The power of stratigraphy in determining biological evolutionary patterns

V Semeniuk[1] & K J McNamara[2]

[1] V & C Semeniuk Research Group
21 Glenmere Road, Warwick, WA 6024

[2] Department of Earth Sciences, University of Cambridge,
Downing Street, Cambridge CB2 3EQ, UK
✉ kjmc@cam.ac.uk

Abstract

Biological evolution can be reconstructed from a number of pathways, including analysis of synoptic species variation, developmental biology (or embryology), palaeontology, and in more recent times use of microbiology and genetic science. The modern environment provides mechanisms and drivers that underpin biological evolution, *viz.*, predation, inter-species competition, intra-species competition, changes in environment, changes in food sources, expansion of species population into neighbouring niches, amongst others. Using the modern environment as an example, there are innumerable and complex processes that result in complexity of stratigraphic sequences and biostratigraphic sequences. If properly addressed and categorised, and applied to the geological record, such information provides a reliable and robust interpretation of the fossil record, and while the synoptic approach for extant and fossil species is useful and has provided insights into speciation, the palaeontologic approach combined with stratigraphy, which is diachronous, holds to be the most useful because it involves tens to hundred of millions of years, and thousands of species. In this paper, the focus is on the use of palaeontology and the use of stratigraphy within which changes in species are recorded, but to begin with we describe some key background principles, processes and factors of geology, biology and evolution that underpin modern ecology, biological evolution, sedimentology and stratigraphy and the use of stratigraphy in evolutionary palaeontological studies; these include: uniformitarianism; gradations; mutations in organisms; biotic assemblages and ecology with respect to habitat; lateral habitat tolerance of organisms and its implications for evolution; skeletal contribution to sediments; the relatively poor record (contribution) of modern assemblages to the fossil record; ecological and population processes underpinning evolution as "drivers" and "determinants"; differential response of organisms to pressures and environmental changes; sedimentology, facies, and habitats; changes in facies laterally and vertically to develop stratigraphic sequences; changes in lithology macrostratigraphically, microstratigraphically, geochemically, or isotopically driven, for instance, by climate and tectonism; and geological processes and the incompleteness of the stratigraphic record. The different types of stratigraphic sequences are explored in their usefulness in interpreting the palaeontological record in terms of trends in biological evolution, and several of the best documented fossil sequences are noted and discussed. Stratigraphy is a powerful and important tool to set the geological stage for inferring evolutionary lineages, understanding evolutionary changes, and separating types of palaeontological sequences useful for interpreting lineages because it helps identify the framework in which the fossils occur, *e.g.*, is a vertical sequence of fossils illustrating anatomical changes the result of stacking of facies and hence a stacking of the synoptic assemblages, or is it the result of diachronous changes?

Keywords: stratigraphy, palaeontology, evolution, stratigraphic types

Introduction

Construction of lineages in biological evolution and development of the theory of biological evolution have been based by a variety of techniques, ranging from interpreting synoptic species variation, palaeontology, embryology, and, more recently, use of microbiology and genetic science (Syvanen 1985; Mitton 1994; Mindell 1997; Weygoldt 1998; Katz 2002; Tishkoff & Kidd 2004; Regier *et al*. 2005; Richardson & Palmer 2007). In point of fact, investigations of biological evolution have proceeded essentially on four broad fronts: 1. that involving

products, such as extant speciation, fossils and their synoptic and diachronous speciation, and biostratigraphy; 2. that involving studies of field ecology and micro-ecology, which have resulted in the understanding of interactions between organisms, such as predator-prey relationships, and species-and-habitat relationships, helping to explain processes that drive evolution; 3. that involving manipulative experiments in the laboratory on organisms such as bacteria or *Drosophila*; and 4. that involving study of microbiological and genetic processes, through the advent of high-resolution microscopy and genetic science techniques, whereby the processes of evolutionary change are genetically and biochemically determined; in fact, major

advances in understanding biological evolution have occurred in recent years with the advent of genetic science, where lineages have been determined by DNA and by exploring mechanisms of genetic transfer. Combined, all have provided strong evidence of the workings and products of biological evolution.

The tenet of this paper, however, is that while the variety of techniques described above, without doubt, have been very useful, and have added enormously to an understanding of the processes and products of biological evolution, it is the palaeontological record, spanning > 500 million years, with many thick sequences of sedimentary accumulations, and encompassing the length and breadth of continental geology and oceanic basins, that holds the largest library of information on the phenomenon of biological evolution. In other words, if biological evolution has been operating since life began on Earth, then it is in the fossil record, in the pages of the book of the Earth, that the evidence is embedded in abundance. Modern analyses of extant synoptic speciation, the various laboratory-based experimental manipulative techniques such as selective breeding or those involving microbiology, and the use of genetics and biochemistry are "here and now" techniques, *i.e.,* they reside and derive from the Holocene, and cannot compare to the wealth of evidence held in the Earth. It is our contention that, to date, the full extent of this palaeontological history has not been systematically explored and utilised, nor explored within a formalised stratigraphic framework.

Fossils are not always readily preserved. In modern and Holocene environments, for instance, the (recent) fossil record is fragmentary, and from a diverse biota of skeletal and non-skeletal organisms, depending on environmental setting and taphonomy, only a small proportion may be preserved. In the modern and Holocene environments there also is (and has been) bioturbation, prevailing erosion, storms, transport, and accumulation of thanatocoenoses, and there are local environmental and climate changes that alter the composition of biological assemblages. These factors have also been present in the geological record, which has rendered the stratigraphic sequences complex, but, in addition, there have been hiatuses, intra-formational erosional episodes, disconformities, angular unconformities, and tectonism that can locally remove sections of stratigraphic sequences and alter an ideal biostratigraphic sequence of fossils (Figure 1). Antagonists of the Theory of Biological Evolution focus on what is missing, and even for many scientists there has been an implicit movement away from using the fossil record in a meaningful way to construct patterns of biological evolution. We argue that rather than concentrating on what is missing in the fossil record, enough is present and enough can be sought for researchers to appreciate what is actually preserved and use that as windows into palaeontologic patterns. If correctly interpreted and used, palaeontology in the stratigraphic record provides a powerful tool to decipher evolutionary patterns diachronously. Consequently, to
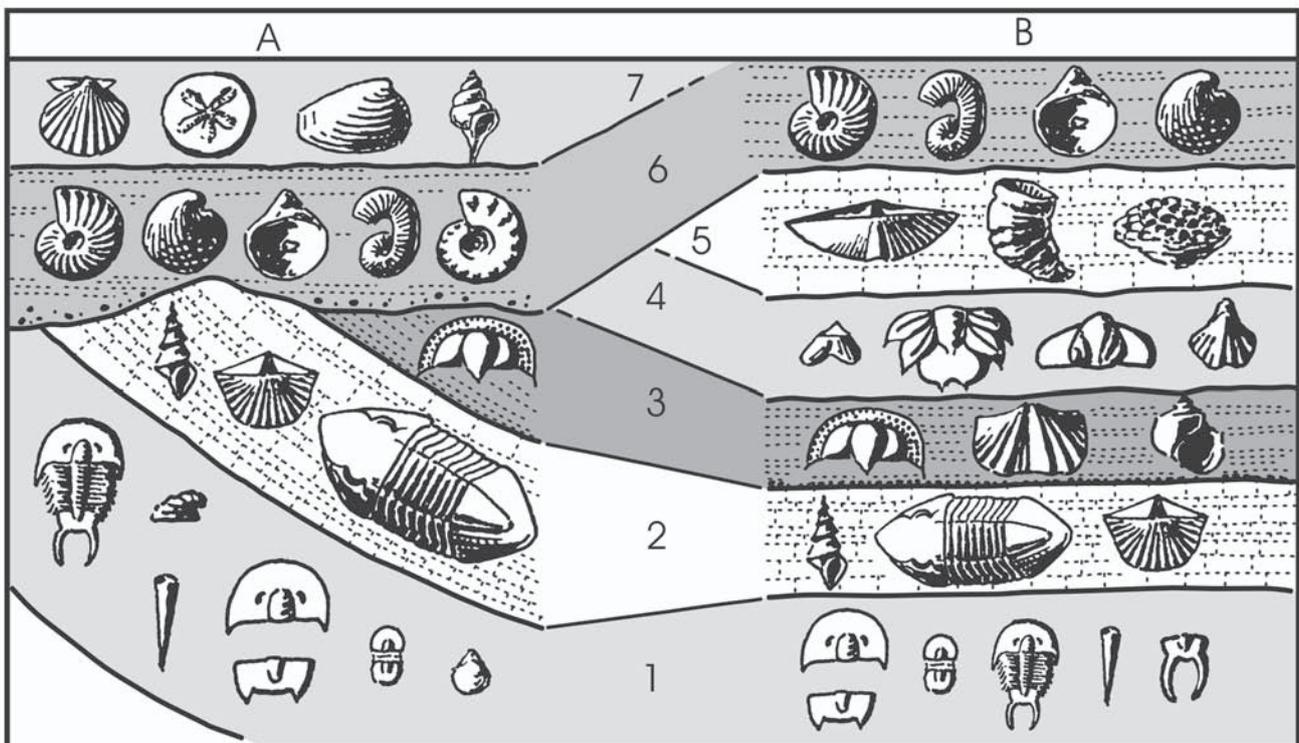

Figure 1. The complexity of the stratigraphic record (adapted and modified from Moore *et al.* 1952). This diagram, originally used by Moore *et al.* (1952) to illustrate complexities involved in using fossil assemblages for stratigraphic correlations, with the occurrences of hiatuses, unconformities and erosional removal of strata, equally could be used to highlight the incompleteness of the fossil record, and also to illustrate that fossils within a stratum occur as "assemblages" (whether biocoenoses, or thanatocoenoses).

assess how evolutionary patterns may be preserved, to assess the robustness of the sequences for use in determining lineages, and to aid palaeontologists and evolutionary biologists and palaeobiologists in their study of lineages, we aim to identify the nature of biological evolution processes (*i.e.,* its "drivers" and "determinants"), the way that evolving organisms may be preserved, and the nature of stratigraphic sequences wherein fossils are embedded.

With the work carried out to date on biological evolution in the palaeontological record there has been a focus on species within a given genus, or genera within a family, often dictated by the nature of the outcrop and the speciality of the researcher. While the results have shown biological evolution operating in the fossil record, the full extent of the complex nature of assemblage interactions, animal-habitat interactions, and the multiplicity of evolutionary patterns present within the strata of the Earth has not been fully explored. For instance, if there were several "drivers" and "determinants" underpinning evolutionary change in a number of species that comprise an assemblage of, say, 100 different organisms within a given habitat, a palaeontologist working in the Palaeozoic and dedicated to studying corals, may not be focusing on the trilobites, graptolites, gastropods, calcareous algae, and other fossils present, which may be manifesting evolutionary changes, while another palaeontologist, if working within the same set of strata may have only focused on gastropods. Yet, proper analysis of the whole assemblage may show changes in many of its components and that evolutionary changes proceeded in a complex, diachronous, and in a temporally variable manner (some following gradualism, some following punctuated equilibria). It may also show different "drivers" and "determinants" underpinning the differential evolutionary changes in the various (now fossil) organisms. Unfortunately, holistic palaeontological studies of assemblages of organisms are not common, and while the studies that have been undertaken have been admirable and useful, there have not been enough palaeontologists to undertake such a dedicated and systematic task worldwide. As such, the story of biological evolution in the palaeontological record, though it has provided important patterns and principles here and there, has been opportunistic and fragmentary.

This paper is partly a review of established concepts, principles and techniques, particularly those in early days of the development of the Theory of Biological Evolution by Darwin, Wallace and others, to illustrate that the early development of the Theory was not based on a robust palaeontological record, and partly a review of the foundations of geological, biological, and ecological science to develop a robust stratigraphic framework to assess palaeontologic changes from a palaeontological (palaeobiology) evolutionary perspective. Thereafter, we focus on types of stratigraphic sequences and fossil sequences and their use in interpreting evolutionary lineages. We describe types of stratigraphy as important tools in reconstructing biological evolution and provide stratigraphic frameworks for deciphering evolutionary patterns. We also emphasise the assemblage approach to unravelling evolutionary patterns, with a focus that different drivers and determinants will be affecting

different organisms in the assemblages. Finally, we revisit some classic palaeontological case studies with focus on equids, *Monograptus, Micraster*, ammonites, and *Gryphaea*, that each in their own way provides different expressions of how palaeontology, biological evolution, and stratigraphy are related and expressed, and how palaeontology in concert with stratigraphy contributes to a more robust understanding of evolutionary lineages and evolutionary associations.

Note that this paper is not concerned with gradualism or punctuated equilibria as phenomena of the palaeontological record, as these focus on rates of appearances of new species or the stability of a given species, and how biological evolution may proceed. Rather we examine the various stratigraphic and biostratigraphic sequences within which the fossil record may be embedded, the reliability of these sequences, and how to use stratigraphy effectively. Thus, regardless of whether gradualism or punctuated equilibrium are the prevailing process of evolutionary change for a given species, or whether it is both, and regardless of whether gradual morphological change is evident, or paedomorphosis or peramorphosis is evident, we focus on stratigraphy, and formally define the various stratigraphic frameworks within which the diachronous assemblages are embedded.

The adjectival descriptor "synoptic" refers to those processes, or products (such as biota) that occur at the same time, or within the same time plane. It is synonymous with "isochronous". Extant biotic assemblages are clearly "synoptic assemblages". Fossil assemblages where they can be shown to have existed in the same time plane are "synoptic fossil assemblages" and the use of such assemblages or other fossil species in the same time plane is "synoptic palaeontology". The adjectival descriptor "diachronous" refers to that processes, or products (such as biota), that occur through time as manifest in the stratigraphic record. The study of fossils through the stratigraphic column, effectively through time, is diachronous palaeontology.

A review of history of early approaches in determining biological evolution

Charles Darwin arrived at his Theory of Biological Evolution from a number of pathways, synthesising information from a range of disciplines (Darwin 1859): information obtained during the voyage of the *Beagle* on extant spatial biological variation (*e.g.,* his conclusions on the *Rhea* and other South American fauna that illustrate modern speciation and the variation across habitats and food types; Darwin 1846); developmental biology; work on beetles; and short term selective breeding with pigeons. Darwin arrived at his conclusions without recourse to detailed palaeontological evidence. This is not to say that the works of geologists and palaeontologists of the time did not influence him, or that he was unaware of the palaeontological record. Indeed, he himself had collected fossils in stratigraphic context, particularly in South America in relation to coral reefs (Darwin 1844), and flightless birds and extinct mammals (Darwin 1846), and Darwin foremost considered himself a geologist rather than a biologist, and thus was well aware of the

palaeontological record available when writing *On the Origin of Species*. But he was also aware of the incompleteness of the fossil record in the 1800s. However, at the time of writing *On the Origin of Species*, palaeontology and geological time could not be used in a robust manner in any detailed analyses because critical information was mostly missing and stratigraphic/palaeontological sequences had not been fully explored at that time (*cf.* Sudbury 1958).

Wallace came to a similar conclusion to Darwin regarding biological evolution and the origin of species, but his focus was on contemporary biota, and he developed his theory mainly from synoptic patterns, with a focus on gradations between species based on his biogeographical observations in South America (Wallace 1852) and the Malay Archipelago (Wallace 1855). While being aware of the palaeontological literature of the time (Wallace 1855), Wallace was primarily a zoologist and did not share Darwin's passion for geology and palaeontology.

In addition to Darwin and Wallace, the main proponents of the principle of natural selection in the Theory of Biological Evolution, were three others who published less developed ideas embodying the principle of natural selection, all of which were derived from different paths of study but involving modern synoptic patterns. These others were: a physician who derived the principle from observations of human skin colour (Wells 1818); an orchardist who developed the principle from experience with culling trees (Matthew 1831); and a zoologist with a special interest in ornithology, particularly the classification of bird varieties (Blyth 1835).

The sources and style of data and information that led Darwin, Wallace and others to their conclusions, while a synthesis of a number of pathways, were simpler than those of today, where microbiology, cell biology, genetics, biochemistry, cladistics, developmental biology, and micro-anatomy of fossils, amongst others, are making contributions to the Science of Biological Evolution.

However, to place the stratigraphic approach we are describing into a context, and refine it as a tool for deciphering evolutionary lineages and patterns from other scientific approaches, we will attempt to categorise the sources and style of data and information that led Darwin and his contemporaries to arrive at the theory of biological evolution. While modern approaches to unravelling, understanding, and supporting biological evolution are based on a number of scientific disciplines, ranging from genetics, biochemistry, embryology, amongst others, in the past, there were four cornerstones in developing evolutionary theory (Figure 2):

1. synoptic species variation
2. developmental biology
3. palaeontology
4. selective breeding

With synoptic species, synthesis of linkages and evolutionary patterns were obtained from interpreting variations in biota, and gradations in the anatomy of biota, adapted for their various modes of living (*i.e.*, speciation, as species adaptation and response to different environments, different food types, and predation, amongst other controls and pressures). Thus, linkages were inferred by analysis of biota within the one time plane. The synoptic approach is particularly powerful if spatial gradations occur in the species, or where speciation can be linked to habitat variation, food types, feeding behaviour, or other animal behaviour. Axiomatically, for Darwin and Wallace, the one time plane for their reconstructions of evolutionary linkages was the contemporary late Holocene. Thus, the modern synoptic species variation was the main approach of Wallace and one of the main approaches of Darwin.

Developmental change, in the form of heterochrony (see McNamara this volume), also has been used as a tool in inferring evolutionary patterns (formerly expressed in the once popular phrase coined by Haeckel (1866): "ontogeny recapitulates phylogeny", or simply "recapitulation" (Gould 1977). Here the element of time is captured in the short term in the ontogeny of the organism (*i.e.*, the life of an individual). Darwin also used developmental change to some extent to develop his Theory, and other authors have explored this component of biological development as an indicator of lineages, and evolutionary trends. Ontogenetic changes are also used in the fossil record where, for accretionary shells (such as molluscs), the earlier stages of shelly organisms are preserved embedded in their interior (*e.g.*, a protoconch). Accepting that developmental change provides clues to evolutionary lineages, fossil developmental change thus also is an important tool in determining palaeontological lineages (McKinney & McNamara 1991; McNamara 1994, 1995, 1997). Developmental palaeontology (ontogeny) has been used successfully in graptolites (Sudbury 1958), trilobites (McNamara 1986; McNamara *et al.* 2003, 2006), echinoids (McNamara 1988, 1990), ammonites (Trueman 1922; Zakharov 1988; Dommergues 1990), and brachiopods (McNamara 1983).

Selective breeding provided short term information that the strongest or fittest or most favourable characteristics could be artificially selected (Matthew 1831; Darwin 1859) thus paving the way to providing a mechanism that could be naturally occurring, a mechanism that Darwin, with later regret, termed natural selection.

Palaeontology as a tool in studies of biological evolution adds the dimension of time to determining evolutionary patterns, and it is particularly relevant to determining lineages because evolutionary trends are best expressed across time (*i.e.*, diachronously). Fossil sequences can span tens to hundreds of millions of years, and so there is the aspect that there is a greater chance that lineages and incremental changes in organisms can be detected. That is, while other pathways of exploring Evolution Science provide good results, and in their own way make significant contributions to the field, they are firmly locked up in the "present", *i.e.*, the "here and now", and there also is a component of having to extrapolate backwards in time to make sense of evolutionary linkages and lineages. Nonetheless, modern biochemical, genetic, and microbiological approaches provide valuable insights into the various mechanisms of biological evolution. The fossil record, on the other hand, holds the key to providing data and information on what has already happened, and has happened over hundreds of millions of years. As mentioned earlier, considering
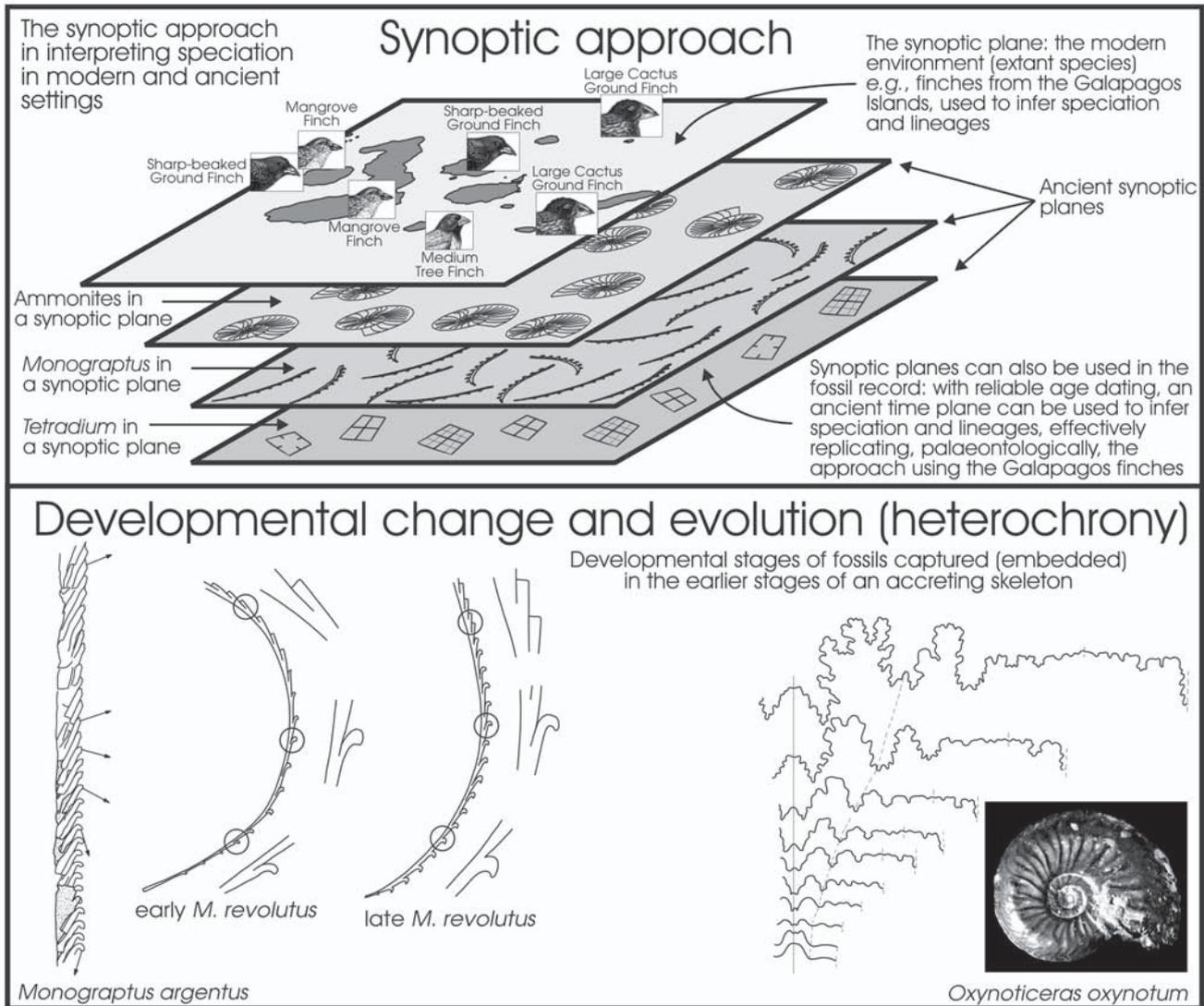
Figure 2. Some of the procedures used in the development of the Theory of Biological Evolution: A. The synoptic approach, in this case, using the finches of the Galapagos Islands, superimposed on a map of the Archipelago, as an example for the modern fauna (Gould 1837, 1841; Darwin 1845), ammonites for a Mesozoic time plane, *Monograptus* for a Silurian time plane, and *Tetradium* for an Ordovician time plane (for *Tetradium* palaeozoogeography see Webby & Semeniuk 1971). B. Developmental changes (heterochrony) evident in *Monograptus revolutus* and *Monograptus argentus* (modified from Bulman 1933; Sudbury 1958), and in the sutures of an ammonite (after Clarkson 1979); arrows on *Monograptus argentus* show the directional change of the orientation of the aperture of the thecae.

the length and breadth of the Earth, and the depth of sedimentary strata accumulated, the stratigraphic record and its fossil content exposed in cliffs and quarries, explored and excavated to date, represents but a fraction of what the Earth holds in archive. We consider that the stratigraphic and palaeontological record holds the best long term evidence and record of biological evolution patterns.

Particularly if well dated, but even in robust sedimentary sequences that are not dated absolutely, palaeontology shows changes in organisms through the stratigraphic record in a temporally absolute, or in a relative way, with the pulses of appearances, extinctions, and anatomical/skeletal changes, effectively adding valuable information to determining evolutionary patterns. This approach can be termed the "diachronous procedure/data/ information".

Where palaeontology is focused within the one time plane, assessing fossil biodiversity (at generic level and species level) would be termed synoptic palaeontology.

Some background principles in geology, ecology, and evolution

Use in stratigraphic sequences of palaeontology and interpretation of the changes in morphology of fossils requires an understanding of some principles in geology, ecology, and ecological processes that underpin evolution. This section provides a brief description of a number of key principles and processes that are required as background to interpreting the palaeontological record from an evolutionary perspective. However, we emphasise that the subject matter to be covered here is wide ranging and to be exhaustively covered would

require a book – we are just providing brief summaries and signposts to the issues underlying a robust interpretation of evolution using palaeontology in the stratigraphic record. For further information on key background processes in geology, ecology and evolution, the reader is referred to Ager (1963), Krumbein & Sloss (1963), Imbrie & Newell (1964), Dunbar & Rodgers (1966), Holmes (1966), Preiss & Siever (1974), Clarkson (1979), Reineck & Singh (1980), Tevesz & McCall (1983), Matthews (1984), Boggs (1987), Emiliani (1992), Underwood (1997), Krebs (2001), Underwood & Chapman (2001), and Odum *et al*. (2004). The key principles, processes, and factors are:

1. uniformitarianism

2. gradations

3. mutations occurring in organisms

4. ecological and population processes underpinning evolution as "drivers" and "determinants"

5. composition of biotic assemblages and their ecology with respect to habitat

6. lateral tolerances of organisms and their implications to evolutionary change

7. contribution of biota to sedimentary sequences as benthos, nekton, and plankton, and exogenic material

8. the relatively poor record (contribution) of modern assemblages to the fossil record

9. differential response of organisms in assemblages to pressures and environmental changes

10. sedimentology, facies, and habitats

11. changes in facies laterally and vertically to develop stratigraphic sequences

12. environmental changes such as climate changes and tectonically-driven sedimentary changes resulting in changes in lithology macrostratigraphically, microstratigraphically, geochemically, or isotopically

13. geological processes and the incompleteness of the stratigraphic record

These are briefly described below, but the reader is referred to other works dealing with the subject matter more fully. In each description, the relevance to understanding evolution in the stratigraphic record in terms of the principles, processes, or factors underpinning evolution is noted.

Uniformitarianism, first espoused as a principle by James Hutton (1788), has been a cornerstone of geology. Essentially it is summarised in the adage: *the present is the key to the past*. As such, interpretation of past sedimentological events, biological processes, development of biotic assemblages, drivers for evolution, expression of hydrochemistry, amongst many others rests on understanding similar or the same processes and products in the modern environment. While it is a clear principle in the geological sciences, *e.g.,* modern models and modern phenomena can be applied to interpreting ancient sequences in disciplines as diverse as sedimentology, volcanology, and stratigraphy (*cf.,* Ginsburg 1975; Reineck & Singh 1980; Cas & Wright 1988), it is also applicable to the biological and ecological sciences, though not as consistently used therein in

comparisons of modern and ancient processes and products. Uniformitarianism is one of the foundations of ideas and principles expressed in this paper.

The identification of gradation between products, regardless of whether they are abiotic or biotic, especially when it is in temporal sequence and if used geographically, is a powerful tool in determining associations and inter-relationships. Abiotically, for instance, grainsize of sediment may gradationally change laterally (synoptically) in response to gradients in energy, providing insights into the relationship between grainsize of substrates and (wave, tidal, or wind) energy levels. In concert, the biological composition within an assemblage may change in response to such grainsize gradations. Gradations may also be expressed at the species level. For instance, an organism may change its form in response to a hydrochemical gradient or grainsize gradients (*e.g., Avicennia marina*, a mangrove, at the local scale physiognomically changes across a tidal flat from tree to shrub to dwarf shrub in response to a salinity gradient, or at the regional scale changes from forest-dominated to heath-dominated in response to a climate gradient; Semeniuk *et al*. 1978; Semeniuk & Wurm 1987). While synoptically a gradation in a product or an organism is reflecting a response to synoptic gradients geographically, climatically, hydrochemically, a gradation if expressed over time (*i.e.,* diachronously), also shows that products are responding to some process or processes temporally. Such gradations, if they occur palaeontologically are important, as they show association of an organism temporally, and that the gradual change of an organism is occurring over time. Gradations between fossils synoptically over large geographic distances, or between facies (habitat) changes are showing inter-relationship of organisms across synoptic gradients. In palaeontology, gradations between species diachronously through a stratigraphic sequence, as well as synoptically across palaeogeographic regions are important tools in determining evolutionary associations and lineages. They show the inter-relationships between species. The evolutionary gradation of the horse foot (MacFadden 1988; MacFadden & Hubbert 1988) and the thecae of monograptids (Sudbury 1958) are good examples of diachronous gradation (Figure 3).

Mutations in organisms are a fundamental tenet of biological evolution (Muller 1932; Freese 1959; Papadopoulos *et al*. 1999; Eyre-Walker & Keightley 2007). The detailed processes involved and how DNA is modified are not relevant to this paper, rather, we focus on the outcome, that is, with mutations, the organism is changing, with the changes occurring potentially in different anatomical and physiological parts of the organism. In time, if the mutations accumulate, new species will derive from ancestral species. Within an assemblage of organisms composed of different species with varying propensity to adapt, or tolerate environmental change, or undergoing various types of mutation, different species will mutate in different ways, or at different rates, or not at all, to the various pressure(s) of the environment. Such differential responses of organisms is exemplified by mammals: within 150 million years since their appearance on Earth, they have developed different mechanisms to deal with
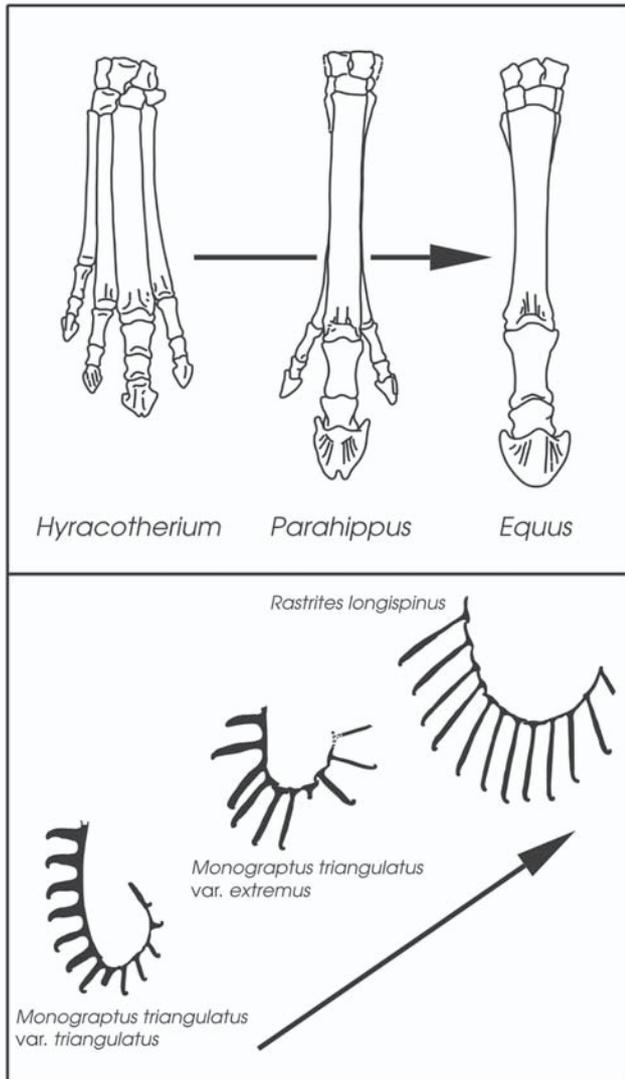
Figure 3. Gradations in form in fossils as a basis for determining lineages. A. Gradation in horse feet (after McFadden 1988 and McFadden & Hubbert 1988). B. Gradations in form of monograptids (after Sudbury 1958). In both examples, the lineages are diachronous.

exothermia generated by the metabolism of their fuel (food) – radiator ears for elephants, epidermal evaporative cooling for humans, evaporative exchange in a labyrinth of nasal passages in camels, and evaporative exchange in the tongue of dogs, amongst others (Willmer *et al*. 2000; Cain III *et al*. 2006; Narasimhan 2008). The importance of the principle of mutation is that organisms within their environment and within the assemblages within that environment are (differentially) mutating, and through time this can be expressed as species changes. Palaeontologists focused on one fossil group will detect such changes within their speciality group, and another will detect changes in another group. The critical factor is that mutations generally will be occurring in all species, though these mutations may not necessarily be expressed as evolutionary changes unless the mutation is beneficial and then it is expressed as a new species. A thorough examination of all biota in well-preserved stratigraphic sequences will find many

organisms changing and that evolution is proceeding on many fronts in many different species. Many of these changes can be attributed to developmental repatterning (heterochrony) (McNamara 1995, 1997, this volume).

In a given environment and within a given biological assemblage, an individual of a species in a population may be subject to predation, the effects of microbiology, intra-species competition, or inter-species competition, changes in environmental conditions, or changes in food sources. The species may also be incrementally expanding into adjoining habitats, expanding its range to exploit new food sources, or more effectively using its existing food resources within its existing habitats (Figure 4). The terms "drivers" and "determinants" actually encompass a range of phenomena, of mixed meaning, *viz*., they may be processes external to the organism (*e.g.*, a predator, or a change in environmental conditions such as the regional cooling of the climate), or may be how an organism (internal to a population) responds to a stable environment, or responds to a locally modifying environment. Combined with various mutations of individuals within a population, these "drivers" and "determinants" can result in anatomical, skeletal, and physiological changes, *i.e.*, the evolution of the species, or the development of new species. Examples of the effects of predation are the co-evolution of cheetah and antelope, where speed and hunting proficiency of the cheetah is being matched by speed and avoidance by the antelopes, or the co-evolution of the string-ray and soldier crab, where soldier crabs develop burrowing behaviour in response to sediment excavation by string-rays (Unno & Semeniuk 2008). In the fossil record McNamara (1994) has shown the importance of predation pressure in the co-evolution of cassid gastropods and spatangoid echinoids. Examples of the effects of microbiology are the resistance to disease in fauna, or the evolving association of soil microflora and nutrient uptake by vascular plant roots.

Intra-species competition, especially sexual competition, can result in development of anatomical features such as bright plumage or coloured crustacean claws. Inter-species competition for habitat space or food sources can result in anatomical modifications in a species to make it more proficient in surviving in its habitat. Changes in environmental conditions, such as in climate, substrates, hydrology or hydrochemistry can underpin species adaptation and anatomical and physiological changes. The evolution of the woolly mammoth is an example of this. Similarly, changes in food sources can drive anatomical changes – the evolution of horse teeth as their food sources changed from forest-dominated conditions to grass-plain conditions and they changed from being browsers to grazers. Species may also be incrementally expanding into adjoining habitats: for example, terrestrial plants belonging to the Verbanacea and the Myrtacea encroached progressively from terrestrial habitats to marginal shore habitats to high tidal habitats (to become *Avicennia marina* and *Osbornia octodonta*), with changes in anatomy, physiology and reproduction strategies; other species, notably the finches of the Galapagos Islands expanded their range and speciated to exploit new food sources. Finally, organisms can develop anatomical changes to more effectively utilise their existing food
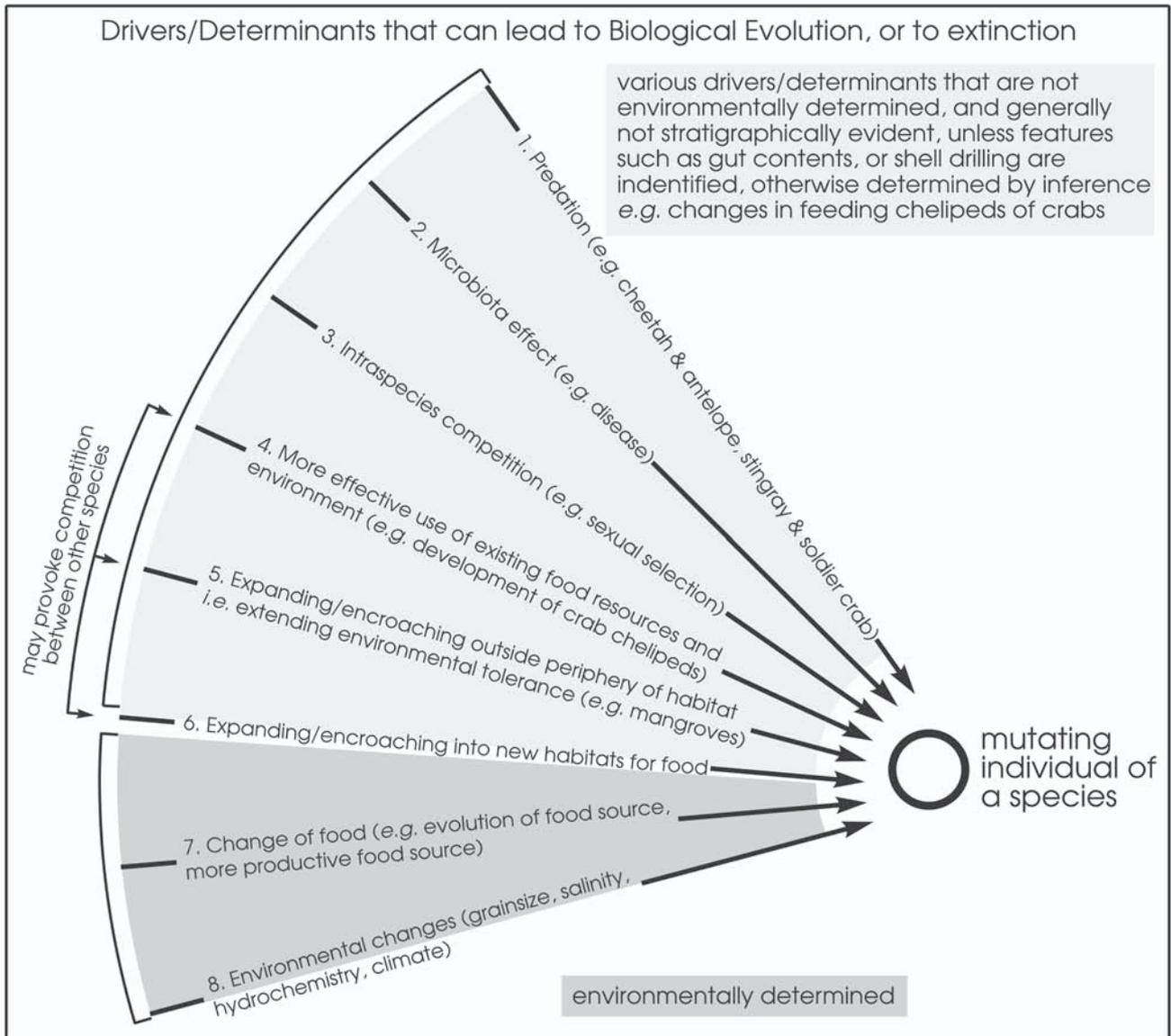
Figure 4. Drivers and determinants that can lead to biological evolution, or to extinction.

resources within their existing habitats. The development of specialised feeding claws and cheliped hairs of the fiddler crab for scraping slime and diatomaceous films off tidal flats, and the cutting claw of crabs that feed on algal-turf on rocky shores are examples. Thus, the "drivers" and "determinants" acting on a species within a habitat can result in extension of the distribution of the organism forming a new species at the periphery of a habitat (peripatric speciation), or through local pressures such as predators, or through more efficient use of food sources (amongst many other examples) can result in development of new species within the habitat (sympatric speciation), as summarised in Figure 5.

A derivative of this concept of "drivers" and "determinants" acting on a species is that not all "drivers" and "determinants" are necessarily environmentally determined, or driven (*e.g.*, intraspecies competition, or more effective use of food resources), and may not be evident stratigraphically. Figure 4 shows that

of the many that act on the organism, the effects generally do not have sedimentological, microchemical, or isotopic signatures. The effects actually will be manifest in the evolution of the species responding to these "drivers" and "determinants". Exceptions are where the stomach contents of predators or browsers or grazers are fossilised, and then there is a direct predator-prey or direct feeder-food relationship and direct evidence of gastropod predation, such as gastropod boreholes in other molluscs or echinoids. Drivers involving changes of food sources and changes in climate, grainsize, and hydrochemistry, are environmentally determined, and may be detected stratigraphically (see McNamara 1990).

Given that the eight "drivers" and "determinants" underpin evolutionary changes within an assemblage of organisms in a given habitat, as described above, there can be differential response of organisms within an assemblage to the "drivers" and "determinants", and
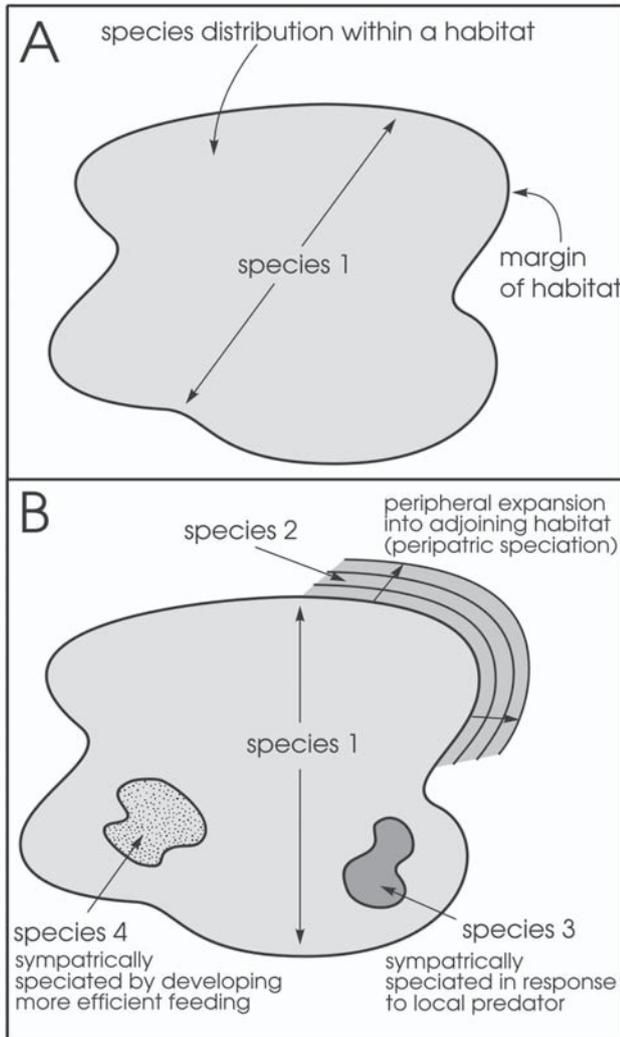
Figure 5. Peripatric and sympatric speciation leading to development of three species within and along the margin of a habitat.

further, different species within an assemblage will be acted upon or influenced by different "drivers" and "determinants". Thus, the ecological pressures and environmental changes can have varying effects on the different species within an assemblage, and the changes induced may proceed at different rates (see later, after description of stratigraphic types).

The species composition of biotic assemblages can markedly vary with habitat, and in fact this is the basis of habitat-focused ecology. There is a wealth of literature recording these patterns. It is well known, for instance, within a given biogeographic region and climate region, for marine environments, for example, that there are distinct benthic biotic assemblages in sandy environments, as compared to muddy sand, or mud environments (Figure 6). Such assemblages are related to substrate types, salinity, and water depth (see Dampier Archipelago; Gulf of California, Gulf of Mexico, Leschenault Inlet estuary; Shark Bay; the Wadden Sea; the Woods Hole region; Semeniuk *et al.* 1982; Jones 2004; Parker 1960, 1964; Dürr & Semeniuk 2000; T A Semeniuk 2000; Semeniuk & Wurm 2000; Logan *et al.* 1970, 1974;

Wolff 1983; Parker 1975). Similar patterns of assemblage-to-habitat relationships exist on tidal flats (sand, muddy or sand-to-mud graded tidal flats), often with biota exhibiting zonation in relationship to environmental gradients (*cf.* mangrove zonation, and benthic fauna zonation; Bezerra *et al.* 2006, Chakraborty & Choudhury 1985, Crane 1975, Degraer *et al.* 2003, Dittmann 2000, Jaramillo & Lunecke 1988, Jaramillo *et al.* 1993, McLachlan 1996, McLachlan *et al.* 1993, Ono 1962, Otani *et al.* 2008, Sassa & Watabe 2008), and in estuaries and coastal environments such as the Wadden Sea (Wolff 1983), the Leschenault Inlet Estuary (Semeniuk & Withers 2000) and the tidal flats of the Canning Coast (Semeniuk 2008; and Figure 6, which shows the variety of molluscan fauna on tidal flats, with the "drivers" and "determinants" superimposed). Similarly, the ecological functioning and processes within a given biogeographic region and climate region can vary markedly according to habitat. The same principles apply to terrestrial environments, such as forested mountains, grassy savannah plains, riverine plains, heathland terrains, wetlands, amongst many others.

Various organisms have varying tolerance to environmental change laterally, and this has major implications in evolutionary development. For instance, within a suite of adjoining habitats varying from sand to muddy sand to mud, and varying from saline to hypersaline, or varying from marine, to estuarine, to tidal flat, some species cross habitat boundaries, while others are environmentally restricted (Figure 7). Local works in Western Australia on the fauna of estuaries (Semeniuk & Withers 2000), mangroves (Semeniuk 1983; Semeniuk & Wurm 1987) and soldier crabs (Unno & Semeniuk 2009) and elsewhere globally on tidal flats (as listed above on the zonation of benthic fauna) exemplify this. Some of these tolerances may have derived from a given species expanding its habitat tolerances, and encroaching into adjoining habitats. The implications are that species with broad environmental and habitat tolerances may be able to cope with habitat changes or other environmental changes, while environmentally restricted species may not, and may be replaced by fitter mutational variants, or become extinct.

Within a stratigraphic sequence of accreted sediment, whether the sequence is homogeneous, multilayered, or complexly heterogeneous, biota can contribute to such sequences as benthos, nekton, and plankton, and exogenic biological material. Not all components may be preserved in sub-recent or pre-Holocene sequences, due to various taphonomic processes, bioturbation, diagenesis, or even low grade metamorphism, but modern environments do show accumulation of benthic biota, nekton and nekton products (such as fragmented shell in excreta), and plankton. The latter may contribute directly as skeletons and skeletal particles (*e.g.*, diatoms, zooplankton exoskeletons, and foraminifera), or as decomposed organic material. Exogenic material may comprise skeletons of terrestrial biota deposited into marine or coastal environments, or tree logs deposited into marine or coastal environments. The result is that in accreting sediments, axiomatically, fossils may accumulate, and the palaeontological assemblages may be wholly benthic, mixed benthic and planktonic/nektonic, or wholly planktonic/nektonic.
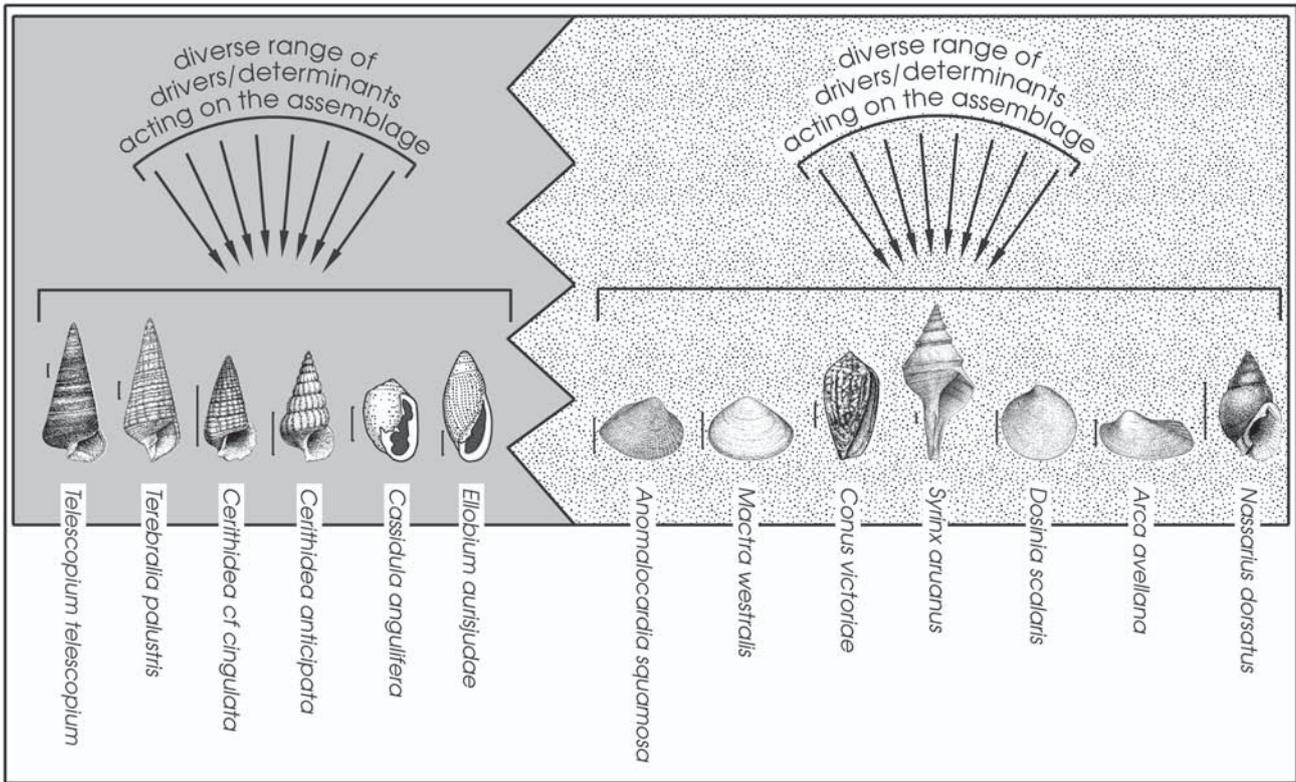
Figure 6. Simplified mollusc assemblages on tidal flats along the Canning Coast, Western Australia (after Semeniuk 2008), showing key species within contrasting but adjoining sediment types, *viz.*, sand *versus* mud, and the complexity of species composition within habitats. Not shown are echinoderms, polychaetes, crustacea, benthic vertebrates, and other fauna within the assemblages. The drivers and determinants above the assemblages illustrate that these factors and processes are operating on all components of the assemblage. Bar scale alongside the molluscs is 1 cm.
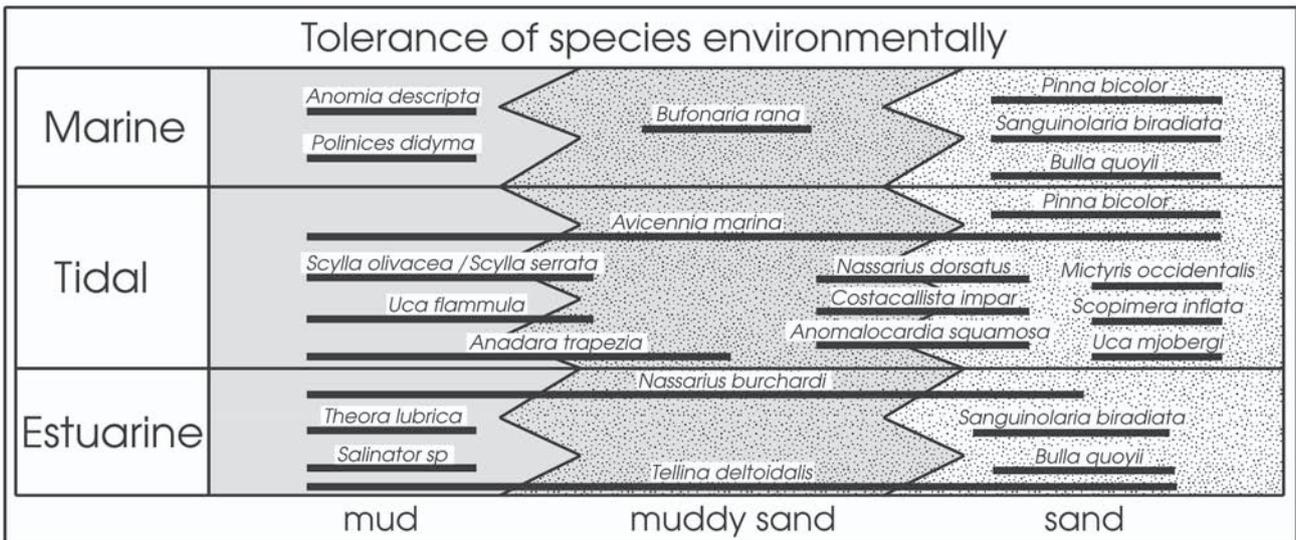

Figure 7. Simplified diagram to illustrate the environmental tolerances of selected species of fauna in subtidal marine, tidal, and estuarine environments in terms of sand, muddy sand, and mud substrates (or habitats). Some species are habitat-restricted, because of grain size influences, food sources, and salinity (see *Mictyris occidentalis* as described by Unno & Semeniuk 2009), while others inhabit a range of substrate (habitat) types (*e.g., Avicennia marina, Tellina deltoidalis*, and *Nassarius burchardi* as described by Semeniuk & Wurm 1987, 2000). Some species cross environmental boundaries, occurring in estuarine and marine settings. This diagram does not address depth occurrence, or (wave and tidal) energy effects on species occurrence. Information on molluscan fauna adapted from Abbott & Dance 2000; Beesley *et al.* 1998; Semeniuk & Wurm 2000; Wells 1984; Wells & Bryce 2000; Wilson 1993, 1993b; Wilson & Gillett 1974).

In terms of benthic (or benthonic), planktonic and nektonic fossils, most palaeontologists focus on the macrofauna, *i.e.*, the benthos, which are the most conspicuous and readily available. However, planktonic or nektonic fossils raining down directly onto the sediment floor also can be important components of the assemblages as they provide primary information in their own right in terms of evolutionary changes, and hold potential to provide supplementary information about the water column and other environmental factors that may not be evident macroscopically in the sediments and in the stratigraphy. Where present, they should be explored hand-in-hand with the macrofauna to assess the environmental stability or consistency of the stratigraphic sequence wherein evolutionary changes in fossils are being investigated. Assemblage changes or species changes in planktonic and nektonic fossils through time, even though the sedimentary pile within which they are accumulating may not show sedimentary evolution or basin evolution, implicate some form of changes in the environment that is not being expressed sedimentologically, *e.g.,* changes in climate, hydrochemistry, or food source changes, or predation pressure that are occurring in the water column. Planktonic or nektonic fossils also can transported to shore or nearshore environments, *e.g.,* the modern cephalopods cuttle-fish *Sepia* and the ramshorn shell *Spirula spirula*, transported from oceanic environments to sandy shores and incorporated into beaches in Holocene and Pleistocene sequences (Semeniuk 1997, 2008). While the shore environments may be sedimentologically and ecologically relatively stable, repetitive and homogenous, the transported fossils may be signalling changes in the water column in the adjoining oceanic regime.

As a consequence of taphonomy (*e.g.*, shell breakage, bioturbation, shell dissolution) and differential synsedimentary diagenesis, there can be generally a relatively poor record of preservation of living modern skeletal assemblages in the sub-recent sedimentary deposits, and by extrapolation, in the fossil record. For instance, the abundance and diversity of the living skeletal faunal assemblages in Shark Bay (Logan *et al.* 1970), Rockingham seagrass bank (Searle *et al.* 1988; Semeniuk 1997), the Dampier Archipelago (Semeniuk *et al*. 1982), Leschenault Inlet Estuary (Semeniuk *et al.* 2000), and the coastal zone of the Canning Basin (Semeniuk 2008), are not as well represented as whole and recognisable skeletal remains in the sub-recent sedimentary deposits. Close examination of the sedimentary deposits neontologically, however, generally shows faunal remains progressively reduced to sand-sized or smaller fragments, or in various stages of pitting on their way to skeletal degradation by dissolution, marine weathering, or algal boring. Skeletal remains in terrestrial environments are even more poorly preserved. This principle applies to the fossil record, and in general, it can be concluded that the fossil record generally is a relatively poor representation of what once existed from the point of view of locating whole and partly fragmented fossils. To circumvent this problem, Semeniuk (1973) in a study of Ordovician fossil assemblages, constructed the palaeo-ecological compositions of the assemblages using whole fossils, fragmented fossils, and sand-sized fragments of fossils where they were petrographically recognisable, and the

same principle applies to sub-recent and Pleistocene skeletal remains in the Quaternary sequences. However, the modern sedimentary-and-skeletal-fragment examples illustrate that while there is degradation of the fossil record, the ancient stratigraphic sequences actually illustrate that enough is preserved to be able to be used palaeontologically and palaeoecologically (*cf.*, the comparisons of Pleistocene and Holocene molluscan fauna in seagrass bank environments described in Semeniuk (1997), and the comparisons of Pleistocene and Holocene foraminiferal assemblages from marginal seagrass bank environments described in T A Semeniuk 2005).

There are a number of ecological and population processes operating in modern environments that underpin biological evolutionary changes. We term these evolution "drivers" and "determinants".

Sedimentology is the study of structures, composition, and grainsizes of sediments, and similar sediments, or suites of inter-related sediments, recurring in a given location are referred to as facies. There can be gravel facies, sand facies, mud facies, or carbonate sand facies *versus* quartz sand facies, and so on. Habitats that benthic biota occupy, for example, in marine and coastal environments, are the result of sediment types (or facies) functioning in combination with hydrological and hydrochemical characteristics. The organism responds to living and feeding on a favourable habitat comprised of a given substrate, and hydrological and hydrochemical setting. The same principle applies to soils – they also form facies, and can be the basis of habitats for soil fauna, soil microbiota, vegetation, and macrofauna.

Sediments and facies can vary laterally and accrete vertically to develop stratigraphic sequences. This is Walther's Rule (Walther 1893–1894; Krumbein & Sloss 1963), where generally sediments in lateral relationships tend eventually to overlie each other. This is best exemplified by shoaling sequences where the sediments are arranged in parallel facies and perpendicular to environmental gradients such as water depth, hydrochemistry, or (wave, tidal, or wind) energy, and as sediments accrete and shoal to shallower water depths, or accrete to become emergent above a waterline, they sedimentologically adjust in response to the progressively changing environmental conditions (Brocx & Semeniuk 2009). The grainsize variation and structure-and-grainsize variation normal to tidal flat shores and sandy beach shores, for instance, form parallel facies that with progradation and shoaling form vertically distinct sedimentary (stratigraphic) sequences that vertically mirror the horizontal facies relationships (Semeniuk 1997, 2008). In this context, habitats, related to facies, and related to sediment distribution are preserved as vertically accreting stratigraphic packages. The palaeontologist and evolutionary palaeontologist just need to read this sequence in terms of a sequence of facies, or a sequence of palaeo-habitats.

However, sediments and facies do not necessarily remain constant and environmental perturbations, such as in climate and tectonism, can result in changes in lithology macrostratigraphically, microstratigraphically, geochemically, or isotopically. Climate changes, for instance, can affect $^{16}O/^{18}O$ ratios in water and in skeletons of biota (and reflected therefore in isotopic

changes in the stratigraphic column). Tectonism can drive and alter sedimentologic effects, bringing in changes of sedimentary style and lithology.

The final matter to discuss is that geological crustal processes can markedly alter the stratigraphic sequences. Uplift, mountain-building, folding, erosion, planation, and so on, can remove sections of the stratigraphic sequences, and result in incompleteness of the stratigraphic record. This has major consequences locally for the fossil record (Figure 1).

A synthesis of these matters described above, as they relate to biological evolution and evolution manifest in the palaeontological record is provided below.

An organism in the modern environment, in its biogeographic range as determined by habitat setting and climate, is complexly interacting with the abiotic factors and with other organisms in its search for living space, harvesting/hunting of food, in evading predators, and reproducing. Also, the sedimentary environment (or habitat) is changing, or shoaling, or in some way being modified lithologically, macrostratigraphically, microstratigraphically, geochemically, or isotopically. Essentially and generally, nothing is static, and the evolutionary biologist and evolutionary palaeontologist must incorporate these factors into their thinking, reconstructions, and interpretations. For instance, from modern considerations of ecological processes, composition of assemblages, changes in assemblages in the short term and the long term, differential response of organisms to environmental and ecological changes and pressures, the complexity of stratigraphy, and the other matters described above, it is clear that interpreting the fossil record in an evolutionary perspective can be a very complicated matter, particularly because it is fragmentary. However, it can be carried out if there is an understanding of ecological processes, of modern dynamics in biological assemblages, and of the types of stratigraphic frameworks that fossils are embedded in and how to use them. We emphasise, again, that the present is the key to the past, and a thorough understanding of modern processes leading to evolutionary change, preservation of fossils, and development of stratigraphy is the key to interpreting the fossil record.

Types of stratigraphic sequences

Fossils reside in sedimentary accumulations that form stratigraphic sequences, and to understand fossil occurrences and evolutionary changes, the various types of stratigraphic sequences and their significance to the palaeontological record need to be described. In a sedimentary basin, where evolutionary changes in fossils are to be described and interpreted, ideally, laterally there would be thousands of kilometres of stratigraphic sequence as rock exposure (*e.g.,* the Permo-Triassic stratigraphy of the Sydney Basin, exposed as the cliff shores along the eastern seaboard of New South Wales, Australia; Packham 1969), and thousands of metres of vertical stratigraphic section extending over time intervals of millions of years of sedimentary accumulation. Such stratigraphic sequences, if fossiliferous, would provide synoptic and diachronous information on fossil species

and fossil assemblages, wherein the various confounding factors generating palaeontological change could be explored and teased apart.

In detail, sedimentary sequences are complex and varied: they record deposition in fluvial, aeolian, lacustrine, glacial, shoreline, marine shelf, and deep-sea environments, amongst others (Reineck & Singh 1980). Depending on tectonism, and occurrence of subsiding basins, they develop as thin sequences, or thick sequences, and depending on whether the external environment (such as climate) and crustal environment are stable, they develop into homogeneous packages, or layered sequences, or heterogeneous and complex packages. In this paper, for purposes of setting the palaeontological record in a context and framework, the stratigraphic sequences relate to those that are relatively thick, *i.e.,* spanning intervals of > 10 m, and ideally spanning intervals > 100 m.

Leaving aside the effects of tectonism and other geological processes that can remove, fragment, or disrupt the ideal sedimentary sequences, and hence complicate stratigraphic sequences and disrupt their vertical and lateral continuity, we recognise various types of stratigraphic sequences hosting fossil deposits. They range from the relatively lithologically homogeneous, to the lithologically repetitive, to the simply layered, to the heterogeneous and complex. The sedimentary sequences we recognised for use in the principles proffered in this paper, ordered from the most simple and homogeneous to the most complex and heterogeneous, are (Figure 8):

Sequence Type 1: macrostratigraphically lithologically homogeneous, as well as microlithologically, microstratigraphically, micropalaeontologically, microchemically, and isotopically homogeneous;

Sequence Type 2: macrostratigraphically lithologically homogeneous, but not homogeneous microlithologically, microstratigraphically, micropalaeontologically, microchemically, and isotopically;

Sequence Type 3: composed of a two-layered or a three-layered sequence, with each layer macrostratigraphically lithologically homogeneous; within each layer, the sediments may or may not be microlithologically, microstratigraphically, micropalaeontologically, microchemically, and isotopically homogeneous, but this factor needs to be noted; the contact between the lithological layers can be sharp, or commonly are gradational;

Sequence Type 4: composed of a lithologically multi-layered sedimentary sequence, often representing the vertical accretion of laterally equivalent facies and hence representing a shoaling-upward package, or a deepening sedimentary sequence; each of the lithologically distinct layers are macrostratigraphically lithologically homogeneous; and generally (depending on the depositional regime) also microlithologically, microstratigraphically, micropalaeontologically, microchemically, and isotopically homogeneous; the contact between the lithological layers can be sharp, or commonly are gradational;

Sequence Type 5: composed of a lithologically coarse-scale repetitive sedimentary sequence, often representing the vertical accretion of alternating sedimentary events
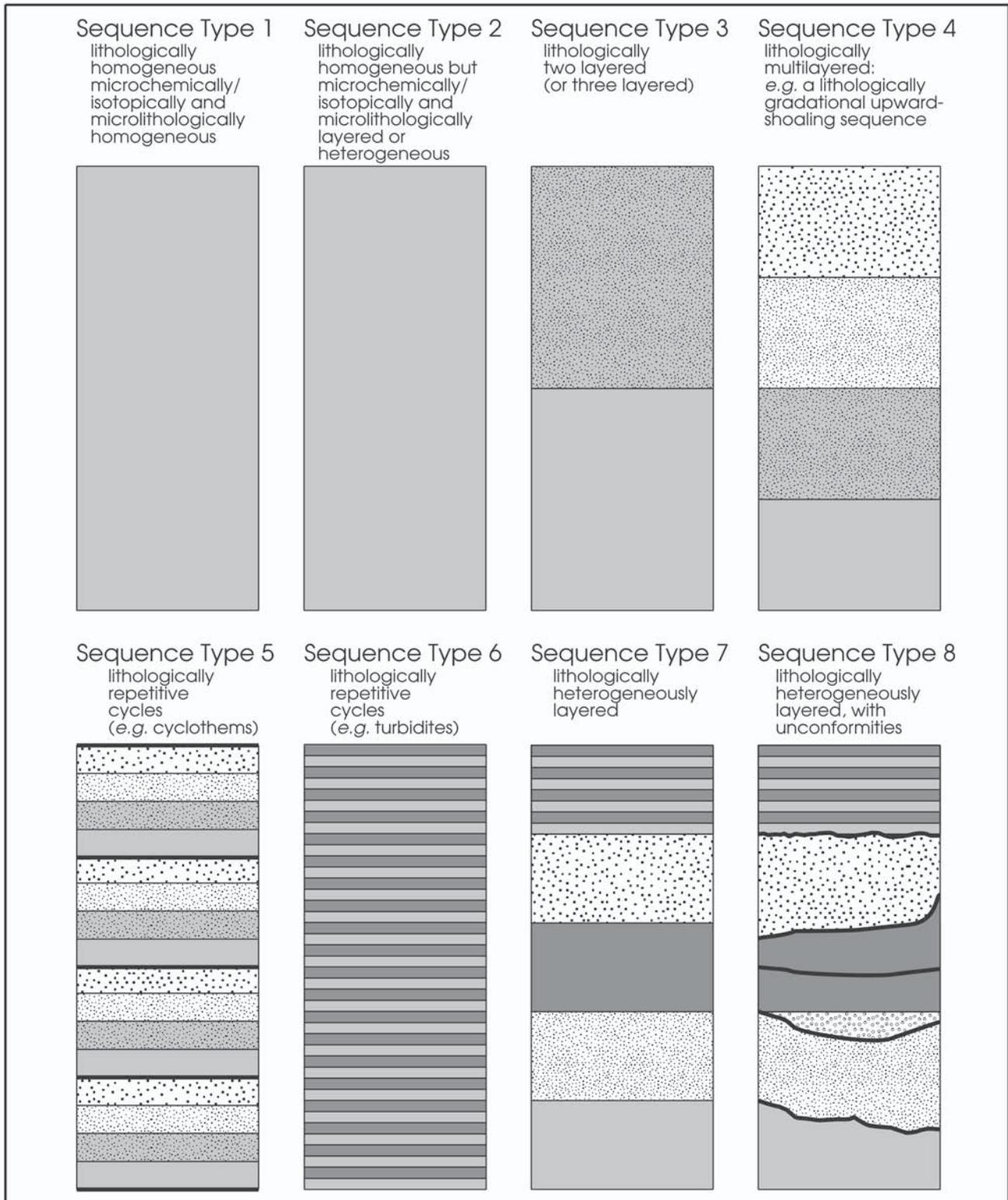
Figure 8. The eight types of stratigraphic sequences. These sequences are generalised and do not refer to specific types of lithology or to environmental setting.

(*e.g.,* relatively moderately thick upward-shoaling packages of marine sediment, with sedimentary units on a metre scale; see Reineck & Singh 1980; or sand to coal cyclic deposition); in the literature these types of sequences have been termed "cyclothems" (see Jackson 1997); each of the lithologically distinct layers may be macrostratigraphically homogeneous; and generally also microlithologically, microstratigraphically, micropalaeontologically, microchemically, and isotopically homogeneous; given the repetitive nature of the alternating lithological sequence and that the lower part of the whole sedimentary package represents the

oldest part of the sequence, and the upper part represents the youngest part; examining each of the individual lithologies in the shoaling package, in turn, diachronously along the sequence effectively provides a similar nature of stratigraphy as Sequences Type 1 and Type 2, though each lithology actually is alternating; where such sedimentary packages accumulate to considerable thickness, and span millions of years, they form a powerful template of sedimentary units within which to study palaeontological changes, because rather than observing fossil changes in one lithology diachronously, these types of cyclic packages provide the opportunity to concurrently study several sediment types (habitats) and their fossil content over the same time interval; further, in a system where the overlying lithologies are in cyclic sedimentary packages, they are part of the lateral facies (habitats) pattern and effectively provide a degree of synchronicity of fossil assemblages in the same stratigraphic column;

Sequence Type 6: composed of a lithologically fine-scale repetitive sedimentary sequence, often representing the vertical accretion of alternating sedimentary events (*e.g.*, accumulating flood-tide and ebb-tide tidal flat sedimentation on a centimetre scale; see Reineck & Singh 1980), or repetitive or episodic catastrophic events, *e.g.*, accumulating submarine turbidites (Krumbein & Sloss 1963; Reineck & Singh 1980; Boggs 1987) triggered perhaps by earthquakes, that record a basal traction flow of sand or coarse silt, grading and fining-upwards to suspension deposited fine silt or clay; these also are called "rhythmites" (see Jackson 1997), referring to their rhythmic layering of lithology; the sequence of sand overlain by muddier layers is also commonly termed a "couplet". Each of the lithologically distinct layers in these turbidites or rhythmites may be lithologically homogeneous; and generally also microlithologically, microstratigraphically, micropalaeontologically, microchemically, and isotopically homogeneous; given the repetitive nature of the alternating lithological sequence, composed say, of sand and silt for tidal flats, or composed of sand and grading to fine silt or clay for turbidites, the lower part of the whole sedimentary package represents the oldest part of the sequence, and the upper part represents the youngest part of the sequence – examining the sequence as an alternating bipartite or tripartite system, these sedimentary sequences are equivalent to the Sequences Type 1 and Type 2, in that focussing on one of the lithologies through the time interval of the stratigraphic sequence provides diachronous fossil information across a relatively homogeneous lithology (albeit consistently sandwiched between the second lithology); in addition, for turbidites, because of the mode of their deposition, the lower part of each fining-upward package may provide benthos-dominated fossil assemblages, and the upper part, plankton-and-nekton-dominated fossil assemblages;

Sequence Type 7: lithologically heterogeneously layered sediments, often representing the vertical accretion of various sedimentary environments; for example, a delta comprised of a heterogeneous package of channel sediments, levee deposits, floodplain sediments, strand plain sediments (beach ridges, lagoonal mud and peat), delta-front, and prodelta mud in itself forms a lithologically complex sedimentary package (Reineck &

Singh 1980), but if the river channel and the deltaic accumulation are laterally migrating with channel switching, then the stratigraphy of sand, shelly sand, gravel, shelly mud and peat can become more complex, and if the delta migrates into a sequence of marine seagrass-style sedimentation that has its own sequence of lithologies (Hagan & Logan 1974), *e.g.*, the contact of the Gascoyne Delta with the Wooramel Seagrass Bank (Davies 1970; Johnson 1982) then the complexity is further increased; without vertical continuity and with vertical disjunctions, these types of sedimentary sequences, though they may be fossiliferous, do not provide a robust stratigraphic framework for detailed diachronous palaeontological studies; at the least with this type of Sequence, if the packages occur within the same time interval (and this is most probable if within the Quaternary), there is some measure of synchronicity of sedimentary environments, even if they represent markedly different facies (habitats);

Sequence Type 8: this sequence is similar to Sequence Type 7, *i.e.*, lithologically heterogeneously layered sediments, often representing the vertical accretion of various sedimentary environments, but with the complication that are numerous hiatuses, disconformities, and erosional intervals disrupting the sedimentary sequences, and removing stratigraphic sections. With the abundance of hiatuses, disconformities, and erosional intervals, Sequence Type 8 is the least reliable for detailed diachronous palaeontological studies for evolutionary purposes; however, if properly dated, the fossils therein can be used for synoptic palaeontological studies.

There has been no implication in the Sequence Types described above that they derive from marine or terrestrial environments, however, because of the heterogeneous nature of processes in terrestrial environments, the best examples of these sequences will be found in marine and coastal environments.

In regards to palaeontological content in stratigraphic sequences, researchers need to be aware of separating fossils that are autochthonous from those that are allochthonous, with the caveat that biota derived from the overlying water column and raining down on to the substrate can be considered to be palaeontologically autochthonous. Often sediments may contain autochthonous and allochthonous components. The shoaling beach sequence illustrates this: with translating wave energy, onshore winds, and general transport shorewards, the sedimentary layers of the beach system may contain autochthonous components such as *Donax* and *Paphies*, and *in situ* sand worm burrows, as well as allochthonous components such as nearshore and shallow subtidal benthos, and at the storm water levels skeletons of *Sepia* and *Spirula spirula* (the latter derived from oceanic waters). Tidal flats, in contrast, are generally of low energy, and contain a higher proportion of autochthonous components.

Difference levels of importance can be ascribed to the Sequence Types in terms of their usefulness to studies in evolution in palaeontology, and Sequence Types 1, 2, 3, 4, 5 and 6, are discussed further below.

Lithologically consistent stratigraphy, such as Sequence Type 1, provides a robust framework for determining evolutionary changes because confounding

factors such as migration of species from adjoining environments due to changes in climate or hydrochemistry or food types, *etc.*, can be eliminated and the changes in the species (*i.e.*, their evolution) can be gauged against an environmentally consistent framework. In this context, the drivers and determinants for evolution may be predators, microbiotic effects, intra-species competition, inter-species competition, and more effective use of food resources. Sequence Type 2 provides a less robust framework to determining evolutionary changes. Microlithological, micropalaeontological, microchemical, and isotopic changes would signal that while macrostratigraphically the habitat appears consistent, there may be changes in climate, or hydrochemistry, or some other environmental parameter, and that the palaeontological changes are due to migration of biota from adjoining environments, or contributions from plankton from warmer (or cooler) water, or chemically different water. The carbonate mud cores from ocean basins extracted over the Quaternary interval exemplify this (Warme *et al.* 1981; Duncan *et al.* 1992): while macrostratigraphically relatively homogeneous, they show changes in foraminiferal assemblages and $^{16}O/^{18}O$ ratios indicating major climate changes (Emiliana 1955, 1966; Ericson *et al.* 1961) related to glacial and inter-glacial cycles (Imbrie & Imbrie 1979). Any fauna that remained in the environment (*i.e.*, tolerant of the temperate change) may have changed due to a variety of drivers and determinants acting on them, but the change in the composition of the planktonic skeletal rain was due to environmental effects.

Sequence Types 3 and 4 show an environmental change, and most commonly are due to the lateral migration of one facies (habitat) into and overlying the other. Any fossil changes across the layers can be due to evolution of a species adjusting to the encroaching new substrates, or simply the change in habitat-linked species migrating as passengers with the migrating habitat.

Sequence Type 5 and 6 manifest some of the best types of stratigraphy for palaeontological studies. Whether composed of a lithologically coarse-scale repetitive sedimentary sequence, or fine-scale repetitive sedimentary sequence, they provide a diachronous sequence of repetitive lithologies that effectively mimic Sequence Types 1 and 2, but with the advantage that the coarse-scale repetitive sedimentary sequences preserve, on a vertical repetitive basis, the sequence of lithologies that are laterally equivalent. Effectively, the sediments of Sequence Type 5 preserve a record of facies (habitats) consistently migrating and remigrating across the site. As such, the fossils contained in each of the facies are re-presented in temporal sequence, and it is possible to determine changes in species diachronously that occur within any given facies (and there may be several to choose from), determine the lateral relation of assemblages with respect to the facies, determine which species were crossing facies boundaries during time of deposition, and which species (in time) eventually crossed facies boundaries. The sediments of Sequence Type 6 preserve a finer-scale record of depositional events that repetitively embed the fossils of the time. If Sequence Type 6 is a turbidite succession, then the repetitive layers embed the benthos in the lower part of the turbidite package or couplet, and the plankton in the upper part of the turbidite package or couplet. By being

repetitive through time, this provides a consistent sequence of lithologies preserving alternating benthic and planktonic components.

Sequence Types 7 and 8 represent the least reliable stratigraphic systems for detailed diachronous palaeontological studies, but they can be still be useful. Even though generally comprised of short sections of stratigraphy, or environmentally un-related sections of stratigraphy, they can be used to infer depositional environments, and if well dated, they can be used to determine synoptic patterns. Fossils of horses and hominids occur in such sequences, and where well dated, they provided an environmental context for the horse fossils, and provide a temporal sequence and a synoptic sequence for the relationships of such fossils.

Types of stratigraphic sequences and their use in interpreting evolutionary lineages

The relationship of species and assemblages to sedimentary facies, and stratigraphic sequences are summarised in idealised diagrams in Figures 9–12. Figure 9A illustrates changes in species of the same genus (species A, B & C) across facies types that are sand, muddy sand, and mud, with no crossing of facies boundaries by any species. This is exemplified by species of *Uca* where, in a given region, they may occupy different substrate types and different tidal levels (Crane 1975). For instance, with the fiddler crabs in Western Australia (George & Jones 1982), *Uca mjobergi* inhabits sandy substrates, *Uca flammula* inhabits muddy sand substrates, and *Uca polita*
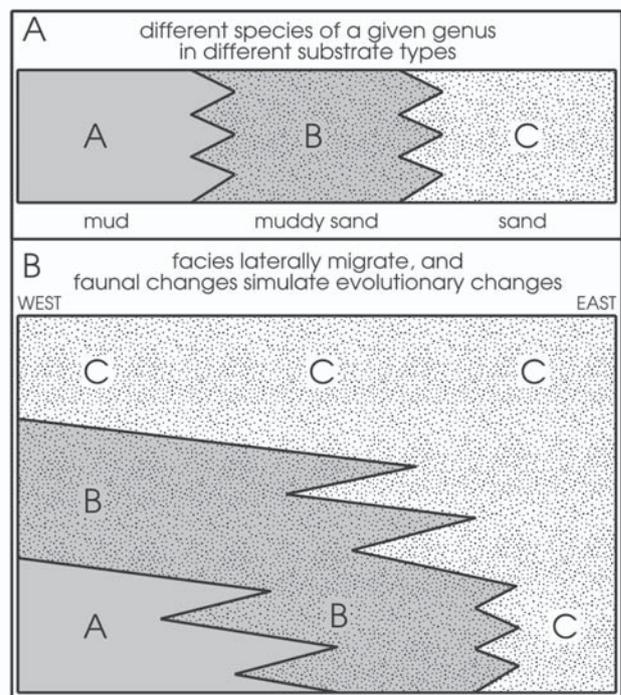

Figure 9. A. Conceptual diagram showing three different species (A, B, C) of a given genus occurring synoptically within three different sediment (substrate) types in a sedimentary basin. B. When the facies migrate or prograde, the sediments form a stratigraphic sequence, and the fossils form a biostratigraphic sequence along the west side of the sedimentary basin.

and *Uca dampieri* inhabit mud substrates. The species diagnostics for these three species are quite marked but illustrate the principle that speciation of a genus is related to substrate type. For other genera, the species diagnostics may not be so marked. With migration of facies to develop a stratigraphic sequence, and with the concomitant habitat-linked species as passengers within the migrating facies, the vertical sequence of fossils may simulate evolutionary changes (Figure 9B). However, diachronous evolutionary relationships have been demonstrated to have occurred in some fossil lineages. One such is the *Paraster-Schizaster* spatangoid echinoid lineage, with the *Paraster* morphotype adapted to coarse sediments, and the derived *Schizaster* morphotype to mud (McNamara 1990). As the stratigraphic record demonstrates, given that the changes occurred over tens of millions of years, they are more than just changes related to facies changes. The *Paraster* morphotype occurs in geologically much older strata than the *Schizaster*, thus the direction of evolutionary change can be determined. The classic evolutionary sequence in the spatangoid echinoid *Micraster* has been reinterpreted by Smith (1984) to show that the morphological changes in that lineage were also an adaptation to the inhabitation of finer sediments in the descendants.

In Figure 10, stratigraphic sections of Sequence Types 1, 2 and 4 are illustrated. In Sequence Type 1, the change
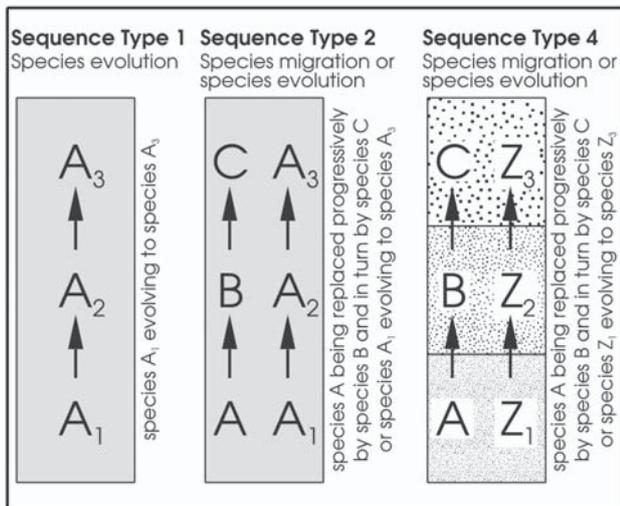

Figure 10. Idealised diagram showing stratigraphic Sequence Types 1, 2 and 4, with fossils. In Sequence Type 1, the change in fossil diachronously within a homogenous stratigraphy most likely will be due to evolutionary processes (change from A1 to A3). In Sequence Type 2, the change in fossil diachronously within a lithologically homogenous stratigraphy, but with microstratigraphic, or geochemical, or isotopic changes, may involve migration of species from adjoining climate zones or habitat zones (species A, B, C), but also can be due to evolutionary processes (change from A1 to A3) where the species has modified to deal with the changing environment. With Sequence Type 4, the change in fossils diachronously within a lithologically shoaling stratigraphy, may involve migration of species from adjoining habitats (species A, B, C), but also can be due to evolutionary processes (change from Z1 to Z3) where the species has modified to survive the changing environment.
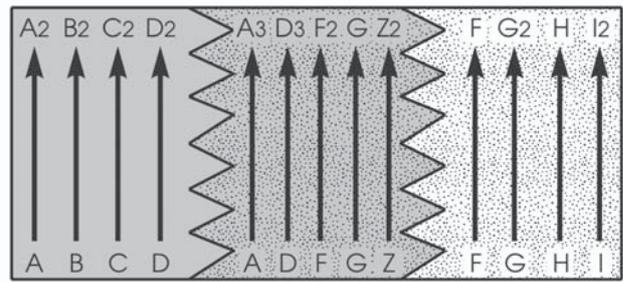

Figure 11. Idealised diagram to show the differential and complicated manner that biological evolution may proceed in assemblages. The diagram shows laterally equivalent sediments (substrates, or habitat) of sand, muddy sand, and mud with several species in each habitat. Some species such as A, D, F and G cross habitat boundaries. The species variably diachronously change into new species in response to the drivers and determinants shown in Figure 6. Some species only change in a given habitat, some do not change at all, and some change into different species when in a different habitat because of the variation in drivers and determinants. This diagram should be viewed in combination with Figures 6 and 9A.

in species (from A1 to A3) within a homogeneous stratigraphy, will most likely represent evolutionary changes. The driver or determinant for the changes may not be able to be deduced. In Sequence Type 2, the change in species within the stratigraphy may represent evolutionary changes (from species A1 to A3), or migration of species from adjoining similar habitats (species A to B to C). In Sequence Type 4, the change in species within the stratigraphy again may represent evolutionary changes (from species Z1 to Z3, as the species adjust to substrate changes), or may reflect migration of species from adjoining similar habitats (species A to B to C).

A more complicated biological response is illustrated in Figure 11. Here, the three facies of sand, muddy sand and mud are represented horizontally as facies equivalents of each other (compare this diagram with Figure 4, where fauna are superimposed). For Figure 11, to illustrate the principle involved, the idealised diagram, shows several species in each facies. Though most are habitat-related (or habitat-restricted), for this illustration, species A and D cross facies boundaries between mud and muddy sand, and species F and G cross facies boundaries between muddy sand and sand. These species may change (or evolve) within the facies through time. In the mud facies, species A, B, C and D all evolve becoming species A2, B2, C2 and D2. Contemporaneously, in the muddy sand facies, species A and D evolve to different species to that in the mud facies, *viz.*, A3 and D3, and species F and Z evolve to become species F2 and Z2, and species G does not change at all. Similarly, contemporaneously, in the sand facies, species G and I evolve to different species, *viz.*, G2 and I2, and species F and H do not change at all. This diagram illustrates the differential evolution of species within assemblages, and the fact that one species that crosses facies boundaries may evolve in time in one facies and not in another.

The various types of evolutionary changes underpinned by the various drivers and determinants within a stratigraphic context of Sequence Types 1, 2 or 3
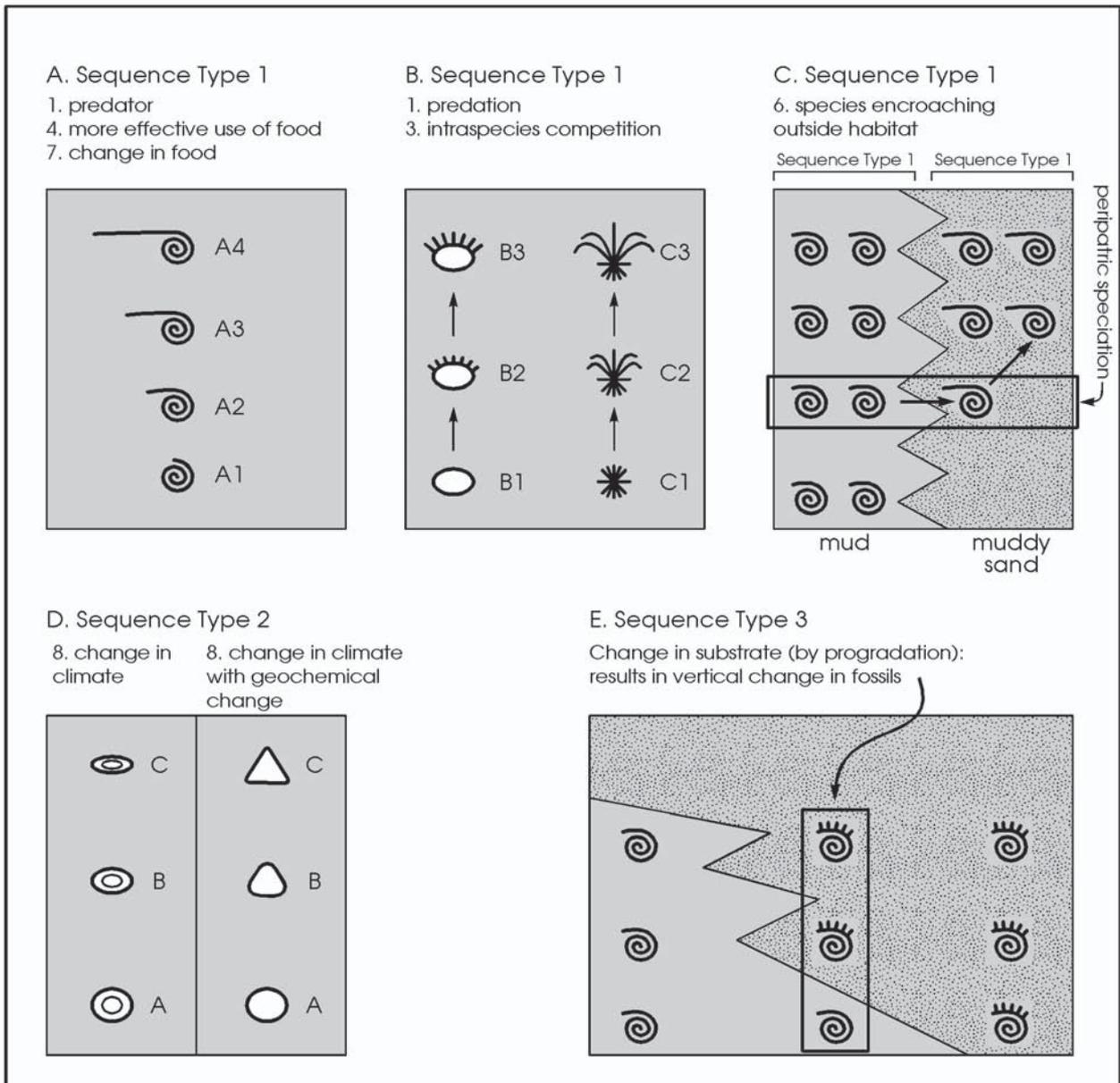
Figure 12. Some theoretical examples of species evolution within the context of the stratigraphic sequence types, and with the type of driver/determinant involved. A. Species evolution within a homogenous stratigraphy, driven by predators, or change in food type, or more effective use of food. B. Species evolution within a homogenous stratigraphy, driven by predation (and the development of spines in species B1, B2, B3), or intra-species competition (and the development of ornamentation in species C1, C2, C3). C. Species evolution (D1 to D2) within two sets of homogenous stratigraphy, with the original species (D1) encroaching to outside its habitat. D. Species change diachronously within a macrostratigraphically homogenous system, with migration of species from adjoining habitats or climate. E. Species change (D1 to D2) diachronously within a macrostratigraphically prograded system, with migration of species D2 from adjoining habitats.

are shown in Figure 12. Evolution of a species in Sequence Type 1 is diagrammatically shown as a species progressively changing from A1 to A4. The driver/determinant may be predators, changes in food, or more effective use of food resources (Figure 12A). Evolution of two species in Sequence Type 1 is diagrammatically shown in Figure 12B, with the species progressively changing from B1 to B3 and C1 to C3, with the driver/determinant in one species being a predator, resulting in the development of protective spines, and intra-species sexual competition in the other, resulting in anatomical ornamentation. The crossing of a facies boundary and peripatric speciation is shown in Figure 12C. Here,

species D1 remains unmodified in the mud facies, but at some stage encroaches into the muddy sand facies, becoming a different species (D2). Thereafter, species D1 and D2 remain unchanged.

The sequence of diagrams Figures 4, 6, 7, 8, 9, 10 and 12 illustrate the complexities of deciphering evolutionary patterns in a stratigraphic context, and the importance of having an understanding of the stratigraphic framework, the types of driver/determinant underpinning evolutionary changes, and the complexity of modern assemblages in terms of biological composition, and the tolerance levels of habitat change for given species.

Table 1

Selected notable fossils used in evolutionary studies and their stratigraphic framework

Fossil group	Stratigraphic Sequence Type	Principle applied
Graptolite *Monograptus* (Sudbury 1958)	Sequence Type 1	diachronous in homogeneous sequence as well as gradation (see Figure 13)
Ammonites (Cobban 1951)	Sequence Types 1 & 2	diachronous in homogeneous sequence
Echinoid *Micraster* (Nichols 1959; McNamara 1989)	Sequence Type 2	diachronous in lithologically homogeneous sequence
Trilobite *Arthricocephalus* (McNamara *et al.* 2003)	Sequence Type 2	diachronous in lithologically homogeneous sequence
Trilobites *Olenellus* and *Olenelloides* (McNamara 1978)	Sequence Type 2	synchronous in lithologically homogeneous sequence
Brachiopod *Tegulorhynchia* (McNamara 1983)	Sequence Type 4	diachronous in lithologically multi-layered sediment sequence
Echinoids *Paraster-Schizaster* (McNamara & Philip 1980)	Sequence Type 4	diachronous in lithologically multi-layered sediment sequence
Bivalve *Gryphaea* (Gould 1980; Rubilar 2005)	Sequence Type 7; Small-scale Sequence Type 1	gradation dominant in diachronous fragmented and scattered stratigraphy, but locally, diachronous in homogeneous sequence
Equids (McFadden 1988; McFadden & Hubbert 1988)	Sequence Types 7 & 8	gradation dominant and synoptic analyses, and diachronous lineages

There have been several classic studies of fossils in sequences that have been used as standards for inferring evolutionary patterns. Some of the notable examples are: fossil horses, the graptolite *Monograptus*, the echinoid *Micraster*, ammonites, trilobites, brachiopods and the oyster *Gryphaea*. Their stratigraphic context is briefly described in Table 1 in terms of the stratigraphic framework in which they are embedded and what principles of analysis were applied.

Stratigraphic sequences within and across sedimentary basins

The focus on stratigraphy in the text above has been on stratigraphic sequence types. Such sequences may be relatively well preserved within a sedimentary basin (such as the example of the sedimentary rocks in the Sydney Basin mentioned above), where there is lateral and vertical continuity, and provide the best settings for the investigations of palaeontology from an evolutionary perspective, bearing in mind that even in well exposed basins, there will be the eight Sequence Types described above. However, in the real geological world of faults, folding, uplift and erosion, stratigraphic sequences are often fragmentary. This is not to say that they cannot be used palaeontologically for evolutionary studies, and indeed, some of the best studied fossils have occurred in such stratigraphic fragments, but in these contexts, the palaeontologist needs to have well-dated sequences, and then rely on gradations, synoptic comparisons, and small scale diachronous sequences. Across sedimentary basins, ordered from the most robust to the most fragmentary, with the latter relying on synoptic information and gradation to reconstruct lineages and associations, we

recognise the seven levels of preservation (Figure 14). These are described with regard to their characteristics, and what techniques are best used to analyse them.

- cyclothems or rhythmites comprising the lithologic sequence, both representing some of the ideal types of stratigraphy to unravel evolutionary lineages;

- homogenous, monotonous lithologic sequence, one of the ideal sequences of stratigraphy to unravel evolutionary lineages;

- homogenous, monotonous lithologic sequence, but with isotopic and microchemical, and microstratigraphic variation – a near ideal sequence of stratigraphy to unravel evolutionary lineages;

- relatively well preserved basin stratigraphy showing gross and subtle facies superposition; fossils therein manifest real and apparent evolution (that is, stacking of already speciated organisms, or true evolutionary change within the stratigraphic sequence);

- relatively well preserved basin stratigraphy, but all in the same time plane (fossil synoptic plane); analysis would include basin facies variation and synoptic speciation (= synoptic plane);

- fragmented isolated stratigraphy but all largely in the same time plane of speciation (fossil synoptic plane) though scattered geographically (across the globe and across basins); and

- fragmented isolated stratigraphy – requires the gradation approach; the fragmentary record of equids is an example.
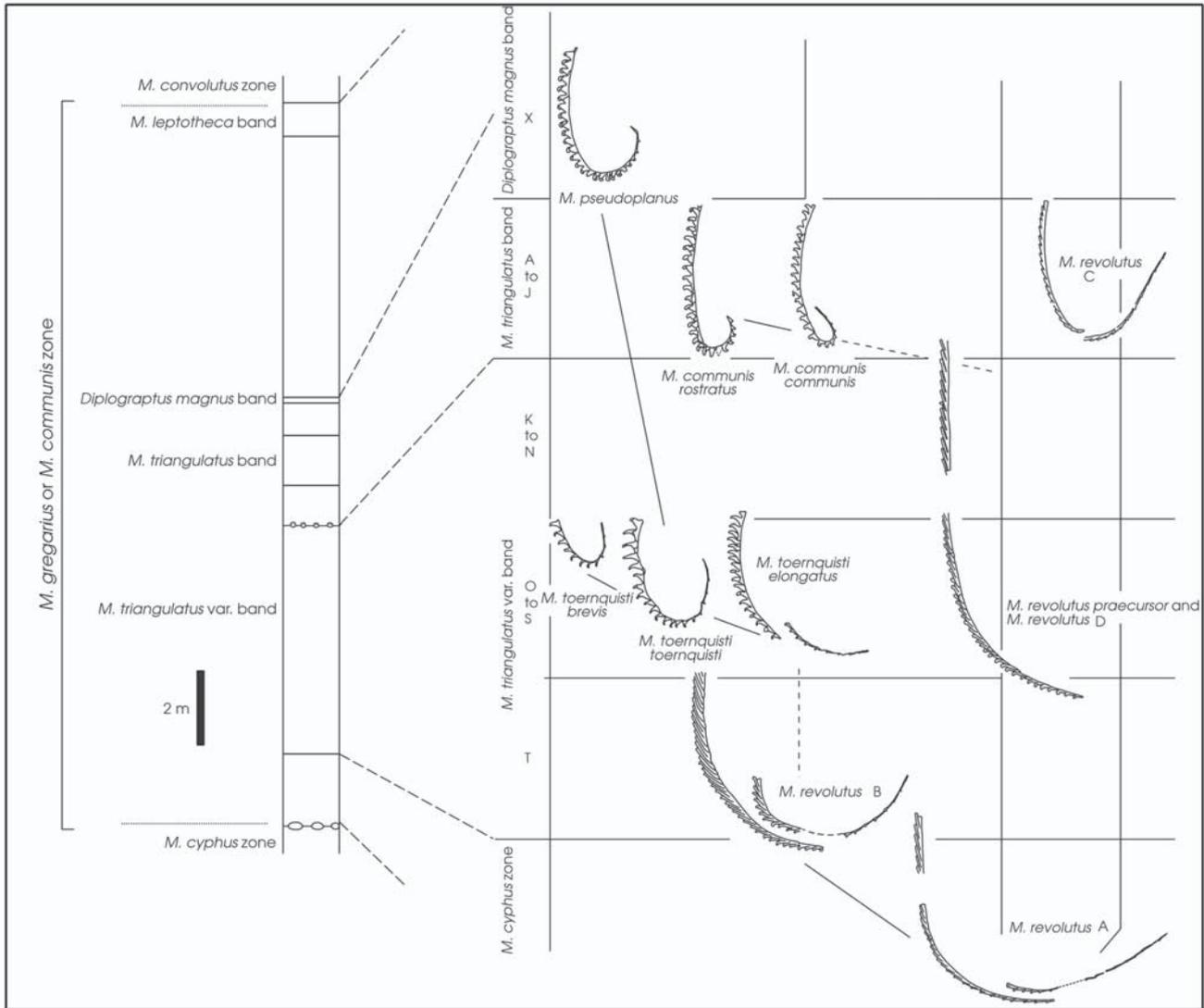
Figure 13. Sequence of *Monograptus triangulatus* from the shales of Rheidol Gorge, showing evolution of the monograptids (adapted after Sudbury 1958).

Discussion and conclusions

Darwin and Wallace focused on modern biota synoptically in interpreting natural species radiation across geographic regions, such as in south-east Asia, or the Galapagos Islands. It was a useful and valid approach and allowed them to interpret speciation in a context of geographic and environmental setting. Darwin, of course, supplemented this approach with taxonomic work on barnacles and beetles, selective breeding of pigeons, and with limited use of palaeontology. If the synoptic approach could be used positively in the modern environment to infer associations, relationships, and lineages, it can also be used palaeontologically to study biodiversity and inter-relationships in the fossil record. With well dated sequences, the identification of the speciation of organisms, say within the same genus, within the stratigraphic record, is utilising the synoptic approach of Darwin and Wallace. While it is palaeontological in scope, if Darwin's approach of synoptic analysis is valid,

then the palaeontological synoptic approach is equally as valid. All that is involved is another time plane, In effect, if Darwin existed a million years into the future, he would have been analysing and explaining the variation in ratites, for instance, in a fossil time plane, by dealing with fossil anatomy and fossil spatial variation and not living anatomy and living spatial variations. However, what is required if a synoptic approach is used in the palaeontological record is an understanding of the palaeoecological setting of the fossils. Interpreting species radiation in the stratigraphic record can be very useful if the fossil bearing horizons are well dated so that the researcher is sure that the variation is within time equivalent horizons, but becomes more powerful when the environmental setting and palaeoecological associations are known. This provides the researcher with insights into the factors underpinning palaeo-biogeographic variations, and separating various strands of environment-induced speciation, *e.g.*, is the species variability related to substrates changes, or faunal associations, or geographic (climatic) variation.
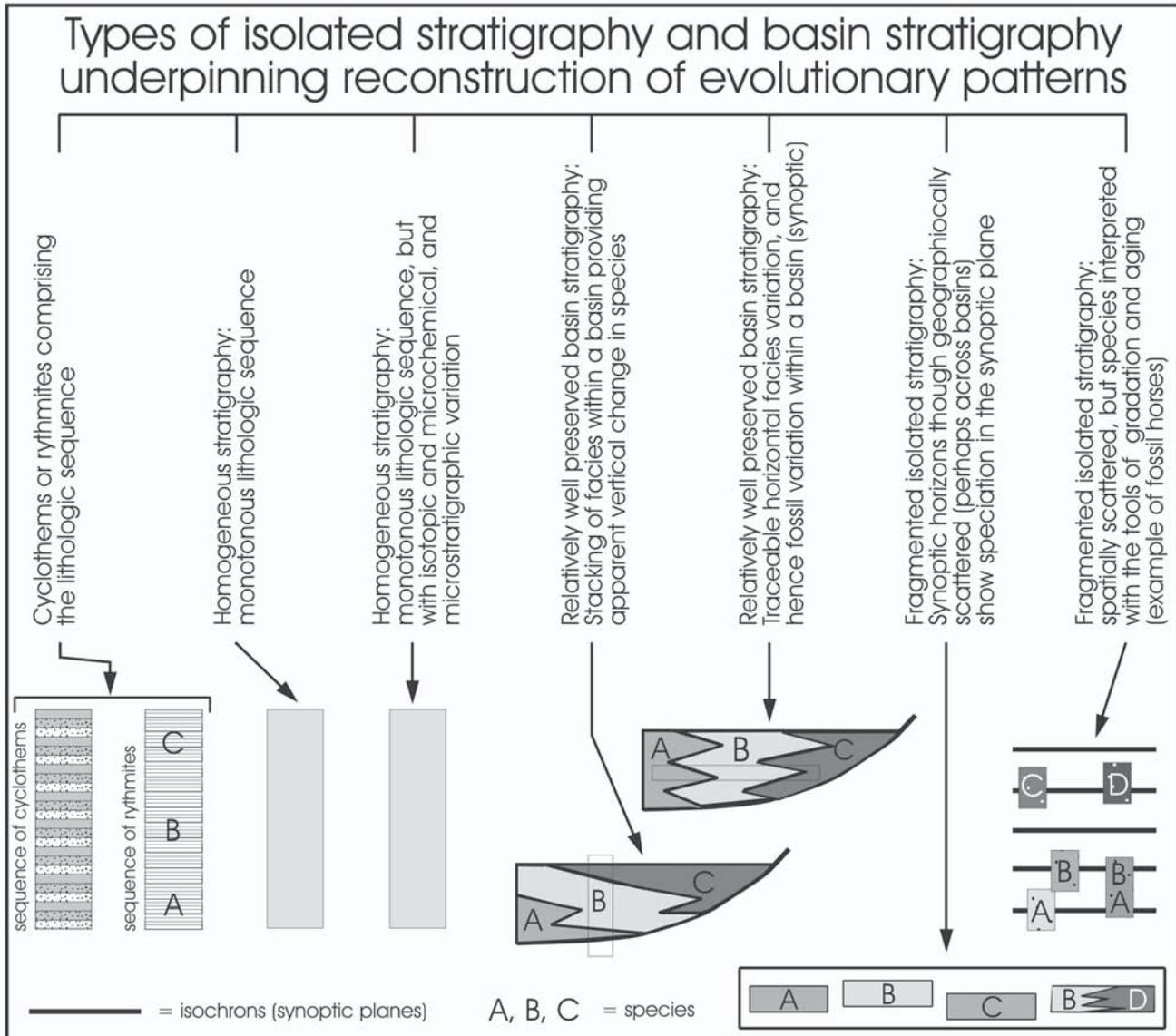
Figure 14. Types of stratigraphy in isolated sections or across sedimentary basins in various states of preservation.

While lineages and relationships can be inferred from anatomy and developmental biology (such as embryology, and even palaeo-embryology, as preserved in the skeletal fossil record), they can be fragmentary, as the palaeontological record often is – but this does not diminish the power of the use of such anatomical comparisons, and nor that of embryology.

Palaeontology provides one of the most power tools to explore biological evolution, as Darwin himself was aware. Fossils cross large time intervals and spatially large tracts of geological basins. Colloquially, they can be viewed as the alphabet of the story of biological evolution in the "pages of the book of the Earth". However, as modern ecology is complex, and the result of many interacting processes and products, then palaeontology, palaeoecology, and palaeo-evolution in the palaeontological record also are complex. The problems that ecologists face in unravelling ecological stories in the modern environment are magnified in the

palaeontological record because of the loss of the record through diagenesis, general taphonomic processes, and the impact of Earth processes (such as crust movements, and erosion) on the stratigraphic record. However, palaeontology as a tool to study biological evolution has one major advantage – it involves large intervals of time, at species, genus, and family levels. To date, however, the material in which fossil are embedded (*i.e.*, the stratigraphy) has not been rigorously enough explored to define the reliability of sequences so that they can be of use in interpreting, in a robust manner, the nature of the palaeontological record from a biological evolution perspective. We hope that in this paper we have pointed a way, in a preliminary manner, to refine and define stratigraphic frameworks so that the nature of the "pages of the book of the Earth" can be assessed, because where palaeontology is linked to a well established stratigraphy, its use becomes more powerful. The vertical changes in organism form/anatomy at species, generic, and family levels, reflecting temporal changes in

organism development, embedded in well dated stratigraphic sequences, provide the best means for interpreting evolutionary changes over time.

Care needs to be exercised in interpreting fossil records where there have been changes induced by lateral facies migration, or climate shifts, or other environmental changes, or missing parts of the stratigraphic record. Where stratigraphic sequences provide a consistent framework of lithology and microlithology (*i.e.*, a relatively homogeneous stratigraphy), or repetitive lithology, spanning large intervals of time, then stratigraphic sequences provide a robust framework for interpreting biological/palaeontological changes that may be manifest across that time interval without having to tenuously interpret or peer through and adjust for regional facies changes, climate changes, or hydrochemical changes.

Additionally, we hope this paper has highlighted that if ecologists need to be aware of sedimentology and abiotic factors that drive ecological functioning and the development of assemblages and the constraining of species to specific habitats, then the reverse needs to be addressed – that palaeontologists working in ancient sequences need to be more holistic, integrating sedimentology, stratigraphy, and evidence of climate changes, and working with assemblages wherein the different organisms are responding differentially to pressures in the environment. If complexity is a reality in modern ecology, then it is a reality in palaeoecology.

To date there has been a focus on individual species, or genera, as examples of evolution, and not a description of the entire assemblage within which the evolution of a given species or genus is embedded. The documentation of evolutionary change also has generally not been undertaken within a framework of stratigraphic sequences, *i.e.*, evolutionary palaeontologists generally have not specialised in palaeo-sedimentology or basin analysis, and conversely, palaeo-sedimentologists, stratigraphers, and basin analysts have generally not specialised in evolutionary palaeontology. In these latter contexts, palaeo-sedimentologists, stratigraphers, and basin analysts have tended to use palaeontology to reconstruct palaeo-environments, or for biostratigraphic correlation. We suggest that the approach to evolutionary palaeontology needs to be more holistic (*i.e.*, multidisciplinary and integrated) in the same way that modern autoecology and ecology tend to be holistic.

Palaeontologists and palaeoecologists need to explore the reasons why there would be faunal changes in the stratigraphic sequences and the answers lie in the modern settings, in the sedimentology, climate changes, facies changes, and ecological assemblages. These provide the information base and models to explain fossil assemblages. In other words, Hutton's adage, "*the present is the key to the past*", needs to be applied to evolutionary palaeontology and palaeoecology. The modern alphabet of autoecology, ecology, ecological functioning, sedimentology, and how stratigraphic sequences develop provides the key to reading the story of evolution in the palaeontological record.

We have also emphasised that different types of stratigraphic sequences may express different types of faunal changes, and hence there will be complexity expressed in stratigraphic/fossil sequences. Some of the complexity in interpreting the fossil record results from variation in the species concept (*i.e.*, whether there are species variation temporarily, or spatially, and thus whether some of the species changes reflect a variable perception of a species by different researchers), but complexity in interpreting the fossil record also can result from interpreting the various expressions of the stratigraphic record, *viz.*, thin *versus* thick homogeneous stratigraphic sequences, thin *versus* thick heterogeneous stratigraphic sequences, shoaling or deepening stratigraphic sequences, and how these effect or are manifest in the palaeontologic record. Additionally, complexity in interpreting the fossil record also can result where there are fragmentary though well dated stratigraphic sequences. There is also a need to separate fossil changes that may be expressed at the species level, at the generic level, and family level. One also needs to separate rapid changes expressed over short time intervals, either in thin stratigraphic sequences or thick stratigraphic sequences, from slow changes in fossil anatomy.

The shifting stratigraphic record can be gross and clearly changing lithologically, or subtle, with both reflecting changes in climate, basin sedimentary patterns, and hydrochemistry. Subtle changes may be the microchemical, or microbiotic, that reflect climate changes while the overall lithology may appear constant. For instance, Quaternary deep sea oozes composed of carbonate mud, and appearing lithologically similar at the gross scale, contain changes in microfossils, or changes in oxygen isotope ratios, or changes in diagenetic patterns, such that the climate record, and species changes are largely locked in at the microscale. For interpreting fossil sequences for use in biological evolution, we have ordered the stratigraphic sequences that host fossils from most fragmentary (wherein one would rely on synoptic information and gradations to reconstruct lineages and associations in combination with radiometric dating), to the most robust involving thick sequences of homogenous lithologies, or cyclothems, or rhythmites (including turbidites).

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