the litho-, bio- and chronostratigraphy of the stratotype section of the Wenlock Series, along Wenlock Edge in Shropshire, UK. This is the internationally accepted standard for the Wenlock Epoch, the third time division of the Silurian Period.
Figure 2.8 Current status of the development of a new, internationally accepted chronostratigraphy for the Ordovician System. New global series and stages are correlated with the comparable chronostratigraphic divisions used in North American and the United Kingdom and Ireland. GSSP, global standard section and point.
Figure 2.9 North American Phanerozoic sequences: the recognition of these large packages of rock or what are termed "megasequences" formed the basis for the modern discipline of sequence stratigraphy, established by the Exxon Corporation. (Based on various sources.)
Figure 2.10 Sequences, system tracts and stratigraphic surfaces defined in relation to base level and transgression–regression curves: (a) stratal architecture across a non-marine to marine transect is related to (b) sequence stratigraphies in the non-marine and marine parts of the transect. (A), positive accommodation (base level rise); BSFR, basal surface of forced regression; c.c., correlative conformity; c.u., coarsening upward; DS, depositional sequence; FR, forced regression; FSST, falling stage systems tract; f.u., fining upward; GS, genetic stratigraphic sequence; HST, highstand systems tract; IV, incised valley; LST, lowstand systems tract; MFS, maximum flooding surface; MRS, maximum regressive surface; NR, normal regression; R, ravinement surface; RST, regressive systems tract; SU, subaerial unconformity; TR, transgressive–regressive sequence; TST, transgressive systems tract. (Based on Catuneanu, O. 2002. *J. African Earth Sci.* **35**.)
Figure 2.11 DCA axis 1 sample scores plotted against the Frankfort composite section. mfs, maximum flooding surface; HST, highstand systems tract; SB/TS, combined sequence boundary and transgressive surface; TST, transgressive systems tract. (From Holland & Patzkowsky 2004.)
Figure 2.12 (a) Illustration of Milankovitch frequencies showing the relationships between eccentricity, obliquity and precession cycles. (b) Outline stratigraphy of Cenomanian Stage Upper Cretaceous chalk facies. Column 1, stages; column 2, cyclostratigraphy; column 3, sequences. (From Gale et al. 1999.)
Figure 2.13 The various methods currently available to construct the geologic time scale 2004 (GTS2004).
Figure 2.14 Carboniferous and Permian distributions of the *Glossopteris* flora and the *Mesosaurus* fauna and the fit of Gondwana. The tight fit of Gondwana and the correspondence of fossil faunas and floras across the southern continents suggested to Wegener and others that South America, Africa, India, Antarctica and Australia had drifted apart since the Permo-Triassic. (Based on Smith, P. 1990. *Geoscience Canada* **15**.)
Figure 2.15 The emergence of the Isthmus of Panama promoted the great American biotic interchange (GABI) between North and South American terrestrial vertebrates together with the radiation of the shallow-water marine benthos of the Caribbean Sea. l, litopterns; n, notoungulates. (Based on Benton 2005.)
Figure 2.16 (opposite and this page) Changing ideas on the development of the Early Paleozoic Iapetus Ocean and its faunas: (a, c, d) paleogeographic reconstructions; (b) the mobility of organisms across a closing ocean; (e) a cluster analysis of the Iapetus and related Early Ordovician brachiopod faunas (tinted blocks in descending order indicate low-latitude, high-latitude, low-latitude marginal and high-latitude marginal provinces); and (f) the possible movement of the Precordilleran terrane in three stages, 1–3. A dataset of early Ordovician brachiopod distribution across the Iapetus terranes is available at http://www.blackwellpublishing.com/paleobiology/. These data may be analyzed and manipulated using a range of multivariate techniques including cluster analysis (see also Hammer & Harper 2005).
(a–d, from Harper, D.A.T. 1992. *Terra Nova* **4**; f, based on Finney 2007.)
Figure 2.17 Displaced faunas in terranes within the North American Cordillera together with changing provincial boundaries on the craton. Postulated latitudinal boundaries on the craton during the Permian, Triassic and Jurassic are indicated and confirm the northern movement of these displaced terranes. A dataset of Jurassic ammonoid distributions

across the cordilleran terranes is available at http://www.blackwellpublishing.com/paleobiology/. These data may be analyzed and manipulated using a range of multivariate techniques including cluster analysis (see also Hammer & Harper 2005). (From Hallam, A. 1986. *J. Geol. Soc.* **143**.)

Figure 2.18 Changing familial diversity of skeletal benthos through time in relation to plate configurations: high diversities are apparently coincident with times of greatest continental fragmentation, for example during the Ordovician, Devonian and Cretaceous-Cenozoic. A, pre-Appalachian-Variscan Ocean; H, Hispanic Corridor; I, Iapetus Ocean; U, pre-Uralian Ocean. (Based on Smith, P. 1990. *Geoscience Canada* **15**.)

Figure 2.19 Strained Cambrian trilobites from Himalaya. (Courtesy of Nigel Hughes.)

Figure 2.20 The Scandinavian Caledonides showing the pre-drift positions of some of the various thrust sheet complexes. During the Early Ordovician (EO) the most seaward, upper parts of the higher thrust sheets (Støren Nappe) contained North American marginal faunas, whereas the lower parts of these thrust sheets (Köli Nappe) contained Celtic (oceanic) type faunas. The lower parts of the nappe pile (e.g. the Valdres Nappe) have Baltic faunas. The Wenlock-Ludlow (MS) marginal molasse deposits (Old Red Sandstone (ORS) facies), for example at Ringerike, have spectacular marine marginal faunas.

Figure 3.1 How a dead bivalve becomes a fossil. The sequence of stages between the death of the organism and its preservation in various ways.

Figure 3.2 The relative rates of decay and mineralization determine the kinds of tissues that may be preserved. At minimum decay rate and with very early mineralization, highly labile muscle tissues may be preserved. When decay has gone to a maximum, and when mineralization occurs late, all that is left are the non-organic tissues such as shells. (Based on Allison 1988.)

Figure 3.3 The conditions for exceptional preservation. (a) The rate of burial and organic content are key controls on the nature of mineralization of organic matter in fossils. Pyritization (high rate of burial, low organic content) may preserve entirely soft-bodied worms, as in an example from the Early Devonian Hunsrückschiefer of Germany (b). Phosphatization (low rate of burial, high organic content) may preserve trilobite limbs such as this example of *Agnostides* from the Cambrian of Sweden (c). Soft parts may be preserved in carbonate (high rate of burial, high organic content), such as polyps in a colonial coral, *Favosites*, from the Early Silurian of Canada (d). If decay never starts, small animals may be preserved organically and without loss of material, such as a fly in amber from the Early Tertiary of the Baltic region (e). (a, based on Allison 1988; b, courtesy of Phil Wilby; c–e, courtesy of Derek Briggs.)

Figure 3.4 Exceptional preservation of muscle in the Jurassic horseshoe crab *Mesolimulus walchi*: (a) the whole specimen showing the rounded headshield (prosoma), with preserved muscle tissues in the middle; (b) muscle fibers; (c) banding across muscle fibers revealed by early decay; and (d) small coccoid microbes associated with the muscle fibers. Scale bars: 20 mm (a), 50 μm (b), 10 μm (c, d). (Courtesy of Derek Briggs.)

Figure 3.5 An imaginary cross-section showing possible sites of exceptional fossil preservation, most of which are conservation deposits, but a few of which are concentration deposits. (Based on Seilacher et al. 1985.)

Figure 3.6 Processes of breakage and diagenesis of fossils. Dead organisms may be disarticulated (a) or fragmented (b) by scavenging or transport, abraded (c) by physical movement, bioeroded (d) by borers, or corroded and dissolved (e) by solution in the sediment. After burial, specimens may be flattened (f) by the weight of sediment above, or various forms of chemical diagenesis, such as the replacement of aragonite by calcite (g) may take place.

Figure 3.7 (a) Numerous examples of deformation of the brachiopod *Eoplectodonta*: in a tectonized mudstone from the Silurian of Ireland. (b) A single deformed example (c. 20 mm wide) of a Cambrian *Billingsella* fossil from the Himalayas (Bhutan) and (c) the same example retrodeformed to its original shape.

Figure 3.8 Different modes of plant preservation. (a) Permineralization, a silicified plant stem from the Rhynie Chert (Early Devonian, Scotland) (× 50). (b) Coalified compression, leaves of *Annularia* from the Late Carboniferous, Wales (× 0.7). (c) Authigenic preservation, a mold of *Lepidostrobus* from the Late Carboniferous, Wales (× 0.5). (d) Direct preservation of a microscopic fossilized diatom in the original silica (scale bar, 20 μm). (a, courtesy of Dianne Edwards; b, c, courtesy of Chris Cleal; d, courtesy of David Ryves.)

Figure 3.9 Mean scores of the stratigraphic consistency index (SCI), the relative completeness index (RCI) and the gap excess ratio (GER) for five geological time partitions of the data set of 1000 cladograms. Note that the SCI and GER indicate no change through time, while the RCI becomes worse (lower values) from the Paleozoic to Cenozoic – but the RCI depends on total geological time, and so is not a good measure for this study. Pz, cladograms with origins solely in the Paleozoic; Pz/Mz, cladograms with origins spanning the Paleozoic and Mesozoic; Mz, cladograms with origins solely in the Mesozoic; Mz/Cz, cladograms with origins spanning the Mesozoic and Cenozoic; Cz, cladograms with origins solely in the Cenozoic. (Based on Benton et al. 2000.)

Figure 3.10 Clade–stratigraphic metrics. Calculation of the three congruence metrics for age versus clade comparisons. SCI is the ratio of consistent to inconsistent nodes in a cladogram. RCI is RCI = 1(ΣMIG/ΣSRL), where MIG is minimum implied gap, or ghost range, and SRL is standard range length, the known fossil record. GER is GER = 1(MIG – G_{min})/(G_{max}

– G_{min}), where G_{min} is the minimum possible sum of ghost ranges and G_{max} the maximum, for any given distribution of origination dates. (a) The observed tree with SCI calculated according to the distribution of ranges in (b). (b) The observed tree and observed distribution of stratigraphic range data, yielding an RCI of 66.0%. GER is derived from G_{min} and G_{max} values calculated in (c) and (d). (c) The stratigraphic ranges from (b) rearranged on a pectinate tree to yield the smallest possible MIG or G_{min}. (d) The stratigraphic ranges from (b) rearranged on a pectinate tree to yield the largest possible MIG or G_{max}. (Based on Benton et al. 2000.)

Figure 3.11 Is the fossil record controlled by the rock record? (a) Plot of number of marine geological formations and extinction rate against the last 500 myr of geological time. Note how closely the rock and fossil curves follow each other. (b) Plot of diversification curves for marine families of animals from analyses by Sepkoski (i) and Benton (ii), compared with (iii) the sea-level curve for the Phanerozoic (fine line) and the percentage of platform flooding (heavy line). Note the approximate matching of diversity and sea-level curves until the past 100 myr. (a, based on Peters & Foote 2002; b, based on Smith 2001.)

Figure 3.12 Paleontological knowledge has improved by about 5% in the 26-year period between 1967 and 1993. According to 1993 data there is 5% less gap, as assessed by a relative completeness index (RCI), implied in the fossil record of tetrapods than in 1967. This figure was obtained by comparing the order of branching points in cladograms with the order of appearance of fossils in the rocks. Will there be a further 5% shift to the right (i.e. towards 100% completeness) by the year 2019? (Based on Benton & Storrs 1994.)

Figure 4.1 Life modes of marine organisms in a living offshore, muddy-sand community in the Irish Sea with a range of bivalves (a–e, l), gastropods (f), scaphopods (g), annelids (h, j), asterozoans (i), crustaceans (k, r), echinoids (m, n) and fishes (o–q). Insets indicate large and small burrowers. (From McKerrow 1978.)

Figure 4.2 The transition from a living assemblage to a death assemblage. Relative proportions of different types of organism change in two living marine assemblages off the Texan coast. Living assemblages are dominated numerically by detritivores and herbivores, death assemblages by suspension feeders. (Based on Staff et al. 1986.)

Figure 4.3 Census of organisms preserved in the Middle Cambrian Burgess Shale. Many groups, such as the priapulid and annelid worms, together with the diverse arthropod biota, are rarely represented in more typical mid-Cambrian faunas, dominated by phosphatic brachiopods and trilobites. (From Whiltington 1980.)

Figure 4.4 Schematic size–frequency histograms: (a) right (positively) skewed, typical of many invertebrate populations with high infant mortality; (b) normal (Gaussian) distribution, typical of steady-state or transported assemblages; (c) left (negatively) skewed, typical of high senile mortality; (d) multimodal distribution, typical of populations with seasonal spawning patterns; and (e) multimodal distribution, with decreasing amplitude, typical of populations growing by molting (ecdysis).

Figure 4.5 Schematic survivorship curves: type I tracks, increasing mortality with age; type II, constant mortality with age; type III, decreasing mortality with age.

Figure 4.6 Size–frequency histogram (a), polygon (b), cumulative frequency polygon (c) and survivorship curve (d) for a sample of 102 conjoined valves of *Dielasma* from the Permian reef base deposit of the Tunstall Hills, Sunderland. (From Hammer & Harper 2005.)

Figure 4.7 Review of modern marine environments and their depth ranges, together with the approximate positions of the main benthic zones. (Based on Ager 1963.)

Figure 4.8 Selection of marine lifestyles above, at the surface, within and at the base of the water column. (Based on Ager 1963.)

Figure 4.9 Epifaunal tiering of marine benthic communities; infaunal tiering recorded in trace fossil assemblages is discussed on p. 205. (From Copper 1988.)

Figure 4.10 Trophic groups, activity of members and their life sites. 1, Primary producers: phytoplankton in surface waters with (a) cyanobacteria and (b) benthic algae. 2, Herbivores: browsing and grazing gastropods. 3, Deposit feeders: (a) deposit-feeding gastropod and (b) shallow infaunal bivalve. 4, Suspension feeders: (a) semi-infaunal, byssally-attached bivalve, (b) shallow infaunal bivalve, (c) crinoid, (d) epifaunal bivalve, and (e) deep infaunal bivalve. 5, Carnivores: (a) nektonic fishes, (b) nekton-benthic fishes, (c) epifaunal gastropod, and (d) infaunal gastropod. (From Brenchley & Harper 1998.)

Figure 4.11 Reconstructions of two different food chain communities. (a) A community with a suspension-feeding food chain, displaying a variety of suspension feeders, collecting food in different ways (bivalves with a mucous trap or setae, bryozoans and brachiopods with lophophores, foraminiferans with cilia, corals with tentacles, and sponges with flagellae). (b) A community with a detritus-feeding food chain dominated by various types of bottom-dwelling deposit feeders and nektonic carnivores represented by a cephalopod and placoderm. (From Copper 1988.)

Figure 4.12 (a) Trophic structures in and around a Late Carboniferous lake complex, Nýřany, Czechoslavakia. (b) Trophic structures in a Late Permian reef complex, northeast England. (a, based on Benton 1990; b, from Hollingworth & Pettigrew

1998.)

Figure 4.13 Shoreline to basin transect showing the relative importance of different factors on the distribution of organisms. (From Brenchley & Harper 1998.)

Figure 4.14 Distribution of living organisms across a depth gradient. (From Brenchley & Harper 1998.)

Figure 4.15 Silurian marine benthic assemblage zones and identifying criteria. (From Brenchley & Harper 1998.)

Figure 4.16 Construction of a rarefaction curve based on data collected from a mid-Devonian brachiopod-dominated fauna, northern France. The main types of brachiopod are illustrated: (a) *Schizophoria*, (b) *Douvillina*, (c) *Productella*, (d) *Cyrtospirifer*, (e) *Rhipidiorhynchus*, and (f) *Athyris*. The curve levels off at about 300 specimens, suggesting this sample size is a sufficient census of the fauna. Magnification approximately ×0.5 for all.

Figure 4.17 In a two-way cluster analysis, an R-mode clusters the genera (bottom) and a Q-mode clusters the community type (right). The original data matrix is in the center of the diagram. The data indicate the reality of a shallow-water biofacies (*Lingula* and *Eocoelia* communities), and mid to deep shelf (*Pentamerus* and *Stricklandia* communities) and outer shelf to slope (*Clorinda* community) assemblages.

Figure 4.18 Commensalism between (a) the gastropod *Platyceras* and a Devonian crinoid and (b) *Spinocyrtia iowensis* with an epifauna primarily located on the fold of the brachial valve adjacent to inhalant or exhalent currents. (Based on Ager 1963.)

Figure 4.19 Selection of fossils from ancient hydrothermal vent sites. All specimens are pyritized and are contained within a matrix of sulfide minerals. (a) Gastropod: *Francisciconcha maslennikovi* from the Lower Jurassic Figueroa sulfide deposit, California. (b) Small worm tubes from the Upper Cretaceous Memi sulfide deposit, Cyprus. (c) Bivalve: *Sibaya ivanovi* from the Middle Devonian Sibay sulfide deposit, Russia. (d, e) From the Lower Silurian Yaman Kasy sulfide deposit, Russia: (d) monoplacophoran, *Themoconus shadlunae* and (e) vestimentiferan worm tube, *Yamankasia rifeia*. Scale bars: 5 mm (a, b), 20 mm (c–e). (Courtesy of Crispin Little.)

Figure 4.20 A cocktail of Jurassic environments. Early Jurassic: (a) sand, (b) muddy sand, and (c) bituminous mud communities. Late Jurassic: (d) mud, (e) reef, and (f) lagoonal communities. (From McKerrow 1978.)

Figure 4.21 Bambachian megaguilds. A near full complement of lifestyles is present in the Modern fauna (c), while fewer are represented in the matrices for the Cambrian (a) and Paleozoic (b) faunas. (d) The numbers of life modes have increased consistently through time.

Figure 4.21 *Continued*

Figure 4.22 Thicknesses of shell concentrations during the Ordovician-Silurian, Jurassic and Neogene. Thick shell beds are a phenomenon of the Modern fauna, mainly generated by
bivalves. (From Kidwell & Brenchley 1994.)

Figure 4.23 Climate change through time, showing alternations between icehouse and greenhouse worlds. (Courtesy of Christopher Scotese.)

Figure 4.24 Some key indicators of climate and temperature. (Courtesy of Christopher Scotese.)

Figure 4.25 Size changes in planktic foraminiferans from high and low latitudes during the last 70 Ma, compared to temperature profiles generated from oxygen isotope data and Mg:Ca ratios. Three phases are recognized, a first (65–42 Ma) with dwarf taxa, a second (42–12 Ma) with moderate-sized taxa, and a third (12 Ma to present) with large-sized taxa. Size increases are correlated with intervals of global cooling. (Courtesy of Daniela Schmidt.)

Figure 4.26 Climate change through time illustrated together with changes in sea level and fluctuations in the intensity of volcanicity. (Based on various sources.)

Figure 4.27 Snowball Earth scenario. (a) Continents are near the equator, increasing precipitation removes CO_2 from the atmosphere, and with falling temperatures ice begins to spread from the poles. (b) Ice continues to spread with temperatures further reduced by the albedo (reflection of solar energy) effect. (c) Atmospheric CO_2 increases due to volcanic activity, prompting a reversal in temperatures. (d) Greenhouse conditions return and the ice sheets recede. (Courtesy of Jørgen Christiansen and Svend Stouge.)

Figure 4.28 Precambrian Gaia and evolution of the biosphere. (a) Changes in climate in a live and lifeless world; there is a sharp fall in temperature when oxygen appears. (b) The changing abundance in atmospheric gases. (c) Changes in the composition of ecosystems: both the photosynthesizers and methanogens increase initially when oxygen appears but the methanogens eventually decline to a much lower level of abundance. (Population is the proportion of the total population in tenths.) (From Lovelock 1998.)

Figure 5.1 (a) Charles Darwin. (b) Branching diagram of phylogeny, the only illustration in *On the Origin of Species* (1859). It shows how two species, A and I, branch and radiate through time. The units I–XIV are time intervals of variable length, and the lower case letters (a, b, c) represent new species.

Figure 5.2 Allopatric speciation models, occurring either symmetrically (a), where the parent species is divided into two roughly equal halves by a geographic barrier, or asymmetrically (b), where a small peripheral population is isolated by a

barrier. In the first case, two new species may arise; in the second, the parent species may continue unaltered, and the peripheral population may evolve rapidly into a new species.

Figure 5.3 Two models of speciation and lineage evolution. (a) Phyletic gradualism, where evolution takes place in the lineages, and speciation is a side effect of that evolution.
(b) Punctuated equilibrium, where most evolution is associated with speciation events, and lineages show little evolution (stasis).

Figure 5.4 Fine-scale evolution in fresh-water snails and bivalves in Lake Turkana, Kenya, through the last 4 myr. The volcanic tuff beds allow accurate dating of the sequence. Major speciation events seem to take place at times of lake-level change: are these examples of punctuational speciation, or merely ecophenotypic shifts? (Based on Williamson 1981.)

Figure 5.5 Phyletic gradualism and speciation in the planktonic diatom *Rhizosolenia*. Today there are two distinct species, *R. bergonii* and *R. praebergonii*, that do not interbreed and that differ in the height of the hyaline area. When tracked back through the past 3.4 myr, the species can be seen to have diverged through a span of up to 500,000 years, from 3.2 to 2.7 Ma. The plot shows samples taken from deep-sea boreholes in the central Pacific, and each measurement of the height of the hyaline area is based on a large sample of hundreds of individuals; the means and 95% error bars for each sample are shown. The rock succession is dated by reference to the magnetostratigraphic scheme of normal (black) and reversed (white) polarity. (Courtesy of Ulf Sorhannus.)

Figure 5.6 Punctuated evolution and speciation in the bryozoan *Metrarabdotos* in the Caribbean. Today, there are three species of this genus, but there have been many more in the past. Careful collecting throughout the Caribbean has shown how the lineages exhibited stasis for long intervals, and then underwent phases of rapid species splitting, especially in the time from 8 to 4 Ma, the Dominican sampling interval (DSI), where records are particularly good. (Courtesy of Alan Cheetham.)

Figure 5.7 Reconstructed phylogeny of African antelopes. Two lineages diverged 6–7 Ma, the slowly evolving impalas and the rapidly speciating gnus and hartebeests. The second group could be said to be evolutionarily more successful than the first, and this might be interpreted as a result of species selection of species-level characters – the rate of speciation. However, the gnus and hartebeests have more specialized ecological preferences than do the species of impalas: perhaps selection has occurred at the individual level (natural selection), and this has had an effect at the species level. Species numbers 14 and 26 are omitted in this study. (Based on Vrba 1984.)

Figure 5.8 Reconstructing the phylogeny of vertebrates by cladistic methods. (a) Are the defining features of vertebrates the possession of bone, a skull and a tail? (b) The tail is found in a wider group, termed the Chordata, but the skull and bone define the Vertebrata.

Figure 5.9 Swimming forepaddles of a variety of reptiles (a–d) and mammals (e–g): (a) *Archelon*, a Cretaceous marine turtle; (b) *Mixosaurus*, a Triassic ichthyosaur; (c) *Hydrothecrosaurus*, a Cretaceous plesiosaur; (d) *Plotosaurus*, a Cretaceous mosasaur; (e) *Dusisiren*, a Miocene sea-cow; (f) *Allodesmus*, a Miocene seal; and (g) *Globicephalus*, a modern dolphin. The forelimbs are all homologous with each other, and with the wing of a bird and the arm of a human. However, as paddles, these are all analogs: each paddle shown here represents a separate evolution of the forelimb into a swimming structure.

Figure 5.10 The relationships of the major groups of vertebrates, tested using six familiar animals. (a) Postulated relationships, based on the analysis of characters discussed in the text.
(b) Phylogenetic tree, showing the cladogram from (a) set against a time scale, and basing the dating of branching points on the oldest known fossil representatives of each group.

Figure 5.11 Relationships of the woolly mammoth based on mitochondrial DNA (mtDNA). This analysis (Rogaev et al. 2006) places the mammoth *Mammuthus primigenius* closest to the Asiatic elephant *Elephas maximus*, while other analyses of mammoth mtDNA place the mammoth closer to the African elephant *Loxodonta africana*. Either way, the relationship to the modern elephants is close, suggesting all three species diverged in the last 5–6 myr. Two samples of mtDNA for the two modern elephants are included, and the outgroups are the sea cow *Dugong dugon* and the hyrax *Procavia capensis*. The sets of digits at each branching point are various measures of robustness: values range from 0 to 1 and 0 to 100, with 1.0 and 100% indicating maximum robustness of the node. Scale bar is 0.1 base-pair substitutions per site. (Courtesy of Evgeny Rogaev.)

Figure 5.12 The number of unique trees for three (a) and four (b) taxa. These cladograms may be written more simply as (A(BC), (B(AC)) and ((AB)C) for the three-taxon cases, and ((AB)(CD)), ((AC)(BD)), ((AD)(BC)), etc. for the four-taxon cases. Note that (A(BC)) and (A(CB)) are identical trees, and both versions count as one.

Figure 6.1 Variation in the Early Silurian brachiopod species *Dicoelosia biloba* from Sweden (o) and *D. hibernica* from Ireland (+), based upon numerous measurements. A principal components analysis plot separates wide and narrow forms along eigenvector 2, so there may truly be two species, although there is considerable overlap between the two.

Figure 6.2 Sexual dimorphism in ammonites, the Jurassic *Kosmoceras*. The larger shell (a) was probably the female, the smaller (b) the male. (Courtesy of Jim Kennedy and Peter Skelton.)

Figure 6.3 Adult female *Ichthyosaurus* (a) from the Lower Jurassic of Somerset, England, showing an embryo that has just

been born (arrow), and detail of the curled embryo (b). (Courtesy of Makoto Manabe.)

Figure 6.4 Tests of allometry in the ichthyosaur *Ichthyosaurus*. (a) Plot of orbit length against skull length, and (b) plot of skull length against backbone length. The Somerset embryo (Fig. 6.3b) is indicated by a solid circle. Both graphs show negative allometry (orbit diameter = 0.355 (skull length)$^{0.987}$; skull length = 1.162 (backbone length)$^{0.933}$), confirming that embryos and juveniles had relatively large heads and eyes. (Courtesy of Makoto Manabe.)

Figure 6.5 Positive allometry in the antlers of the giant Irish deer *Megaloceros*. (a) A famous photograph of an Irish deer skeleton mounted in Dublin in Victorian times. (b) Positive allometry in the antlers of modern deer, showing that *Megaloceros* (M) falls precisely on the expected trend of its closest living relatives. Note that the fallow deer (D) plots above the slope (i.e. antlers are larger than expected from its height), and the European and American moose (A) plot below the line (i.e. antlers are smaller than expected from their height). Two regression lines, the reduced major axis (steeper) and least squares regression, are shown. The allometric equation is antler length = 0.463 (shoulder height)$^{1.74}$. (Based on information in Gould 1974.)

Figure 6.6 Hints of ancestry in modern animals. (a) Extra toes in a horse, an example of an atavistic abnormality in development, or a throw-back, to earlier horses which had more than one toe; normal horse leg (left), extra toes (right). (b) The vestigial hip girdle and hindlimb of a whale; the rudimentary limb is the rudiment of a hindlimb that functioned 50 Ma.

Figure 6.7 Heterochronic evolution in the Cenozoic brachiopods *Tegulorhynchia* and *Notosaria*. Adults of more recent species are like juveniles of the ancestor. Hence, pedomorphosis ("juvenile formation") is expressed in this example. (Based on McNamara 1976.)

Figure 6.8 Heterochronic evolution in the Triassic rhynchosaurs. The skull of adult (A) Late Triassic forms developed beyond the size and shape limits seen in earlier Triassic adult forms. Here, the juveniles (J) of the descendants resemble the ancestral adults, and this is thus an example of peramorphosis ("beyond formation"). (Based on Benton & Kirkpatrick 1989.)

Figure 6.9 *Hox* genes and the development of the tetrapod limb. (a) The sequence of growth of a tetrapod limb bud, reading from top to bottom, showing how the stylopod (humerus/femur), zeugopod (forearm/calf) and autopod (hand/foot) differentiate. The pattern is determined by turning on (filled squares) and off (open squares) of *Hox* genes *D*-9 to *D*-13. (b, c) Interpretation of the forelimbs of the osteolepiform fish *Eusthenopteron* (b) and the tetrapod *Acanthostega* (c) in terms of development. The developmental axis (solid line) branches radial elements (dashed lines) in a pre-axial (anterior) direction in both forms, and the digits of tetrapods condense in a post-axial direction. (a, based on Shubin et al. 1997; b, c, courtesy of Mike Coates.)

Figure 6.10 The use of a modern analog to interpret a mysterious fossil. (a) A colony of the pseudoplanktonic crinoid *Traumatocrinus* attached to a fossil piece of driftwood, from the Late Triassic of China. (b) Reconstruction of the crinoids in life, showing how the wind pulled the log to the left, and the dangling crinoids captured plankton like a net. (c) A tow-net used to maximize catches of fish, a possible modern analog that explains the feeding mode of the fossil colony. (Courtesy of Wang Xiaofeng.)

Figure 6.11 Basic mechanical models for biological structures. There are different kinds of levers in use in everyday appliances, and these styles may be seen in biological structures. (a) In a class 1 lever the effort and load are on opposite sides of the fulcrum. (b, c) In class 2 and 3 levers the effort and load are on the same side of the fulcrum, with the effort furthest away in a class 2 lever (b), and closest in a class 3 lever (c).

Figure 6.12 Finite element analysis of the skull of *Tyrannosaurus rex*. The skull (a) was converted into a cell mesh (b), and biting forces applied (c). In the stress visualization (c), high stresses are indicated by pale colors, low stresses by black. Each bite, depending on its strength and location, sends stress patterns through the skull mesh and these allow the paleobiologist to understand the construction of the skull, but also the maximum forces possible before the structure fails. (Courtesy of Emily Rayfield.)

Figure 6.13 The running stride of *Tyrannosaurus rex*. (a) The main components of a stride, showing the stance phase when the foot touches the ground, and the swing phase. (b–d) Three positions of the limb in early stance, mid-stance and late stance, as the body moves forward, and showing the main forces, including the ground reaction force (GRF). (e–g) Three alternative postures for the limb, with the body held high or low. Read more, and see the movies at http://www.rvc.ac.uk/AboutUs/Staff/jhutchinson/ResearchInterests/beyond/Index.cfm. (Courtesy of John Hutchinson.)

Figure 6.14 Evidence for a rodent–plant interaction from the Eocene. (a) Seed of the water plant *Stratiotes* carrying a neat hole gnawed by a rodent, from the Eocene Bembridge Limestone Formation of the Isle of Wight, southern England. (b) A hole gnawed by a modern woodmouse, showing the same kind of perpendicular narrow grooves made by the tips of the upper incisors. Scale bars, 1 mm. (Courtesy of Margaret Collinson.)

Figure 7.1 An image of a dodo from another era. Lewis Carroll introduced the dodo as a kindly and wise old gentleman in *Alice Through the Looking Glass*, although at the time most people probably regarded the dodo as rather foolish. Driven to extinction in the 17th century by overhunting, the dodo is now an image of human thoughtlessness.

Figure 7.2 Mass extinctions through the past 600 myr include the enormous end-Permian event 251 Ma, which killed two or three times as many families, genera and species (50% of families and up to 96% of species) as the "intermediate" events. These were global in extent, and involved losses of 20% of families and 75–85% of species. Some of the minor mass extinctions were perhaps global in extent, causing losses of 10% of families and up to 50% of species, but many may have been regional in extent, or limited taxonomically or ecologically.

Figure 7.3 (a) The classic collector curve showing the sigmoid (or logistic) shape of the curve of cumulative new species plotted against effort (number of specimens collected/number of days spent looking/number of investigators), with a rapid rise and then a tailing off to an asymptote. (b) Rarefaction curve that shows the number of species likely to be identified from samples of a particular size. (b, based on Hammer & Harper 2005.)

Figure 7.4 Patterns of extinction of foraminifera in a classic KT section spanning about 1.5 myr. A species loss of 53% occurred in two steps close to the KT boundary and iridium anomaly. Dating is based on magnetostratigraphy, and the KT boundary falls in the C29R (reversed) zone. Planktonic zones (P0, P1a, P1b) are indicated; sediment types are mudstones (darker grey) and limestones (pale grey); meter scale bar shows height above and below a particular extinction level, 0. (Based on Keller
et al. 1993.)

Figure 7.5 Gaps and missing data can make gradual extinction events seem sudden (a) or sudden events seem gradual (b). In both diagrams the vertical lines represent different species. (a) The real pattern of fossil species distribution is shown on the left, and if there is a large or small hiatus, or gap, at the KT boundary (middle diagram), a gradual loss of species might seem artificially sudden (right-hand diagram). (b) It is likely that the very last fossils of a species will not be found, and a sudden extinction might look gradual; this can only be detected by intense additional collecting in the rocks that include the supposed last fossils (shaded gray).

Figure 7.6 Periodic extinctions of marine animal families over the past 250 myr. The extinction rate is plotted as percent extinction per million years. A periodic signal may be detected in a time series like this either by eye, or preferably by the use of time series analysis. There are a variety of mathematical techniques generally termed spectral analysis for decomposing a time series into underlying repeated signals. The techniques are outlined in chapter 7 of Hammer and Harper (2006), and a practical example that repeats the classic Raup and Sepkoski (1984) analysis is given at http://www.blackwellpublishing.com/paleobiology/. (Based on the analysis by Raup & Sepkoski 1984.)

Figure 7.7 The end-Permian mass extinction in China. (a) The pattern of extinction of 333 species of marine animals through 90 m of sediments spanning the PT boundary in the Meishan section, showing radiometric ages and carbon isotopes. Three extinction levels, A, B and C are identified. Vertical lines are recorded stratigraphic ranges of marine species in the sections. (b, c) Block diagrams showing typical species in China at the very end of the Permian (b), and immediately after the crisis (c). (a, based on Jin et al. 2000; b, c, drafted by John Sibbick.)

Figure 7.8 The possible chain of events following the eruption of the Siberian Traps, 251 Ma. Volcanism pumps carbon dioxide (CO_2) into the atmosphere and this causes global warming. Global warming leads to reduced circulation and reduced upwelling in the oceans, which produces anoxia, productivity decline and extinction in the sea. Gas hydrates may have released methane (CH_4) which produced further global warming in a "runaway greenhouse" scenario (shaded gray). (Courtesy of Paul Wignall.)

Figure 7.9 The iridium (Ir) spike and fern spike, as recorded in continental sediments in York Canyon, New Mexico. The Ir spike, measured in parts per trillion (ppt), an enhancement of 10,000 times normal background levels, is generally interpreted as evidence for a massive extraterrestrial impact.
The fern spike indicates sudden loss of the angiosperm flora, and replacement by ferns. (Based on Orth et al. 1981.)

Figure 7.10 The KT impact site identified. Location of the Chicxulub Crater on the Yucatán peninsula, Central America, and sites of tempestite deposits around the coastline of the proto-Caribbean (open circles). Continental KT deposits are indicated by triangles.

Figure 7.11 Evidence for a KT impact in the Caribbean. (a) Shocked quartz from a KT boundary clay. (b) A glassy spherule from the KT boundary section at Mimbral, northeast Mexico, evidence of fall-out of volcanic melts from the Chicxulub Crater (about 1.5 mm in diameter). (Courtesy of Philippe Claeys.)

Figure 7.12 Disaster taxa after the end-Permian mass extinction: the brachiopod *Lingula* (a), and the bivalves *Claraia* (b), *Eumorphotis* (c), *Unionites* (d) and *Promyalina* (e). These were some of the few species to survive the end-Permian crisis, and they dominated the black anoxic seabed mudstones for many thousands of years after the event.

Figure 7.13 The rate of historic extinctions of species for which information exists, counted in 50-year bins. Note the rapid rise in numbers of extinctions in the period 1900–1950; the apparent drop in the period 1950–2000 is artificial because complete counts have not been made for that 50-year period yet.

Figure 8.1 The biochemical theory for the origin of life, as proposed by I. A. Oparin and
J. B. S. Haldane in the 1920s. Biochemists have achieved steps 1–3 in the laboratory, but scientists have so far failed to

create life. ATP, adenosine triphosphate.

Figure 8.2 The model behind "RNA world", where an RNA replicase and a self-replicating membrane-bound vesicle combine to form a protocell. Inside the vesicle, the RNA replicase functions, and might add a function to improve the production of the vesicle wall through a ribozyme. At this point, the RNA replicase and the vesicle are functioning together, and the protocell has become a living cell, capable of nutrition, growth, reproduction and evolution. Read a general introduction to RNA world at http://www.blackwellpublishing.com/paleobiology/. (Based on information in Szostak et al. 2001.)

Figure 8.3 Time scale showing major events in the history of the Earth and of life. Most of the time scale is occupied by the Precambrian, whereas the well-known fossil record of the Phanerozoic (Phan.) accounts for only one-seventh of the history of life.

Figure 8.4 The universal tree of life, based on molecular phylogenetic work. The major prokaryote groups are indicated (Bacteria, Archaea), as well as the major subdivisions of Eucarya. Among eukaryotes, most of the groups indicated are traditionally referred to as "algae", both single-celled and multicelled. The metaphytes (land plants), fungi and metazoans (animals) form part of a derived clade within Eucarya, indicated here near the base of the diagram. Mb, megabase (= 1 million base pairs). (Courtesy of Sandie Baldauf.)

Figure 8.5 Postulated prokaryotes from the Apex Chert of Western Australia (c. 3465 Ma) showing filament-like microbes preserved as carbonaceous traces in thin sections. All are examples of the prokaryote cyanobacterium-like *Primaevifilum*, which measures 2–5 μm wide. (Courtesy of Bill Schopf.)

Figure 8.6 Stromatolites, a Precambrian example from California, USA (magnification ×0.25). (Courtesy of Maurice Tucker.)

Figure 8.7 The oldest fossils on Earth? A mass of thin thread-like filaments found in a massive sulfide deposit in Western Australia dated at 3.2 Ga. The fact the threads occur in loose groups and in tight masses, and that they are not oriented in one direction, suggests they are organic. The filaments are lined with minute specks of pyrite, showing black, encased in chert. Field of view is 250 μm across. (Courtesy of Birger Rasmussen.)

Figure 8.8 Prokaryote fossils from the Gunflint Chert of Ontario, Canada (c. 1.9 Ga): (a) *Eosphaera*, (b) *Kakabekia*, and (c) *Gunflintia*. Specimens are 0.5–10 μm in diameter. (Redrawn from photographs in Barghoorn & Taylor 1965.)

Figure 8.9 Eukaryote characters: a typical prokaryote cell (a) differs from a eukaryote plant cell (b) in the absence of a nucleus and of organelles. (c) The endosymbiotic theory for the origin of eukaryotes proposes that cell organelles arose by a process of mutually beneficial incorporation of smaller prokaryotes into an amoeba-like prokaryote (steps 1, 2 and 3). (Based on various sources.)

Figure 8.10 Diagram showing the evolutionary relationships and divergence times for the red, green, glaucophyte and chromist algae. These photosynthetic groups are compared with the Opisthokonta, the clade containing animals and fungi. The tree also shows two endosymbiotic events. Some time before 1.5 Ga, the first such event took place, when a photosynthesizing cyanobacterium (CB) was engulfed by a eukyarote. The second endosymbiotic event involved the acquisition of a plastid about 1.3 Ga. Plastids in plants store food and may give plants color (chloroplasts are green). (Courtesy of Hwan Su Yoon.)

Figure 8.11 Early fossil "eukaryotes". (a) The thread-like *Grypania meeki*, preserved as a carbonaceous film, from the Greyson Shale, Montana (c. 1.3 Ga). (b, c) Single-celled eukaryotes from the Bitter Springs Chert, Australia (c. 800 Ma): (b) *Glenobotrydion* showing possible mitosis (cell division in growth), and (c) *Eotetrahedrion*, probably a cluster of individual *Chroococcus*-like cyanobacteria. (d) Branching siphonalean-like filament. Scale bars: 2 mm (a), 10 μm (b–d). (Courtesy of Martin Brasier, based on various sources.)

Figure 8.12 A filamentous alga from the Lakhanda Group, Siberia (c. 1000 Ma), 400 μm wide. (Courtesy of Andy Knoll.)

Figure 8.13 The oldest multicellular eukaryote, *Bangiomorpha*, from the 1.2 Ga Hunting Formation of Canada. (a) A colony of whiskery filaments growing from holdfasts attached to a limestone base. (b) A single filament showing a single-series filament making a transition to multiple series, with sets of four wedge-shaped cells; note the sets of four disk-shaped cells in the single-series part of the strand. (Courtesy of Nick Butterfield.)

Figure 9.1 Protist positions on the tree of life. In this tree, developed by Patrick Keeling, University of British Columbia, the protozoans (foraminiferans and radiolarians) lie within the Cercozoa far divorced from the chromists (diatoms and dinoflagellates) within the Chromalveolates. (From Keeling et al. 2005.)

Figure 9.2 Stratigraphic ranges of the main protist groups. (From Armstrong & Brasier 2005.)

Figure 9.3 Main types of foraminiferan test walls: (a) the composition and structure of test walls and (b) lamellar construction.

Figure 9.4 Main types of foraminiferan chamber construction.

Figure 9.5 Some genera of foraminiferans: (a) *Textularia*, (b) *Cribrostomoides*, (c) *Milionella*, (d) *Sprirolina*, (e) *Brizalina*, (f) *Pyrgo*, (g) *Elphidium*, (h) *Nonion*, (i) *Cibicides*, (j) *Globigerina*,

(k) *Globorotalia*, and (l) *Elphidium* (another species). Magnification ×50–100 for all. (Courtesy of John Murray (b, d, e, g, h, j, k) and Euan Clarkson (a, c, f, i, l).)

Figure 9.6 Modeling foraminiferan tests: part of a theoretical three-dimensional morphospace for foraminiferans. GF, growth factor; TF, translation factor; $\Delta\phi$, deviation factor. (From Tyszka 2006.)

Figure 9.7 Foram test and environments: distribution of test types and genera of Foraminifera against environmental gradients. (From Armstrong & Brasier 2005.)

Figure 9.8 Stratigraphic ranges of the main foraminiferan groups. (Based on various sources.)

Figure 9.9 Descriptive morphology of the radiolarians.

Figure 9.10 Some radiolarian morphotypes: *Lenosphaera* (×100), *Actinomma* (×240), *Alievium* (×180), *Anthocyrtidium* (×250), *Calocyclas* (×150) and *Peripyramis* (×150).

Figure 9.11 Haeckel's radiolarians: plate 12 from *Die Radiolarien (Rhizopoda Radiaria)* by Ernst Haeckel (1862).

Figure 9.12 Descriptive morphology of the acritarchs.

Figure 9.13 Some acritarch morphotypes: *Multiplicisphaeridium* (×800), *Baiomeniscus* (×200), *Leiofusa* (×400) and *Villosacapsula* (×400).

Figure 9.14 Acritarch and invertebrate diversity through Ordovician Period. (Courtesy of Thomas Servais.)

Figure 9.15 Descriptive morphology of (a) a dinoflagellate, and (b) a dinoflagellate theca (left), unpeeled (middle) to reveal the corresponding cyst (right).

Figure 9.16 A prasinophyte (a) and some dinoflagellate taxa (b–h): (a) *Tasmanites* (Jurassic), (b) *Cribroperidinium* (Cretaceous), (c) *Spiniferites* (Cretaceous), (d) *Deflandrea* (Eocene), (e) Wetzeliella (Eocene), (f) *Lejeunecysta* (Eocene), (g) *Homotryblium* (Eocene), and (h) *Muderongia* (Cretaceous). Magnification ×250 (a, d, e), ×425 (b, c, f, g, h). (Courtesy of Jim Smith.)

Figure 9.17 Morphology of some tintinnids in cross-section from limestones (×100–200).

Figure 9.18 Some coccolith morphotypes:
(a) coccospheres of the living *Emiliana huxleyi*, currently the most common coccolithophore (×6500), and (b) Late Jurassic coccolith limestone (×2000). (c) Coccolith plate styles:
1 and 2, *Coccolithus pelagus*; 4 and 5, *Oolithus fragilis*; 5 and 6, *Helicosphera carteri*. In
C. pelagus and *H. carteri* growth was upwards and outwards with the addition of layer upon layer of calcite; in *O. fragilis* growth was different with curved elements, in non-parallel to crystal cleavage directions. (a, b, courtesy of Jeremy Young; c, courtesy of Karen Henriksen.)

Figure 9.19 Descriptive morphology of the diatoms.

Figure 9.20 Some diatom morphotypes: *Coscinoconus* (×250), *Asterolampra* (×400), *Cocconeis* (×360), *Achnanthes* (×150), *Surirella* (×200) and *Eunotia* (×400).

Figure 9.21 Descriptive morphology of the chitinozoans: (a) Operculatifera (simplexoperculate), *Lagenochitina*, and (b) Prosomatifera (complexoperculate), *Ancyrochitina*.

Figure 9.22 Chitinozoan apparatus: a large cluster of *Desmochitina nodus* interpreted as an egg clutch of the chitinozoan animal; the opercula are not present suggesting that the animals had already hatched (×70). (Courtesy of Florentin Paris.)

Figure 9.23 Some chitinozoan morphotypes: *Sphaerochitina* (×160), *Urnochitina* (×160), *Conochitina* (×80), *Ancyrochitina* (×240) and colonial arrangements (×40).

Figure 10.1 Time scale and tempo of early animal evolution: the key metazoan groups are shown with the putative age of their last common ancestor, together with an estimate of the respective numbers of classes and orders indicated against a stratigraphy indicating key biological and chemical events. N–D, Nemakit-Daldynian; T, Tommotian; A, Atdabanian; B/T, Botomian. (Courtesy of Kevin Peterson.)

Figure 10.2 Putative trace fossils from the Precambrian of Australia, showing *Myxomitodes*, a presumed trail of a mucus-producing multicellular organism about 1.8–2 billion years old from Stirling Range, Western Australia. (Photo is approximately 65 mm wide.) (Courtesy of Stefan Bengtson.)

Figure 10.3 Animal embryos from the Doushantou Formation, China. (a) Surface of embryo based on tomographic scans together with (b) an orthoslice revealing subcellular structures analogous to modern lipids and (c) an orthoslice at the boundary between two cells. (c, f) Two-cell embryo of the sea urchin *Heliocidaris* showing lipid vesicles for comparison. (e) Orthoslice rendering of a possible embryo revealing internal structures. (g–i) Models of tetrahedrally arranged cells. Relative scale bar (see top left): 170 μm (a–d, f), 270 μm (e), 150 μm (g–i).
(Courtesy of Philip Donoghue.)

Figure 10.4 Appearance of the main animal phyla and some other high-level taxonomic groups. Geological period abbreviations are standard, ranging from Cambrian (C) to Cretaceous (K). (Based on Valentine 2004.)

Figure 10.5 Main invertebrate body plans and larvae: upper and lateral views of spiral (a) and radial (b) patterns of cell

cleavage; development of the mesoderm in the spiralians (c) and radialians (d); diploblastic (g) and triploblastic (h) body plans and trochophore-type (e) and dipleurula-type (f) larvae.

Figure 10.6 Phylogenetic relationships among the main invertebrate groups. (Phylogeny courtesy of Kevin Peterson.)

Figure 10.7 Stratigraphic distribution of the Ediacara biota. Solid triangles, glaciations; C, calcified metazoans; T, position of the Twitya disks. (Based on Narbonne 2005.)

Figure 10.8 Some typical Ediacara fossils: (a) the Radiata, which have been associated with the cnidarians, and (b) the Bilateria, which may be related to the annelids and arthropods. *Ediacaria* (×0.3), *Charnia* (×0.3), *Rangea* (×0.3), *Cyclomedusa* (×0.3), *Medusinites* (×0.3), *Dickinsonia* (×0.6), *Spriggina* (×1.25), *Tribrachidium* (×0.9) and *Praecambridium* (×0.6). (Redrawn from various sources by Anne Hastrup Ross.)

Figure 10.9 Vendozoan constructional morphology, recognizing unipolar, bipolar and radial growth modes within the Ediacara-type biota. Scale bars, 10 mm. (From Seilacher 1989.)

Figure 10.10 An Ediacara community including a fixed and mobile tiered benthos.

Figure 10.11 The calcareous tube *Cloudina* displaying indications of predation. (Courtesy of Stefan Bengtson.)

Figure 10.12 Elements of the Tommotian-type or small shelly fauna. Magnification approximately ×20 for all, except *Fomitchella* which is about ×40. (Based on various sources.)

Figure 10.13 Coelosclerites. Chancelloriids: 1 and 2, *Chancelloria*; 3, *Archiasterella*; 4, *Eremactis*. Sachitid: 5, *Hippopharangites*. Siphonoguchitids: 6, *Drepanochites*; 7, *Siphogonuchites*; 8, *Maikhanella*. Scale bars, 100 μm. (Courtesy of Stefan Bengtson.)

Figure 10.14 Stratigraphic distribution of Late Precambrian and Early Paleozoic metazoan taxa, some key morphological transitions and the carbon isotope record ($\delta^{13}C$). PDB, Vienna Pee Dee beleminite, the standard material for relative carbon isotope measurements. (Based on various sources.)

Figure 10.15 Comparison of Ediacara and Cambrian landscapes: (a) fitness landscapes; (b) locally optimal morphologies (Nicklas' plants); and (c) locally optimal morphologies (bilaterian animals). (Based on Marshall 2006.)

Figure 10.16 Modes of the Cambrian explosion. (Based on Budd & Jensen 2000.)

Figure 10.17 The Cambrian (a) and Ordovician (b) seafloors. (Based on McKerrow 1978.)

Figure 10.18 Origin of larval types and the Ordovician radiation as deduced from the fossil record and molecular clock data. The numbers of genera of key suspension-feeding taxa are indicated on the histogram in light tint, and, in dark tint, the numbers of genera of trace fossils. (Based on Peterson 2005.)

Figure 10.19 Significance of the diverse worm-like animals at the Precambrian–Cambrian boundary and the postulated origins of some major clades. (Based on Dzik, J. & Krumbiegel, G. 1989. *Lethaia* **22**.)

Figure 11.1 Basic sponge morphology.

Figure 11.2 Main grades of sponges.

Figure 11.3 Some examples of the main groups of sponges: *Archaeoscyphia* (×0.25), *Siphonia* (×0.4 and 0.8), *Protospongia* (×0.4), *Hydnoceras* (×0.25), *Prismodictya* (×0.6), *Rhaphidonema* (×0.8), *Corynella* (×0.8) and *Astraeospongium* (×0.4).

Figure 11.4 Sponge paraphyly. (a) The more traditional view presenting both the eumetazoans and poriferans as monophyletic groups; feeding strategies cannot be polarized since all the outgroups are non-metazoan. (b) If, however, poriferans are paraphyletic and calcisponges are more closely related to eumetazoans then the water canal system is a primitive character and the gut is more derived.

Figure 11.5 Main categories of spicule morphology. Magnification approximately ×75 for all, except microscleres which are about ×750.

Figure 11.6 Stratigraphic distribution of reef-building sponges and related parazoans, together with the scleractinian corals.

Figure 11.7 Stromatoporoid morphology.

Figure 11.8 Stromatoporoid growth modes. (Based on Kershaw, S. 1984. *Palaeontology* **27**.)

Figure 11.9 The Archaeocyatha: (a) morphology and (b) classification, function and growth modes of the main groups. (Based on Wood et al. 1992.)

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Figure 16.14 Matching fins and legs of the first tetrapods: the pectoral fin of the Devonian sarcopterygian fish *Eusthenopteron* (a) shows bones that are probable homologs of tetrapod arm bones, such as in the Devonian amphibian *Acanthostega* (b). *Acanthostega* had eight fingers and *Ichthyostega* had seven toes on its hindlimb (c). (d) The early tetrapod *Acanthostega*. (Courtesy of Mike Coates.)

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Figure 16.20 Synapsids of the Permian: (a) the carnivorous pelycosaur *Dimetrodon*; (b) the carnivorous gorgonopsian *Lycaenops*; and (c) the herbivorous dicynodont *Dicynodon*. (a, based on Gregory 1951/1957; b, c, courtesy of Gillian King.)

Figure 16.21 Transition to the mammals: (a) the Early Triassic cynodont *Thrinaxodon*; (b) the Early Jurassic mammal *Megazostrodon*; and
(c, d) skulls of an early synapsid (c) and a mammal (d) to show the reduction in elements in the lower jaw and switch of the jaw joint. (a, based on Jenkins 1971; b, based on Jenkins & Parrington 1976; c, d, based on Gregory 1951/1957.)

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Figure 17.2 Lepidosaurs: (a) the Late Triassic sphenodontid *Planocephalosaurus*; (b) the Late Jurassic lizard *Ardeosaurus*; and (c, d) skulls of a modern lizard (c) and snake (d), showing the points of mobility that permit wide jaw opening. (a, based on Fraser & Walkden 1984; b, based on Estes 1983.)

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Figure 17.4 Measuring the growth rate of a sauropod dinosaur. (a) Cross-section through the bone wall of the femur of the sauropod *Janenschia* from the Late Jurassic of Tanzania; the animal was full grown and the femur was 1.27 m long. The section was made by drilling into the bone and extracting a core that was then cut through; the center of the bone is to the left, the outside to the right. Lines of arrested growth are the darker bands, where the bone structure is tighter, indicating a slow-down in growth. These are marked off with tick marks on the side of the slide. (b) Growth curve for the sauropod *Apatosaurus* based on sections from the limb bones and ribs of several individuals, juveniles and adults, showing how the animal reached adult size with a spurt of growth from years 5 to 12. (Courtesy of Martin Sander and Greg Erickson.)

Figure 17.5 Cretaceous theropod dinosaurs:
(a) *Deinonychus*, and (b) *Tyrannosaurus*. (a, based on Ostrom 1969; b, based on Newman 1970.)

Figure 17.6 Armored ornithischian dinosaurs from the Jurassic (a) and Cretaceous (b, c):
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Figure 17.7 Skull of the Late Cretaceous hadrosaur *Edmontosaurus*.

Figure 17.8 Photograph of one of the *Massospondylus* eggs with a complete embryo skeleton inside, measuring some 15 cm in total length. It died just before hatching. As an adult, it would have grown to a length of 5 m. (Courtesy of Robert Reisz.)

Figure 17.9 Jurassic marine reptiles: (a) the ichthyosaur *Stenopterygius* and (b) the plesiosaur *Cryptoclidus*. (Courtesy of Rupert Wild.)

Figure 17.10 The oldest bird, *Archaeopteryx*, from the Late Jurassic. (Courtesy of Andrzej Elzanowski.)

Figure 17.11 Two examples of the Early Cretaceous bird *Confuciusornis* from Liaoning, China, showing a male (below, with long tail streamers) and a female. (Courtsey of Zhou Zhonghe.)

Figure 17.12 The dog-sized triconodont mammal, *Repenomamus*, from the mid-Cretaceous
of Liaoning, China: (a) reconstruction of this mammal eating a small *Psittacosaurus*, and

(b) specimen showing *Psittacosaurus* bones inside the rib cage. (Courtesy of Hu Yaoming.)

Figure 17.13 Extinct marsupials: (a) the sabretooth *Thylacosmilus* from South America, and (b) the giant herbivore *Diprotodon* from Australia. (Based on Gregory 1951.)

Figure 17.14 Cladogram of the major orders of placental mammals based on molecular evidence. The four deep splits among modern orders happened in the Late Cretaceous, but modern placentals did not become diverse until after the extinction of the dinosaurs.

Figure 17.15 Afrotheres and xenarthrans: (a, b) skulls of the Eocene proboscidean *Moeritherium* (a) and the Miocene proboscidean *Deinotherium* (b); and (c, d) Pleistocene edentates from Argentina, *Glyptodon* (c) and *Mylodon* (d). (Based on Gregory 1951.)

Figure 17.16 Diverse laurasiatherians: (a) the Eocene bat *Icaronycteris*; (b) the small four-toed artiodactyl *Messelobunodon*, showing the complete skeleton and a mass of chopped plant material in the stomach area, from the oil shale deposit of Messel, Germany; (c) the Pleistocene giant Irish deer *Megaloceros*; (d) the middle Eocene whale *Ambulocetus*; (e) the late Eocene whale *Basilosaurus*; (f) the Miocene horse *Neohipparion*; (g) the Pleistocene sabre-toothed cat *Smilodon*; (h) the Eocene dog *Hesperocyon*; and (i) the Miocene "seal" *Allodesmus*. (a, based on Jepsen 1970; b, courtesy of Jens Franzen; c, e–i, based on Gregory 1951; d, based on Thewissen et al. 1994.)

Figure 17.17 Diverse euarchontoglirans: (a) the Eocene rodent *Paramys*; (b) the Paleocene primate *Plesiadapis*; and (c) the Miocene ape *Proconsul*. (a, based on Wood 1962; b, based on Lewin 1999.)

Figure 17.18 Phylogeny of the primates, showing some of the main fossil and living groups (a), and the detail of one view of human evolution (b). *A.*, *Australopithecus*; *H.*, *Homo*; M, Mesozoic; Q, Quaternary.

Figure 17.19 Our oldest ancestor? The spectacular skull of *Sahelanthropus* from the upper Miocene of Chad, over 6 Ma. (Courtesy of Michel Brunet.)

Figure 17.20 The origin of bipedalism in humans: (a) the Pliocene hominid *Praeanthropus afarensis*, known as "Lucy"; and (b) comparison of the hindlimb of an ape (left), Lucy (middle) and a modern human (right). (Based on Lewin 1999.)

Figure 17.21 Skulls of fossil humans in front and side views: (a) *Australopithecus africanus*; (b) *A. boisei*; (c) *Homo habilis*; (d) *H. erectus*; (e) *H. sapiens*, Neandertal type; and (f) modern *H. sapiens*. (Based on Lewin 1999.)

Figure 17.22 Skulls of Flores man, *Homo floresiensis* (left), and of a typical modern human, *H. sapiens*, to show the great difference in size. (Courtesy of Paul Morwood.)

Figure 18.1 Examples of fossil fungi:
(a, b) *Palaeomyces*, a possible oomycete fungus from the Early Devonian Rhynie Chert of Scotland, showing branching non-septate hyphae terminated by enlarged vesicles (a) and a resting spore (b); and (c) *Palaeancistrus*, with basidiomycete-like clamp connections, from the Pennsylvanian of North America. (a, b, courtesy of Thomas N. Taylor; c, based on Stewart & Rothwell 1993.)

Figure 18.2 The oldest evidence of vascular plants on land? Spores from the Mid Ordovician (470 Ma) of Oman, scanning electron microscope images of a mass of spores (a) and close-up of one spore tetrad (b), and light microscope view of a spore tetrad (c). (Courtesy of Charlie Wellman.)

Figure 18.3 *Sporogonites*, an Early Devonian bryophyte, seemingly showing numerous slender sporophytes (20 mm tall) growing from a basal gametophyte portion. (Based on Andrews 1960.)

Figure 18.4 Cladogram showing the postulated relationships among the major groups of vascular land plants. Some synapomorphies that define particular nodes are: Chlorobionta (chlorophyll *b*), Charophyceae + Embryophyta (cell structure), Embryophyta (alternation of generations), Tracheophyta (vascular canals (tracheids) and secondary thickening) and Spermatopsida (seeds). Read more about the "deep green" project to establish a complete phylogeny of green plants at http://ucjeps.berkeley.edu/bryolab/GPphylo/.

Figure 18.5 Phylogenetic tree of the main groups of vascular land plants. The pattern of postulated relationships is based on the cladogram (Fig. 18.4), and details of known stratigraphic range and species diversity are added.

Figure 18.6 The origin of vascular land plant (tracheophyte) life cycles: (a) simplified plant life cycle showing alternation of phases; (b) life cycle of a hypothetical tracheophyte, with a dominant sporophyte phase and reduced gametophyte, in comparison with the life cycle of a hypothetical bryophyte (c), where the dominant phase is the gametophyte, and the sporophyte is a reduced dependent structure. (Based on various sources.)

Figure 18.7 Early vascular plants. (a–d) The oldest land plant, *Cooksonia* from the Silurian to Early Devonian. Early Devonian examples from Wales, showing a complete sporangium at the end of a short stalk (a), a stoma (b) and spores (c). The sporangium is 1.6 mm wide, the stoma is 40 μm wide and the spores are 35 μm in diameter. (d) Reconstruction of *Cooksonia caledonica*, a Late Silurian form, about 60 mm tall. (e) *Zosterophyllum*, a zosterophyllopsid from the Early Devonian of Germany, 150 mm tall. (a–d, courtesy of Dianne Edwards; e, based on Thomas & Spicer 1987.)

Figure 18.8 Reconstructed scene in the Early Devonian Rhynie ecosystem showing the commonest vascular plants *Rhynia* and *Asteroxylon* in the foreground, and a selection of small arthropods that lived in the water and in and on the plants

(scale bars, 100 μm). (Drawing by Simon Powell, based on information from Nigel Trewin.)

Figure 18.9 Reconstructing the arborescent lycopsid *Lepidodendron*, a 50 m-tall tree from the Carboniferous coal forests of Europe and North America. No complete specimen has ever been found, but complete root systems, *Stigmaria*, and logs from the tree trunk are relatively common. The details of the texture of the bark, branches, leaves, cones, spores and seeds are restored from isolated finds.

Figure 18.10 Giant Carboniferous horsetails:
(a) *Calamites*, a 10 m-tall tree; (b) *Annularia*, portion of a terminal shoot bearing 10 mm-long leaves; and (c) *Palaeostachya*, diagrammatic cross-section of a cone-like structure, 15 mm in diameter, bearing small numbers of megaspores. (Based on Thomas & Spicer 1987.)

Figure 18.11 The tree fern *Psaronius*, a 10 m-tall fern from the Pennsylvanian of North America. (Based on Morgan 1959.)

Figure 18.12 A typical gymnosperm seed, the ovule of *Pinus*, the pine, showing the archegonia (fertile female structures) surrounded by a substantial food store. Sperm enter through a narrow gap in the protective integument, and pass through pollen tubes to the archegonia.

Figure 18.13 Basic morphology and terminology of spores and pollen, shown in polar and equatorial (eq.) views.

Figure 18.14 Stratigraphic distribution of the main pollen and spore types.

Figure 18.15 Some Devonian and Carboniferous spore taxa: (a) *Retusotriletes*, (b) *Retusispora*, (c) *Spinozonotriletes*, (d) *Raistrickia*, (e) *Emphanisporites*, (f) *Grandispora*, (g) *Hystricosporites*, (h, i) *Ancyrospora*, and (j) *Auritolagenicula*. Magnification ×400 (a–d, f, i), ×750 (e), ×90 (g), ×125 (h), ×40 (j). (Courtesy of Ken Higgs.)

Figure 18.16 Some Jurassic spore and pollen taxa: (a, b) *Klukisporites*, (c) *Dettmanites*,
(d) *Dictyophyllidites*, (e) *Retusotriletes*, (f) *Callialasporites*, (g) *Classopolis*, (h) *Podocarpidites*, and (i) *Protopinus*. Mgnification ×400 for all. (Courtesy of Ken Higgs.)

Figure 18.17 The seed fern *Glossopteris*, a
4 m-tall tree, from the Late Permian of Australia. (Based on Delevoryas 1977.)

Figure 18.18 Carboniferous wildfires and the use of the SEM: (a) ancient charcoal can reveal spectacular details under the SEM, such as cross-field pitting, which provides evidence for which species of plants burned; and (b) part of a tree-ring. Note the transition from thin-walled "early wood" (left) to thick-walled "late wood" (center). The rings of growth may indicate a seasonal tropical environment like northern Australia or East Africa. Study of these plant remains and the sediments shows that wildfires happened every 3 to 35 years, and especially in drier uplands (c). PDP, poorly-drained coastal plain; WDP, well-drained coastal plain. (Courtesy of Howard Falcon-Lang.)

Figure 18.18 *Continued*

Figure 18.19 The early conifer *Cordaites*, about 25 m tall. (Based on Thomas & Spicer 1987.)

Figure 18.20 Diverse gymnosperms: (a) leaves of the modern ginkgo, *Ginkgo biloba* and (b) of the Jurassic ginkgo, *Sphenobaiera paucipartita*; (c) reconstruction of the 1.5 m-tall cycad *Leptocycas gigas* a from the Late Triassic of North America; and (d) reconstruction of the 2 m-tall bennettitalean *Cycadeoidea* from the Cretaceous of North America. (Based on Delevoryas 1977.)

Figure 18.21 Evolution of the angiosperm flower: (a) cone of the Jurassic bennettitalean *Williamsoniella*, showing the female fertile structure, the ovule, contained in a central receptacle, and surrounded by the male fertile structures, the microsporophylls; (b) flower of the gnetale *Welwitschia*, showing the central ovule, and surrounding male elements; and (c) flower of the angiosperm *Berberis*, showing the same pattern, but with the seed enclosed in
a carpel.

Figure 18.22 The coevolution of floral structures and of pollinating insects during the entire span of the Cretaceous and the early part of the Tertiary. Some of the major floral types are (a) small simple flowers, (b) flowers with numerous parts, (c) small unisexual flowers, (d) flowers with parts arranged in whorls of five, (e) flowers with petals, sepals and stamens inserted above the ovary, (f) flowers with fused petals, (g) bilaterally symmetric flowers, (h) brush-type flowers, and (i) deep funnel-shaped flowers. Pollinating insects include (j) beetles, (k) flies, (l) moths and butterflies, and (m–q) various groups of wasps and bees: (m) Symphyta, (n) Sphecidae,
(o) Vespoidea, (p) Meliponinae, and (q) Anthophoridae. (Based on information in Friis et al. 1987.)

Figure 18.23 Fossil angiosperm remains from North America. (a) Flower of an early box-like plant, *Spanomera*, from the mid-Cretaceous of Maryland (×10). (b) Leaf of the birch, *Betula*, from the Eocene of British Columbia (×1). (Courtesy of Peter Crane.)

Figure 18.24 Rapid radiation of the angiosperms during the Cretaceous, shown by the rise in the number of angiosperm families, from none at the beginning of the Cretaceous to more than 35 by the end of the period. Neocom, Neocomian; B, Barremian; Ce, Cenomanian; T, Turonian. (Based on information in various sources.)

Figure 18.25 The evolution of angiosperm leaf shape and paleoclimate. (a) Samples of typical leaf shapes from North American floras spanning the mid-Cretaceous, showing variations in length, margins and shapes. The average leaf size declines, suggesting an increase in temperature. (b) The leaf size index (percentage of entire-margined species and average leaf size) for low-latitude North American floras through the Late Cretaceous shows fluctuations. These are interpreted as the result of changes in temperature. (Based on information in Upchurch & Wolfe 1987.)

Figure 19.1 Slab of fine sandstone from the Robledo Mountains Formation (Lower Permian) of New Mexico, showing the trace fossil *Tonganoxichnus*, the hopping trace of a basal wingless insect such as *Dasyleptus* (inset). (Courtesy of Nic Minter.)

Figure 19.2 One animal may make many different kinds of trace fossils. The modern fiddler crab *Uca* makes: (a) a J-shaped living burrow (domichnion; *Psilonichnus*), (b) a walking trail (repichnion; *Diplichnites*), (c) a radiating grazing trace with balls of processed sand (pascichnion), and (d) fecal pellets (coprolites). (Based on Ekdale et al. 1984.)

Figure 19.3 One trace fossil may be produced by many different organisms. Here, all the traces are resting impressions, cubichnia, of the ichnogenus *Rusophycus*, produced by (a) the polychaete worm *Aphrodite*, (b) a nassid snail, (c) a notostracan branchiopod shrimp, and (d) a trilobite. (Based on Ekdale et al. 1984.)

Figure 19.4 Variations in the physical nature of the sediment may create variations in the appearance of a trace fossil. Here, a subsurface, patch-feeding burrow develops different morphologies, and therefore has different names, when preserved: (a) in sand (*Scalarituba*), (b) at a sand–mud interface in firm sediment (*Nereites*), (c) at a sand–mud interface in wetter sediment (*Neonereites*), and (d) at a mud–sand interface, seen from below (*Neonereites*). (Based on Ekdale et al. 1984.)

Figure 19.5 Terminology for trace fossil preservation, depending on the relationship of the trace to sediment horizons. (Based on Ekdale et al. 1984.)

Figure 19.6 Typical trace fossils of the Lower Silurian sediments of the Welsh Basin (*Nereites* ichnofacies): (a) *Helminthopsis*, (b) *Paleodictyon*, (c) *Nereites*, (d) *Gordia*, and (e) the pre- and post-turbidite trace fossil assemblages. (Courtesy of T. P. Crimes.)

Figure 19.7 Experimental ichnology: (a) graduate student Jesper Milàn, trying to persuade an emu to walk where he wants it to walk, and (b) the tracks and undertracks of the emu – results of an experiment where an emu stepped on a package of alternating layers of concrete and sand. After the concrete hardened, the sand was flushed out and replaced with silicone rubber. The top print (left) made an impression on several layers below, shown as undertracks at depths of up to 40 mm. Notice how the impressions of the digits become wider and less well-defined along each subjacent horizon. (Courtesy of J. Milàn.)

Figure 19.8 Trace fossils of the deep ocean floor. The patch-feeding trace (pascichnia) *Helminthopsis* meanders on one horizon, and the network burrow system (agrichnia) *Paleodictyon* is seen at a different level, in this field photograph from the Lower Silurian Aberystwyth Grits, Wales. (Courtesy of Peter Crimes.)

Figure 19.9 Theropod dinosaur tracks from the Late Triassic of Greenland. (a) A three-dimensional computer reconstruction (top) shows a theropod foot at three stages in the creation of a deep track, moving from right to left. A photograph of a deep Greenland footprint is shown below. (b) A three-dimensional computer image reconstructing theropod foot movements through sloppy mud. The first toe creates a rearward pointing furrow (1, 2) as it plunges down and forward. The sole of the foot leaves an impression at the back of the track (3) because it is not lifted as the foot sinks. All toes converge below the surface and emerge together from the front of the track (4). (Courtesy of Stephen Gatesy.)

Figure 19.10 The behavioral classification of trace fossils, showing the major categories, and some typical examples of each. Illustrated ichnogenera are: 1, *Cruziana*; 2, *Anomoepus*; 3, *Cosmorhaphe*;
4, *Paleodicyton*; 5, *Phycosiphon*; 6, *Zoophycos*; 7, *Thalassinoides*; 8, *Ophiomorpha*; 9, *Diplocraterion*; 10, *Gastrochaenolites*; 11, *Asteriacites*; 12, *Rusophycus*. (Based on Ekdale et al. 1984.)

Figure 19.11 Diagram showing how to measure stride length (SL) and foot length (FL) on a dinosaur track.

Figure 19.12 The major ichnofacies, and their typical positions in a hypothetical diagram of marine and continental environments. Typical offshore marine soft-sediment ichnofacies, from deep oceanic and basinal locations to the intertidal zone, include the *Nereites* (N), *Skolithos* (Sk), *Zoophycos* (Z) and *Cruziana* (Cr) ichnofacies, which may occur in various water depths and in different conditions of sedimentation. A storm-sand fan and a turbidite fan are indicated. The *Psilonichnus* (Ps) ichnofacies occurs in supratidal marshes and the *Scoyenia* (Sc) ichnofacies includes all lacustrine and related continental settings. The *Glossifungites* (G) ichnofacies is typical of firmgrounds, the *Trypanites* (Tr) ichnofacies consists of borings in limestone, and the *Teredolites* (Te) ichnofacies consists of borings in wood. (Modified from Frey et al. 1990, and other sources.)

Figure 19.13 Block diagrams showing typical trace fossils of the major ichnofacies: (a) *Nereites* ichnofacies, viewed as molds on a turbidite bed bottom; (b) *Zoophycos* ichnofacies;. (c) *Cruziana* ichnofacies; (d) *Skolithos* ichnofacies; (e) *Psilonichnus* ichnofacies; (f) *Scoyenia* ichnofacies;
(g) *Glossifungites* ichnofacies; (h) *Trypanites* ichnofacies; and (i) *Teredolites* ichnofacies, characterized by vertical bulbous burrows of bivalves (*Teredolites*) and subhorizontal burrows. (Based on Ekdale et al. 1984; Frey et al. 1990, and other sources.)

Figure 19.13 *Continued*

Figure 19.14 Sediments and trace fossils in the Late Cretaceous Cardium Formation of Alberta. Normal, fine-grained sediments (A, C) are associated with *Cruziana* ichnofacies trace fossils,
while intermittent, coarse, sandstone, storm beds (B) show trace fossils of the *Skolithos* ichnofacies. 1, *Chondrites*; 2,

Cochlichnus; 3, *Cylindrichnus*; 4, *Diplocraterion*; 5, *Gyrochorte*; 6, *Paleophycus*; 7, *Ophiomorpha*; 8, ?*Phoebichnus*; 9, *Taenidium*; 10, *Planolites*; 11, *Rhizocorallium*; 12, *Rosselia*; 13, *Skolithos*; 14, *Thalassinoides*; 15, *Zoophycos*. (Based on Pemberton & Frey 1984.)

Figure 19.15 Examples of trace fossil tiering, in which burrowers choose specific depth horizons below the sediment–water interface. (a) In the Middle Ordovician limestones of Öland, Sweden, there are three tiers. (b) In the Early Jurassic Posidonienschiefer of Germany, there are also three tiers. (c) In the Late Cretaceous Chalk of Denmark, there are at least nine tiers. (Based on Ekdale & Bromley 1991, and other sources.)

Figure 19.16 Trace fossils may help to define the Precambrian–Cambrian boundary, and to flesh out detail about the Cambrian explosion. Jensen (2003) identified seven trace fossil zones, each characterized by trace fossils of increasing complexity. Evidence for trilobites, and arthropods in general, is signaled first by trace fossils and then by body fossils. Prot, Proterozoic. (Drawing by Simon Powell.)

Figure 19.17 Ichnofabric indices for different sedimentary/ichnofacies settings. These diagrams show the proportions of sediment reworked by bioturbation, as seen in vertical section and numbered from top to bottom: 1 (no bioturbation) to 5 (intensely bioturbated). (Courtesy of Mary Droser and Duncan McIlroy.)

Figure 19.18 Interpreting trace fossils in borehole cores can be difficult. Vertical (a) and horizontal (b) cuts across a core may show rather obscure burrow impressions, but these make sense when interpreted in three dimensions (c). These are indications of the U-shaped burrow *Diplocraterion*, typical of the *Skolithos* ichnofacies, and so an indicator of the intertidal zone. (Courtesy of Duncan McIlroy.)

Figure 20.1 Two models for the diversification of marine invertebrate life over the past 600 myr of good-quality fossil records. (a) The empirical model, in which the data from the fossil record are plotted directly, and (b) the bias simulation model, in which corrections are made for the supposedly poor fossil record of ancient rocks. (Based on information in Valentine 1969; Raup 1972.)

Figure 20.2 The diversification of four groups of multicellular organisms during the Phanerozoic: (a) marine animals, (b) vascular land plants, (c) non-marine tetrapods, and (d) insects. All graphs show similar shapes, with a long initial period of low diversity, and then rapid increase since the Cretaceous. Geological period abbreviations are standard, running from Vendian (V) to Tertiary (T). (Based on various sources.)

Figure 20.3 Theoretical models for the diversification of life plotted as if for the last 600 myr (a) in the absence of major perturbation and (b) with two mass extinctions superimposed.

Figure 20.4 The history of family diversity of the three great "faunas" of marine animals, showing a Cambrian phase, a Paleozoic phase and a "modern" phase. The three phases add together to produce the overall pattern of diversification in Fig. 20.2a. Geological period abbreviations are standard, running from Vendian (V) to Tertiary (T). (Based on Sepkoski 1984.)

Figure 20.5 Sepkoski's three-phase coupled logistic model for diversification of animal life in the sea. (a) The family-level diversification curve for marine animals, showing the three evolutionary "faunas" from Fig. 20.4, each shaded differently. Numbers I to V are the five big mass extinctions, in sequence from left to right, Late Ordovician, Late Devonian, end-Permian, Late Triassic and Quaternary-Cretaceous. (b) The handover from the Cambrian to the Paleozoic "fauna" involved a shift in equilibrium diversity ($\hat{D}$); equilibrium diversity is achieved when origination (k_s) and extinction (k_e) rates match. (c, d) The coupled logistic model gives a simple representation of the broad outlines of the progress of the three evolutionary "faunas" 1, 2 and 3 (c), and perturbations, shown by vertical arrows, may be added to correspond to the mass extinctions (d). (Based on information in Sepkoski 1979, 1984.)

Figure 20.6 The evolution of the horses has been interpreted as a simple one-way trend towards large size, single toes and deep teeth. The reality is more complex: horse evolution has followed a branching pattern, and the line to the modern horses, *Equus*, was not preordained: notice the diversity of North American horses in the late Miocene and Pliocene. The evolutionary steps did not all occur in parallel: *Merychippus* was a grazing horse, with deep-rooted teeth, but retained a three-toed foot. (Based on MacFadden 1992, and other sources.)

Figure 20.7 A classic example of a radiation, the pattern of diversification of the placental mammals after the Cretaceous-Tertiary mass extinction. Mammals originated in the Triassic, and diversified at a modest rate during the Jurassic and Cretaceous. Modern placental superorders originated in the Late Cretaceous, and the orders began to diversify. Only after the dinosaurs had died out did the placental mammals really diversify and become abundant worldwide. (From Benton 2005.)

Figure 20.8 A classic example of competitive replacement? Articulated brachiopods were the dominant seabed shelled animals in the Paleozoic, whereas bivalves take that role today. It was assumed that the bivalves competed long term with the brachiopods during the Paleozoic, even in the Permian, and eventually prevailed. (a) A plot of the long-term fates of both groups shows a steady rise in bivalve diversity, and a drop in brachiopod diversity. However, brachiopods were also diversifying during the Paleozoic, although they were hard hit by the Permo-Triassic mass extinction (arrowed). (b) The

bivalves managed to recover after the mass extinction event, while the brachiopods did not. Geological period abbreviations are standard, running from Vendian (V) to Tertiary (T). (Based on information in Gould & Calloway 1980.)

Figure 20.9 The diversification of life, with the timing of the 10 major biological advances indicated: 1, origin of life; 2, eukaryotes and the origin of sex; 3, multicellularity; 4, skeletons; 5, predation; 6, biological reefs; 7, terrestrialization; 8, trees and forests; 9, flight; 10, consciousness. The diversification of life is plotted for the whole of the past 4000 myr (a), and for the Phanerozoic (b). Geological period abbreviations are standard, running from Vendian (V) to Tertiary (T).

Appendix

Collage of the main provinces through time. The Early Paleozoic was characterized by low- and high-latitude provinces separated by the Iapetus Ocean. During the Late Paleozoic, the Rheic Ocean separated the Old and New World provinces, whereas the Mesozoic was characterized by Boreal (high-latitude) and Tethyan (low-latitude) provinces. (These maps were produced by Professor Trond Torsvik, Center for Geodynamics, Geological Survey of Norway and the Center for Advanced Study, Norwegian Academy of Sciences and Letters, at the request of the authors.)