1 • Work-flows in applied palaeontology

A generic work-flow in applied palaeontology is shown in Fig. 1.1.

It will be seen that the key constituent elements are: project specification and management; sample acquisition, processing and analysis; and analytical data acquisition. Each of these elements is discussed in turn below (and interpretation and integration in Chapters 2–10).

1.1 PROJECT SPECIFICATION AND MANAGEMENT

Project specification involves, firstly, the identification of the technical and business objectives of the project; and secondly, the formulation of a plan and budget appropriate to the timely delivery of these objectives to the customer, taking into account such factors as timing, resourcing and third-party involvement.

Project management involves assurance of adherence to the plan and budget. It also involves assurance of quality, and of compliance with Health, Safety and Environmental, or HSE, standards, as appropriate.

1.2 SAMPLE ACQUISITION

The sample acquisition strategy is determined by the technical or research objectives of the project, and by the available budget. In most cases, the principal factor to be considered is the number and spacing of samples, which will determine the ultimately achievable biostratigraphic resolution, and hence the value of the project, as well as the cost.

1.2.1 Surface sample acquisition

Acquisition of surface samples for their fossil content is required to constrain surface geological mapping and correlation, among other reasons.

Equipment. The (more-or-less) technical equipment required or useful for the palaeontologist in the field is as follows: a global positioning satellite (GPS) system; a topographic map or aerial photographs or satellite images of the area of interest; a compass/clinometer; an altimeter; a range-finder; a pair of binoculars; a digital camera or video; a portable lap-top computer on which to upload digital images; a portable solar panel with which to recharge electronic equipment; a measuring tape; a $\times 10$ to $\times 20$ magnifying glass or a pocket microscope; a bottle of dilute hydrochloric acid to test for carbonates; a sledge or 4-lb (2-kg) lump hammer; a 2-lb (1-kg) hammer; a set of chisels; a set of dental tools; a pick-axe; an entrenching tool; an auger; a supply of sample bags; a supply of indelible pens for labelling them; a waterproof notebook and a supply of pencils for recording observations (Jones, 2006; Coe, in Coe, 2010).

Safety. Safety equipment should include clothing and footwear appropriate to the season and terrain; sun-cream; personal protection equipment, including a hard hat or climbing helmet, and goggles for use when hammering; sufficient food and water to see out an emergency; fire-lighting equipment; a survival blanket; a torch (flashlight); a whistle, for attracting attention; and a first-aid kit (Goldring, 1999; Oliveri & Bohacs, 2005; Jones, 2006; Coe, in Coe, 2010).

Recommended safety procedures are as follows (Goldring, 1999):

> Listen to the daily weather forecast (including wind direction), which may determine where it is prudent to work. Take account of the time and height of tides when planning coastal work. Write down each day your approximate route, working area and time of return, and leave it for others to see. In worsening conditions, do not hesitate to turn back if it is still safe to do so. If you get lost, disabled, benighted, or cut off by the tide, … stay where you are until conditions improve or until you are found. Supposed short cuts can be lethal.

Distress codes are as follows (Goldring, 1999):

> On mountains: 6 long blasts, flashes, shouts or waves in succession, repeat(ed) at minute intervals. At sea: 3 short then 3 long, then 3 short blasts or

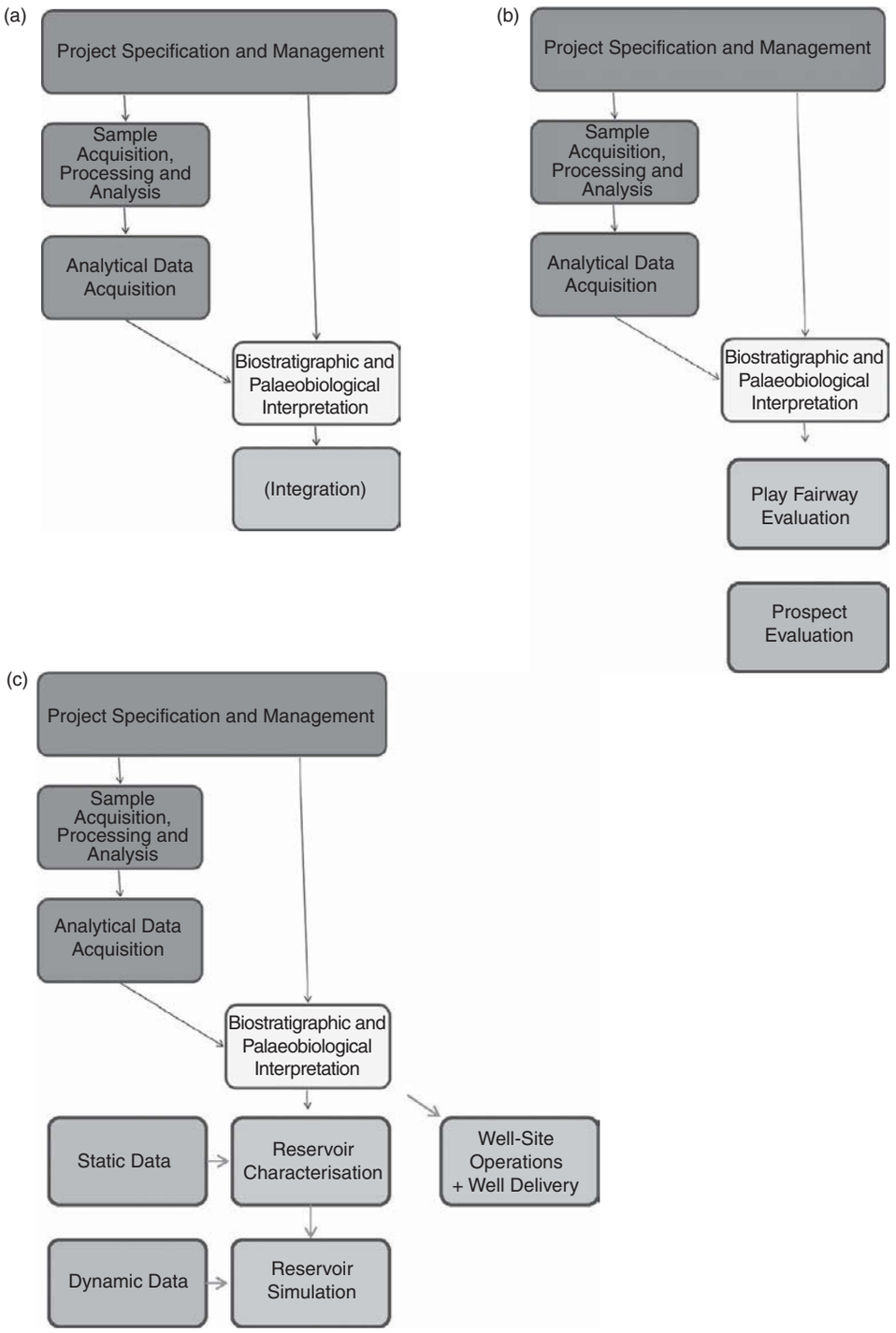

Fig. 1.1 **Work-flows in applied palaeontology**. (a) General; (b) petroleum exploration, as discussed in Section 5.2; (c) reservoir exploitation.

flashes [Morse code for SOS], ... repeat(ed). Rescuers reply with 3 blasts or flashes repeated at minute intervals.

Acquisition of surface samples for their macrofossil content

Acquisition of surface samples for their macrofossil content, and of macrofossils, has to be responsible and sustainable, so as to conserve or preserve what is a finite natural resource for future generations, preferably in place (Goldring, 1999; Jones, 2006; Spicer, in Coe, 2010). In the United Kingdom, acquisition in designated 'Sites of Special Scientific Interest' or SSSIs is restricted to that for genuine and justifiable scientific purposes only, otherwise it would constitute an 'operation likely to damage' (OLD) the resource. Elsewhere in the United Kingdom, it is restricted by recommendation or voluntary code of conduct. The Geologists' Association 'geological fieldwork code' of conduct recommends the following actions. Firstly, 'Observe and record, and *do not hammer indiscrimately*.' Secondly, 'Keep collecting to a minimum. Avoid removing *in situ* fossils, unless they are *genuinely* needed for serious study.' Thirdly, 'The collecting of actual specimens should be restricted to those localities where there is a plentiful supply, or to scree, fallen blocks and waste tips.' Fourthly, 'Never collect from walls or buildings. Take care not to undermine fences, walls, bridges or other structures.' In Germany, acquisition in so-called 'geotopes' ('parts of the geosphere ... clearly distinguishable from their surroundings in a geoscientific fashion') is restricted by nature conservation and by national monument protection legislation.

Macrofossils are generally large enough to be seen in surface outcrops or in float. However, careful observation may be required in order that they may actually be seen. The angle of the Sun is important in this regard. Early mornings and late afternoons, when the Sun is low and the shadows long, are often the best times for searching for fossils. (Similarly, tilting slabs can cast shadows that throw previously unseen and unsuspected fossils into unexpected relief.) Intensive searching can commence once extensive searching has revealed a fossiliferous horizon. Hard rocks can be broken open using a lump hammer, or split along bedding planes using a hammer and chisel, in both cases carefully, so as not to damage specimens. Contained fossils are typically harder than containing rocks, and can be readily extracted. In the event that the fossils are softer than the rock, thay can nonetheless still be extracted, carefully, using dental tools, a process often started in the field and finished in the laboratory. Collecting fossils from certain hard rocks, such as massive limestones, can be effectively impossible. Specimens are probably better photographed than removed from these rocks. Soft rocks can be trenched and samples removed for laboratory preparation.

Acquisition of surface samples for their microfossil content

Special care must be taken in the acquisition of surface samples for their microfossil content so as to avoid contamination, which can arise from, for example, the failure to clean hammers or other tools, or the use of cloth rather than plastic sample bags.

Sample spacing. The overall objectives of the fieldwork should be considered when determining the appropriate strategy for sampling. For example, if the objective is reconnaissance mapping, spot sampling might be all that is required, whereas if the objective is detailed logging, targeted or close systematic sampling would be required. As a general comment, the biostratigraphic or palaeoenvironmental resolution of the analytical results will depend as much on the sampling density as on the fossils themselves. Partly on account of this, and partly on account of the logistical effort and financial cost of mobilising field parties, it is always advisable to collect what might be thought of as too many rather than too few samples. However, any restrictions on access or sampling imposed by the land-owner should be respected, as should the code of conduct (see above). The particular microfossil groups to be expected in the ages and environments of the rocks expected to be encountered should also be considered, together with any sampling requirements specific to those groups (see below).

Sample size. The size of sample required depends to an extent on the group targeted (see also below). Samples for most micropalaeontological or palynological analysis should generally be at least 30–60 g, or 'One Standard British Handful', while those for nannopalaeontological analysis should be at least 5–10 g (and more in areas of high sedimentation

rate and dilution of fossil content). Note, though, that samples for conodont analysis should be at least 500 g or 0.5 kg, and, in the case of the Devonian, which contains only rare specimens, 10 kg.

Sample lithology. The lithologies most likely to be productive for microfossils are fine-grained clastics such as shales and mudstones, especially where calcareous, and fine-grained limestones such as lime mudstones, wackestones and packstones. Those least likely to be productive are coarse-grained clastics such as sandstones and conglomerates, coarse-grained limestones such as grainstones, rudstones and framestones, altered dolomites, and evaporites. Note, though, that coarse-grained clastics can contain reworked microfossils that can provide useful information as to provenance.

Importantly, weathered rocks of any lithology are less likely than unweathered rocks to be productive for calcareous microfossils, on account of the likelihood of leaching; and are unlikely to be productive for organic-walled microfossils, on account of the likelihood of oxidation (which can also occur in the sample processing laboratory or storage facility, and which can be species-selective in its effects: Kodrans-Nsiah *et al.*, 2008). This is a particular problem in tropical climes, for example in the Kufra basin in southeast Libya, where surface weathering can affect up to 50–75 m of section, necessitating digging, trenching, auguring or even drilling, using appropriate tools, to obtain fresh, unweathered samples. (Note also that 'palaeo-weathering' affected up to 50 m of section below the Permo-Carboniferous unconformity in the North Sea.) Unweathered rocks can be recognised by their generally blocky rather than slabby, platy, fissile or earthy texture. Note that if it is simply not possible to access unweathered rocks, because the effects of weathering have pervaded so deep, it is nonetheless still worth sampling any calcareous concretions that might be present, since experience has shown that these can be productive for calcareous microfossils.

Thermally altered rocks of any lithology are less likely than unaltered rocks to be productive, particularly for organic-walled microfossils. The effects of thermal alteration can be either local or regional.

Specific groups of microfossils. Calcareous microfossils are locally so abundant in rocks of the appropriate age-range and facies as to be rock-forming, as in the case of '*Globigerina*' or planktonic foraminiferal oozes. They are common in essentially all fine-grained marine limestones and marls, and even in indurated ones, which cannot be easily disaggregated and which are therefore best studied in thin-section (although they may be difficult to identify in altered dolomites). Calcareous microfossils are also common in essentially all fine-grained marine calcareous mudstones, and, in the case of agglutinated foraminifera, in non-calcareous mudstones. Even non-marine, lacustrine calcareous mudstones can contain calcareous microfossils, in the form of ostracods and branchiopods, which may be sufficiently large to be discernible on bedding planes with the aid of a hand-lens. Samples are best collected by chiselling along bedding planes rather than hammering, so as to avoid damage to specimens. One large sample bag is generally sufficient to ensure recovery of calcareous microfossils, especially if the material is fresh and unweathered. It is invariably worth the effort ensuring that this is so.

Siliceous microfossils are locally so abundant in rocks of the appropriate age-range and facies as to be rock-forming, as in the case of diatomites, radiolarian cherts or radiolarites, and spiculites. Diatomites often resemble volcanic tuffs when weathered. Diatoms can be common not only in diatomites but also in siliceous mudstones, such as those of the Miocene of California, or in so-called 'opokas', such as those of the Miocene of Sakhalin. Radiolarians can be common not only in radiolarites but also in shales and in calcareous rocks of marine origin. Unfortunately, the silica of which diatoms is composed is an unstable variety (Opal-A), which converts to a more stable variety (cristobalite or Opal-CT) under the sort of pressure and temperature conditions encountered at burial depths of the order of 2 km, often resulting in the destruction of diagnostic morphological features. Even under these conditions, though, diatoms can be preserved, with their diagnostic morphological features intact, through recrystallisation, replacement – typically by pyrite or calcite – or entombment in concretions. Radiolarians are generally more robust, and more resistant to diagenetic alteration.

Phosphatic microfossils such as conodonts are at least locally common in most marine rocks of the

appropriate age-range and facies. They are perhaps most common in limestones, especially bioclastic wackestones or packstones. The occurrence of macrofossils such as crinoids or brachiopods in a rock is an encouraging sign that it will be productive for conodonts. Cherts are also sometimes productive for conodonts on treatment with hydrofluoric acid. Conodonts are generally resistant to chemical attack, and also to diagenetic dolomitisation and thermal alteration. They can occasionally be seen on bedding planes with the aid of a handlens. They can be concentrated in lag deposits such as bone beds. The abundance of conodonts varies through time, such that sample sizes need to be adjusted accordingly (see above) The facies preference of conodonts also varies through time. Older conodonts are more common in shallower-water, younger ones in deeper-water, deposits.

Organic-walled microfossils or palynomorphs are present to common in most clastic rocks of the appropriate age and facies that contain clay-sized particles and that have not been subject to excessive oxidation or thermal alteration (carbonates are generally poorly productive). Organic-walled microfossils can be extremely abundant, with up to 100 000 grains per gram present in some carbonaceous deposits, such that small samples are generally sufficient. Even individual conglomerate clasts can be analysed, in order to provide an indication of provenance of reworking. Organic-walled microfossils are prone to reworking on account of their small size and resistance to chemical attack.

Calcareous nannofossils are locally so abundant in marine rocks of the appropriate age-range and facies as to be rock-forming, as in the case of calcareous nannofossil oozes and chalks. They are common in essentially all fine-grained marine limestones, marls and calcareous mudstones. Recrystallised limestones and dolomites should be avoided, though, as they are likely to have had their original calcareous components destroyed by diagenesis. Marine red beds deposited below the calcite compensation depth should also be avoided.

1.2.2 Subsurface sample acquisition

In the petroleum industry, acquisition of subsurface samples for their fossil content is required to constrain the biostratigraphic, or age, interpretation, and the palaeobiological, palaeoecological or palaeoenvironmental, or facies, interpretation, of subsurface wells, either during or after drilling, and to calibrate subsurface seismic interpretation, among other reasons (see Chapter 5 below).

Sample type. Conventional and side-wall core samples are generally preferred over cuttings samples (see Section 5.2). This is because cuttings samples are prone to contamination by material in the drilling mud and also by material sloughing off the walls of the bore and caving down-hole. For example, in my working experience, cuttings samples from the Pedernales field in the eastern Venezuelan basin were contaminated by mangrove pollen in drilling mud formulated from local river water that were indistinguishable from those in the reservoir (Jones, in Jones & Simmons, 1999; see also sub-section 5.3.3 below). Note, though, that contamination of cuttings samples appears to be much less of a problem with modern than with historical mud systems. Note also that in many ways cuttings are more representative and informative than core samples, as they provide continuous rather than point coverage. Wet cuttings are generally preferred over washed and dried, unless an oil-based drilling mud has been used.

Sample spacing. The generally preferred spacing of cuttings samples is every 10 m or 30′, with a contingency to close to every 3 m or 10′ over intervals of interest, such as the reservoir target (Fig. 1.2). The preferred spacing of conventional and side-wall core samples is every 1 m or 3′, with a contingency to close to every 0.3 m or 1′ over intervals of interest (Fig. 1.2).

Sample size. As noted above, the size of sample required depends to an extent on the group targeted. Cuttings and conventional core samples for micropalaeontological or palynological analysis should generally be at least 30–60 g, while those for nannopalaeontological analysis should be at least 5–10 g. Side-wall core samples for micropalaeontological or palynological analysis should be approximately half the size of the core, while those for nannopalaeontological analysis should be approximately a quarter of the size of the core.

Sample lithology. Again as noted above, the lithologies most likely to be productive for microfossils are fine-grained clastics and fine-grained limestones,

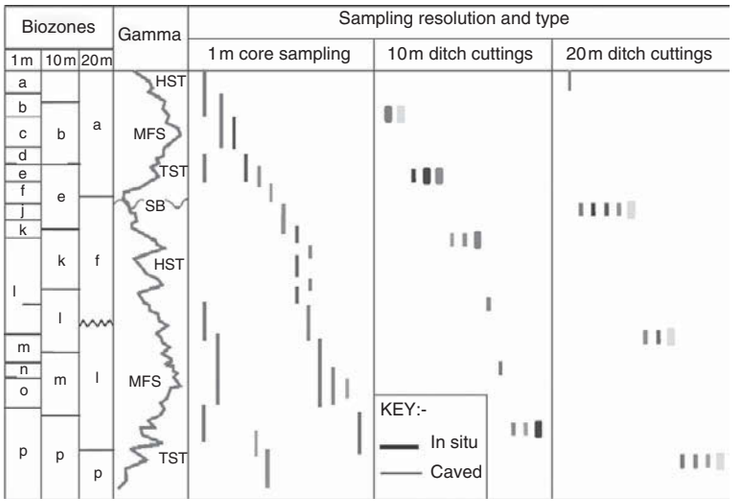

Fig. 1.2 **The effect of sampling on biostratigraphic resolution (and hence value).** Only fine sampling (down to 1 m) is sufficient to resolve fine detail such as thin rock units or systems tracts, or short-lived biozones. HST, high-stand systems tract; TST, transgressive systems tract, as defined in Section 4.1. Biozones a–p are invented categories, included for illustrative purposes only. Caving refers to down-hole contamination (see 1.2.2). Modified after Sturrock, in Emery and Myers (1993).

and those least likely to be productive are coarse-grained clastics, coarse-grained limestones, altered dolomites and evaporites.

Drilling environment. In the petroleum industry, the drilling environment also needs to be considered, as the drilling technology, bit type and mud system can all impact sample quality.

In terms of drilling technology, conventional drilling, controlled mud pressure drilling and riserless mud recovery (RMR) drilling have no or low impact on sample quality; coiled tubing drilling, drilling with casing and underbalanced drilling (UBD) can have a moderate impact; and managed pressure drilling (MPD) has a high impact, as it essentially does not permit the return of samples to the surface. Note, though, that coiled tubing, slim-hole and UBD technologies have recently been successfully employed in combination in the drilling of the Sajaa field in Sharjah in the United Arab Emirates, without impacting the quality of the samples used in micropalaeontological analysis and in 'biosteering' (Jones *et al.*, in Koutsoukos, 2005; see also 5.4.1 below).

In terms of bit type, roller cone bits have no or low impact; diamond bits, polycrystalline diamond compact (PDC) bits, and PDC bits with down-hole motors can have a moderate impact; and PDC bits with turbines can have moderate to high impact, as they can effectively metamorphose samples and render them useless for analytical purposes.

In terms of mud systems, water-based and polymer-based systems can have a moderate impact; and oil-based systems can have a moderate to high impact.

1.3 SAMPLE PROCESSING

In the petroleum industry, in the case of micropalaeontological sample processing, for example for calcareous microfossils such as foraminifera and ostracods, samples should generally be simply disaggregated in water, with or without the addition of a solution of washing soda or of hydrogen peroxide, or of heat, to speed the process (Jones, 2006). The individual microfossils should then be picked out of the sieved residue with a moistened artist's brush, and sorted into numbered squares on a cardboard slide for identification under a reflected light microscope. Indurated limestone samples should be thin-sectioned for analysis under a transmitted light microscope.

In the case of nannopalaeontological processing, for calcareous nannofossils, samples should again be simply disaggregated in distilled water. The disaggregated sample should then be strewn onto a glass slide with a cover slip for identification under a powerful transmitted light microscope.

In the case of conventional palynological processing for organic-walled microfossils or palynomorphs, the non-palynomorph components of the sample should be dissolved in hydrochloric, hydrofluoric and fuming nitric acids. The sieved residue should then be strewn onto a glass slide with a cover slip for identification under a transmitted light microscope.

The use of hydrochloric, hydrofluoric and fuming nitric acids in conventional palynological sample processing raise some serious Health, Safety and Environmental (HSE) issues (see Box 5.6).

It is important that sample processing is undertaken by a best-in-class facility, both to ensure compliance with HSE standards, and also to ensure that no palaeontological information is lost, because if it is lost, it is lost irretrievably.

1.4 SAMPLE ANALYSIS

In the petroleum industry, it is also important that sample analysis is undertaken by best-in-class analysts, so as to maximise the quality and value of the analytical data acquired. It is sometimes undertaken in-house in oil and gas companies, but more often externally by third party consultancies.

1.5 ANALYTICAL DATA ACQUISITION

In the petroleum industry, where, as noted above, analysis is often undertaken by third parties, it is important that the full suite of raw analytical data is acquired rather than simply an interpretation or summary thereof, so as to enable independent in-house quality assurance and interpretation.

It is preferable that the full suite of data is acquired in a digital format, for ease of manipulation, display and storage.

2 • Biostratigraphy and allied disciplines, and stratigraphic time-scales

Biostratigraphy involves the use of fossils in establishing the ordering of containing rocks in time and in relation to evolving Earth history (McGowran, 2005; Jones, 2006). It is one of the principal bases for chronostratigraphic subdivision and correlation of lithological units, thus providing a spatio-temporal context for their interpretation, and is a fundamental building block of Earth science.

I make no formal distinction between biostratigraphy (which essentially records relative age, or time) and lithostratigraphy (which records rock), in the characterisation of sequences, that is, intervals of time represented by rock, such as the Devonian Old Red Sandstone. I do so only in the characterisation of non-sequences, that is, intervals of time unrepresented by rock, such as that between the Late/Upper Devonian Old Red Sandstone and underlying Silurian greywacke observed at 'Hutton's Unconformity' at Siccar Point in East Lothian in Scotland. Note in this context that the absolute age, or extent in time, of the intervals of time either represented or unrepresented by rock can only be determined by absolute chronostratigraphy or geochronology, which actually measures time rather than simply recording or representing it (or by biostratigraphy calibrated against the absolute chronostratigraphic or geochronological time-scale).

I make no distinction at all between time- and rock-stratigraphic nomenclature. Note, though, that other authors do, and use the descriptors 'early', 'middle' and 'late' only when referring to time-stratigraphic units, and 'lower', 'middle' and 'upper' only when referring to rock-stratigraphic units.

2.1 SUMMARY OF BIOSTRATIGRAPHIC SIGNIFICANCE AND USEFULNESS OF PRINCIPAL FOSSIL GROUPS

The biostratigraphic significance and usefulness of the principal fossil groups is discussed in this section and in Sections 2.2–2.6 below, and summarised in Fig. 2.1 (from Jones, 2006; see also 'Chronos' website, www.chronos.org).

The ranges over which they are biostratigraphically significant are shown by broad bands. It is evident that most are only biostratigraphically significant over certain time intervals, and then only in the appropriate facies. Note also that the potential biostratigraphic significance of fossils can be impaired by natural factors, such as *post-mortem* transportation and diagenetic effects, and reworking. The biostratigraphic significance of fossils can also be impaired by artificial factors, such as sample acquisition and processing, and subjectivity in specific identification.

The particular usefulness and applicability of some groups is in not only biostratigraphy, but also palaeobiology, discussed in Chapter 3, and sequence stratigraphy, discussed in Chapter 4. Case studies of applications of these groups in industry and elsewhere are discussed in Chapters 5–10.

Characteristics of biostratigraphically significant and useful fossil groups

Biostratigraphically significant and useful fossil groups share two common characteristics: firstly, relatively rapid rates of evolutionary turnover, and hence restricted stratigraphic distributions, and/or essentially isochronous first and last appearances; and secondly, essentially unrestricted ecological distributions (for example throughout the marine realm, and across a range of biogeographic provinces, in the case of many planktonic or nektonic forms). The most useful groups for practical purposes are also, typically, abundant, well preserved, and easy to identify. These are referred to as 'marker fossils' or 'index fossils'. Conversely, the least stratigraphically useful groups characteristically exhibit relatively slow rates of evolutionary turnover, and/or diachronous or time-transgressive first and last appearances. Alternatively, they may exhibit restricted ecological distributions (for example to individual bathymetric zones, in the case of many benthic forms). Note, though, that the very ecological restriction exhibited by these groups renders them palaeobiologically useful 'facies fossils' (see Chapter 3 below).

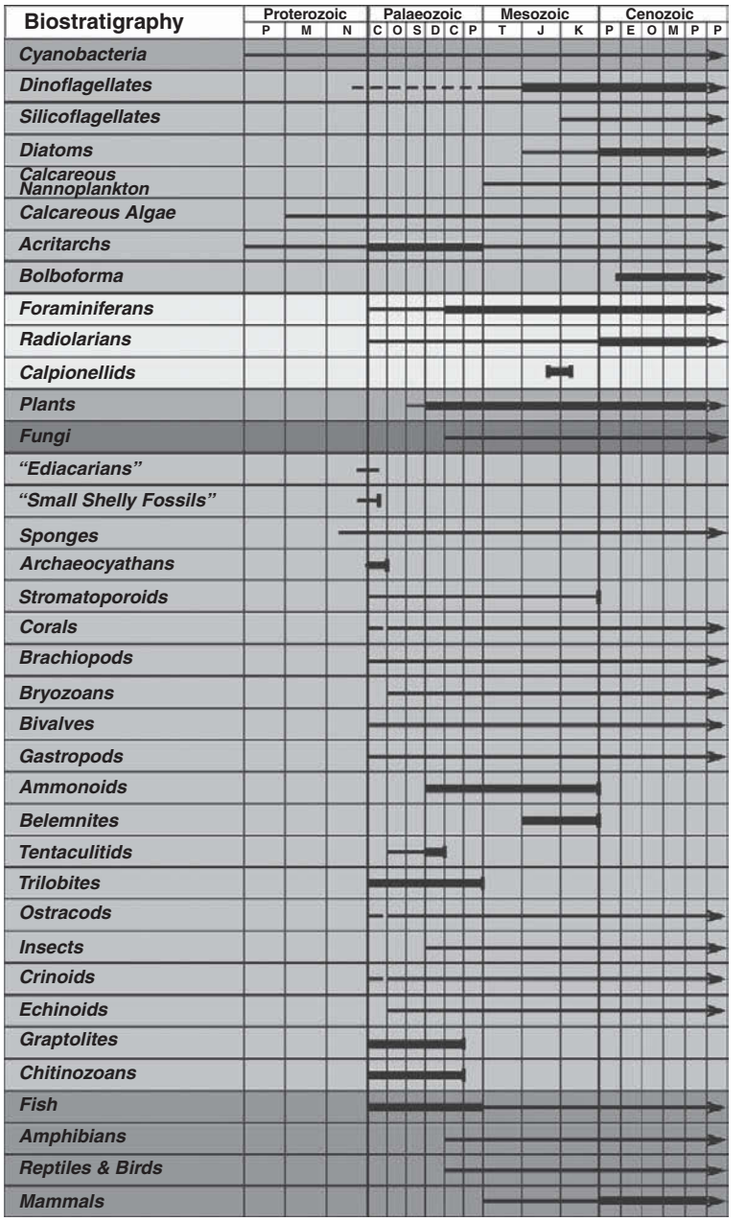

Fig. 2.1 **Stratigraphic distribution of selected fossil groups**. Modified from Jones (2006).

2.1.1 Bacteria

Cyanobacteria

Cyanobacteria evolved in the Archaean, approximately 3500 Ma, and have ranged through to the Recent (Batistuzzi & Hedges, in Hedges & Kumar, 2009). They diversified through the Palaeoproterozoic, Mesoproterozoic and Neoproterozoic, but underwent something of a decline in the Neoproterozoic, from around 1000 Ma. Some authors have speculated that this decline was due to

excessive grazing of stromatolitic mats by early 'ediacarans'. However, other authors have hypothesised that it was brought about by environmental change associated with a series of glaciations, resulting in a so-called 'Snowball Earth' in the 'Cryogenian' period of the Neoproterozoic (Moczydlowka, 2008). Incidentally, it has also been hypothesised that diversity promotes environmental stability, and therefore that low-diversity biotas, like those of the Proterozoic, are more susceptible to such external environmental factors than high-diversity biotas, like those of the Phanerozoic.

The oldest known Cyanobacteria and/or microbialites are those from the Pilbara craton of Western Australia, dated to approximately 3500 Ma; and from the Barberton greenstone belt of South Africa and Swaziland, dated to approximately 3500–3300 Ma (Brasier *et al.*, 2005; Allwood *et al.*, 2007; Konhauser, 2007; Schopf *et al.*, 2007; van Kranendonk *et al.*, 2008; de Gregorio *et al.*, 2009). Incidentally, organic material of somewhat questionable origin has been found in the Witwatersrand supergroup of South Africa, which overlies the Barberton supergroup and is dated to approximately 2900–2700 Ma. It has been hypothesised that this material originated either from Bacteria or Algae, or from lichen-like organisms (the observed columnar form as representing *in situ* growths, the particulate or 'fly-speck' form as dispersed spores). Whether or not this is the case, it is clear that whatever organism was responsible for the organic material was also somehow responsible for the observed concentration of gold in the organic material, for which the Witwatersrand is rather more famous.

The exceptionally slow rate of evolutionary turnover exhibited by the Cyanobacteria renders them of limited use in biostratigraphy.

In my working experience in the petroleum industry, Cyanobacteria have proved of use in the following areas:

Proterozoic – the Neoproterozoic, Tonian of east Siberia, and the Neoproterozoic, Tonian–Cryogenian of the Jagbub High, Cyrenaica, northeast Libya, North Africa;

Proterozoic or Palaeozoic – the 'Infracambrian' of the Middle East, and of Mauritania in northwest Africa;

Palaeozoic – the Carboniferous of Libya in north Africa;

Mesozoic – the Cretaceous of the western margin of the British Isles.

'Archaebacteria'

'Archaebacteria' have no known fossil record. However, molecular sequencing evidence indicates that they are among the most primitive forms of life on earth, and may have been among the earliest (Batistuzzi & Hedges, in Hedges & Kumar, 2009). This is supported by the observation that many modern species inhabit the sorts of extreme environments that would have existed on the early earth.

2.1.2 Plant-like protists (Algae)

Dinoflagellates

Molecular evidence in the form of arguably dinoflagellate-derived dinosteranes in oil source-rocks and in oils indicates a possible Precambrian origin for the dinoflagellates (Moldowan *et al.*, 1996; Moldowan *et al.*, in Zhuravlev & Riding, 2001; Delwiche, in Falkowski & Knoll, 2007). Indeed, possible dinoflagellates have been recorded from the Precambrian Wynniatt formation of Victoria Island in the Canadian Arctic, dated to between 1081 and 721 Ma, from the Cambrian MacLean Brook formation of Nova Scotia in the Canadian Atlantic, and from the Cambrian Oville formation of Spain (Palacios *et al.*, 2009). (Note also that the existence of zooxanthellates as long ago as the Ordovician is indirectly indicated by the occurrence of corals, with which the group at present has a symbiotic relationship.) However, definite dinoflagellates do not appear in the rock record until the Triassic. The overall pattern of dinoflagellate evolution has been one of ever-increasing diversification through the Mesozoic and Cenozoic, with comparatively little loss of diversity other than that associated with the Late Cenomanian mass extinction, and, more especially, the end-Cretaceous mass extinction. Interestingly, dinoflagellates appear to have evolved (possibly iteratively) through the incorporation by a protist of a haptophyte, arising