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A Solution to Darwin’s Dilemma: Differential taphonomy of Palaeozoic and Ediacaran non-mineralised discoidal fossils

Volume 1 of 2

Breandán Anraoi MacGabhann

Supervisor: Dr. John Murray

Earth and Ocean Sciences, School of Natural Sciences, NUI Galway

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Taxonomic Statement

This work is not issued for public and permanent scientific record, or for purposes of zoological nomenclature. Taxonomic acts within are therefore not valid by the ICZN until published for public and permanent scientific record.
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The problem with writing acknowledgements these days is that all the good lines have been taken. The one I want to use is:

“If I have seen further than others, it is by standing on the shoulders of giants”

reportedly said by Isaac Newton. Wikipedia now tells me that it had been used before then, which is slightly disappointing, though it does make me feel a little better about copying it here! Newton supposedly meant this as a veiled insult to his contemporary Robert Hooke, who, we are led to believe, was somewhat vertically challenged. I, on the other hand, would like to use it sincerely.

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This thesis is brought to you by the soundtrack to ‘Inception’. Time for me to wake from the dream…
Abstract

The eldonides, a group of non-mineralised asymmetrical discoidal fossils characterised by a coiled alimentary canal with circumoral tentacles and radially arranged internal lobes, are perhaps the least-well known major group of Palaeozoic organisms. Their fossil record is primarily known from sites of exceptional preservation, ranging from the Cambrian to the Devonian. Eleven species are known in eight genera and three families (the Eldoniidae, Maoyanidiscidae, and Paropsonemidae), all placed in the Order Eldonida, Class Eldoniata, and the early deuterostome stem-group Cambroernids.

The eldonides are of little biostratigraphical or palaeoecological utility. However, they are significant in that while eldoniids are generally preserved as compressions in shales, most paropsonemid specimens are found as moulds and casts in sandstones, a poorly-understood taphonomic mode previously thought to be unique to the oldest known animal fossils, of Ediacaran age. Paropsonemids from the Tafilalt Lagerstätte (Ordovician, Morocco), were apparently exceptionally preserved in this style by the adsorption of iron ions, produced during decay by iron reduction, to tissues composed of complex biopolymers. These ions provided sites for the nucleation of aluminosilicate clay minerals, and the formation of iron sulphides (by reaction with hydrogen sulphide produced during subsequent decay by sulphate reduction). These formed moulds of the paropsonemid dorsal surfaces, which were cast by adjacent sediment following the completion of decay. Importantly, comparison to Ediacaran-aged fossils indicates that these were preserved by the same processes, while comparison to fossil eldoniids confirms that this taphonomic style can only preserve tissues composed of complex biopolymers.

This suggests that the oldest known animal fossils cannot have been the oldest animals, but merely the first animals to evolve such tissues. It thus appears that Charles Darwin was correct in his proposal that the oldest known animal fossils were preceded by a long period of animal evolution not represented in the fossil record.
Darwin’s Dilemma

“There is another and allied difficulty, which is much graver. I allude to the manner in which numbers of species of the same group, suddenly appear in the lowest known fossiliferous rocks. Most of the arguments which have convinced me that all the existing species of the same group have descended from one progenitor, apply with nearly equal force to the earliest known species. For instance, I cannot doubt that all the Silurian trilobites have descended from some one crustacean, which must have lived long before the Silurian age, and which probably differed greatly from any known animal. Some of the most ancient Silurian animals, as the Nautilus, Lingula, etc., do not differ much from living species; and it cannot on my theory be supposed, that these old species were the progenitors of all the species of the orders to which they belong, for they do not present characters in any degree intermediate between them.

If, moreover, they had been the progenitors of these orders, they would almost certainly have been long ago supplanted and exterminated by their numerous and improved descendants.

Consequently, if my theory be true, it is indisputable that before the lowest Silurian stratum was deposited, long periods elapsed, as long as, or probably far longer than, the whole interval from the Silurian age to the present day; and that during these vast, yet quite unknown, periods of time, the world swarmed with living creatures.

To the question why we do not find records of these vast primordial periods, I can give no satisfactory answer.”

The abrupt and apparently simultaneous appearance of a diverse range of skeletal fossils near the base of the Cambrian System has engendered much comment and discussion amongst evolutionary biologists and palaeontologists since the 19th Century, when such remains were the oldest known fossils, with older rocks firmly believed to be devoid of any evidence of life. The significance of this debate, in a historical context, is difficult to overstate; indeed, this ‘Cambrian Explosion’ (also referred to as the ‘Cambrian Radiation’), as it is known, remained an insurmountable enigma to Darwin (1859). Darwin believed that if his theory of evolution was correct, then the oldest skeletal fossils (in strata then referred to as the Silurian, as the Cambrian had not yet been defined) could not be fossils of the oldest animals, but merely the oldest animals known to be preserved as fossils. In particular, he was concerned by the diversity within groups, such as the trilobites, and believed that this diversity could only have been produced by an extended period of prior evolution. He had, however, no explanation for why this supposed earlier stage of evolution had left no fossil record.

Decades of research since Darwin’s time have, of course, fundamentally altered our comprehension of early animal evolution. High-resolution lithostratigraphy and biostratigraphy of the Cambrian (e.g. Landing, 1994; Geyer and Shergold, 2000; Peng et al., 2004; Shergold and Cooper, 2004; Babcock et al., 2005; Jago et al., 2006; Zhu et al., 2006) – in particular trilobite (e.g. Palmer, 1977; Öpik, 1979; Jago and Haines, 1998; Zang et al., 2001; Peng and Babcock, 2005; Terfelt et al., 2008), archaeocyathan (e.g. Debrenne and Rozanov, 1983; Zhuravlev and Gravestock, 1994; Zhuravlev, 1995; Brock et al., 2000; Zang et al., 2001), ‘small shelly fossil’ (e.g. Matthews and Missarzhevsky, 1975; Landing et al., 1988; Khomentovsky and Karlova, 1993; Steiner et al., 2003; Elicki, 2005) and acritarch (e.g. Moczydłowska, 1991; Zang, 1992; Vidal et al., 1995; Moczydłowska, 1999; Geyer and Shergold, 2000; Zang et al., 2001; Moczydłowska, 2002; Moczydłowska and Zang, 2006) biostratigraphy – have significantly advanced our knowledge of the relative timing of geological and biological events and Cambrian evolution. Chemostratigraphy, particularly δ13C and 87Sr/86Sr isotope stratigraphy (e.g. Nicholas, 1996; Montañez et al., 2000; Ebneth et al., 2001; Zhu et al., 2004; Alvaro et al., 2008; Maloof et al., 2010), have allowed intercontinental correlation of rock
sequences with a remarkable degree of precision. This has further enhanced our understanding of the sequence of geological and biological events, and has also provided insights into the chemistry of ancient seawater, the nature of continental weathering, seafloor oxidation conditions, atmospheric oxygen levels and biogeochemical cycling during the late Precambrian and Cambrian. Technological advances in the field of radiometric geochronology, particularly thermal ionisation mass spectrometry (TIMS) methods of analysing the uranium-lead isotope system in magmatic zircon crystals (e.g. Mattinson, 2000; Bowring and Schmitz, 2003; Mattinson, 2005; Schoene et al., 2006; Mattinson, 2010), have enabled the dating of Cambrian events with a precision unimaginable for Darwin and his contemporaries (e.g. Compston et al., 1992; Bowring et al., 1993; Isachsen et al., 1994; Davidek et al., 1998; Jago and Haines, 1998; Landing et al., 1998; Encarnación et al., 1999; Amthor et al., 2003; Maloof et al., 2010) (Fig. 1.01).

Advances in the field of biochemistry and genetics have led to the development of so-called 'molecular clocks' (e.g. Runnegar, 1982a; Wray et al., 1996; Conway Morris, 1997; Ayala et al., 1998; Bromham et al., 1998; Bromham and Hendy, 2000; Smith and Peterson, 2002; Peterson et al., 2004; Peterson and Butterfield, 2005; Peterson et al., 2008; Park et al., 2012), which use the hypothesis of a steady (on average) mutation rate in genetic material to estimate the age of the last common ancestor of pairs or groups of species (and thus of the higher-level taxa to which those species belong) by analysing the numbers of mutations of the same genetic code in each species, and using the known fossil record to calibrate the clock by estimating the average rate of mutations in that particular code.

The discovery of Hox genes (which regulate anatomical development patterns during embryonic stages) and micro-RNAs (non-coding RNA genes which appear to have strongly influenced metazoan macroevolution by controlling genic precision) have also fundamentally changed the understanding of metazoan evolution and development (e.g. Davidson et al., 1995; Valentine et al., 1996; Valentine et al., 1999; Davidson, 2001; Valentine, 2001; Martindale et al., 2002; Coutinho et al., 2003; Valentine and Jablonski, 2003; Peterson et al., 2005; Peterson et al., 2009; Sperling and Peterson, 2009; Wheeler et al., 2009).
Perhaps most importantly, the discovery of Cambrian Konservat-Lagerstätten (including the Burgess Shale of British Columbia, Canada (Gould, 1989; Briggs et al., 1994), Sirius Passet in Greenland (Ineson and Peel, 2011; Peel and Ineson, 2011), and the Maotianshan Shale of Chengjiang, China (Seilacher, 1991; H. Luo et al., 1999; Hou et al., 2004), arguably some of the best-known sites of exceptional fossil preservation in the world) have phenomenally increased our knowledge of Cambrian biodiversity, particularly amongst the usually cryptic non-mineralised animals which constitute the vast majority of marine organisms.

Yet for all this, the Cambrian Explosion is discussed and debated even more today than it was in the time of Darwin (e.g. Conway Morris, 1989; Gould, 1989; Erwin, 1991; Conway Morris, 1992; Tucker, 1992; Conway Morris, 1993a, 1997; Bromham et al., 1998; Conway Morris, 1998; Lieberman, 1999; Valentine et al., 1999; Bromham and Hendy, 2000; Valentine, 2002; Conway Morris, 2003; Kirschvink and Raub, 2003; von Bloh et al., 2003; Dzik, 2005; Peterson et al., 2005; Conway Morris, 2006; Marshall, 2006; Shu et al., 2006; Squire et al., 2006; Budd, 2008; Lieberman, 2008; Maruyama and Santosh, 2008; Meert and Lieberman, 2008; Shu, 2008; Peterson et al., 2009; Maloof et al., 2010).

Many potential causes have been advanced for the Cambrian Explosion, including:

1. A rise in atmospheric oxygen levels (e.g. Cloud, 1968; Towe, 1970; Canfield and Teske, 1996; Knoll, 2003; Kennedy et al., 2006; Canfield et al., 2007);
2. The evolution of biomineralisation (e.g. Rigby and Milsom, 2000);
3. The evolution of predatory lifestyles (e.g. Stanley, 1973; Dzik, 2005; Peterson et al., 2005);
4. The increase in size of a Precambrian metazoan microfauna (e.g. Boaden, 1989; Conway Morris, 1993a; Davidson et al., 1995; Fortey et al., 1997; Cooper and Fortey, 1998);
5. The evolution of homeobox (Hox) genes (e.g. Davidson et al., 1995; Knoll and Carroll, 1999; Davidson and Erwin, 2006);

6. Massive methane hydrate release following an episode of inertial interchange true polar wander (Kirschvink and Raub, 2003); and

7. A global reorganisation of oceanic biogeochemical cycles (e.g. Logan et al., 1995; Kennedy et al., 2006; Canfield et al., 2007).

Broadly speaking, as noted by Conway Morris (2006), these hypotheses fall into two categories: those which regard the Cambrian Explosion as a real evolutionary radiation; and those which instead regard it as a taphonomic artefact, with the origin of the Metazoa occurring further back in time in the Precambrian.

Theories supporting a deep time origin of the Metazoa, and thus Darwin’s hypothesis, are strongly supported by molecular clock data, which has consistently produced estimates for the origin of various metazoan lineages which considerably pre-date the first appearance of these lineages in the fossil record. While original estimates (e.g. Runnegar, 1982a; Wray et al., 1996) produced divergence dates for metazoan phyla at around 1 Ga or even older, most recent estimates place the origin of some bilaterian phyla around the base of the Cambrian, bringing molecular clocks closer in line with fossils – particularly in the case of arthropods, echinoderms, and vertebrates (Erwin et al., 2011). However, even this most recent estimate places the origin of the Bilateria at around 670 Ma, the Cnidaria around 690 Ma, the Demospongia around 700 Ma, and the Metazoa around 780 Ma, in clear contrast with the palaeontological record (Fig. 1.02). Significantly, the close concordance between the Cambrian estimates for the origin of particular bilaterian phyla crown groups and the fossil record in Erwin et al. (2011)'s study lend credence to the Cryogenian estimates for the origin of crown group metazoans and major groups, suggesting that the delay between the origin of the Metazoa and the appearance of the modern phyla is real, and not an artefact of the molecular clock methodology. This contrast between the fossil record and molecular clock data, suggesting a long Precambrian history of metazoans without a known fossil record, is effectively a modern re-statement of Darwin’s dilemma.
Perhaps the most significant advance in understanding the Cambrian Explosion (in terms of Darwin’s dilemma, closing the gap between molecular clocks and the fossil record, and understanding the form of early animal evolution) has been the discovery of macroscopic unmineralised fossils in Precambrian sediments (e.g. Narbonne, 2005). Such remains could be interpreted as part of the Precambrian history of metazoans alluded to by Darwin (1859). However, these fossils have proven very difficult to classify, with some researchers interpreting them as lichens (Retallack, 1994), giant protists (Zhuravlev, 1993; Seilacher et al., 2003), or members of an extinct non-metazoan Kingdom of life (Seilacher, 1984, 1989, 1992) separated from the succeeding Cambrian biotas by a mass extinction. Moreover, such fossils are known only from an interval of around 575-541 Ma (late Ediacaran: Fig. 1.2) (Narbonne, 2005); hardly

“as long as, or probably far longer than, the whole interval from the Silurian age to the present day”

as suggested by Darwin (1859, p. 309), nor does this significantly close the gap between the fossil record and molecular clock estimates for the origin of major metazoan groups. Recent research has strongly supported the hypothesis that at least some of these non-mineralised fossils may represent ancestral stem- or crown-group metazoans (e.g. Gehling, 1987, 1988; Gehling and Rigby, 1996; Fedonkin and Waggoner, 1997; Lin et al., 2006; Fedonkin et al., 2007). However, the astonishing complexity and particularly the disparity of these fossils within only a few million years of their first appearance suggests that a metazoan interpretation of these remains would, at best, merely shift the focus of the debate 30 million years back in time from the base of the Cambrian to the mid-late Ediacaran. Rather than solving Darwin’s dilemma, therefore, these fossils appear to have further compounded the enigma.

1.1 The non-mineralised fossils of the Ediacaran System

It is now known that macroscopic unmineralised Precambrian fossils had in fact been discovered prior to the publication of *On the Origin of Species* (Darwin, 1859); the first known report of such remains was contained in a report by R.A. Eskrigge
Differential taphonomy of Palaeozoic and Ediacaran non-mineralised fossils

(1868), which noted that with respect to the Precambrian rocks of Charnwood Forest in England (my emphasis):

“The only traces of organic remains which have been found in the slaty rocks are the remarkable rings seen at Woodhouse Eaves, discovered by myself and the late James Harley in April 1848. They occur with two raised rings, commencing with a sort of central boss, going round, and varying in diameter from six inches to one foot.”

(Eskridge, 1868, quoted in Ford, 2008)

Shortly afterwards, non-mineralised specimens were reported from the Avalon zone of Newfoundland by E. Billings (1872). Unfortunately, neither of these reports gained widespread attention, with both sets of fossils being regarded by others as inorganic structures (see discussions in Ford, 1999, and Narbonne, 2005). It is likely that this was due principally to their Precambrian age – by that stage, the notion that strata older than the Cambrian Explosion were uniformly devoid of evidence of life had become quite entrenched. Indeed, when the first undoubted non-mineralised fossils were discovered and described in Precambrian strata in Namibia by Paul Range and Hans Schneiderhöhn in 1908 (Schneiderhöhn, 1920; Range, 1932; Turner and Oldroyd, 2009) and subsequently George Gürich (Gürich, 1929, 1933; Grazhdankin and Seilacher, 2005), and in South Australia by Reg Sprigg (Sprigg, 1947, 1948, 1949) and later Martin Glaessner (Glaessner, 1958), it was initially believed that the occurrence of these fossils automatically indicated a late Cambrian age for the host sediments. It was not until the rediscovery of the unequivocally Precambrian fossils of Charnwood Forest in England by schoolboy Roger Mason, and their systematic description by Trevor Ford (Ford, 1958, 1963, 1999, 2008) that it became readily accepted that animal life had actually existed in the Precambrian, and it was realised that both the Australian and Namibian fossils were also Precambrian in age (Glaessner, 1959).

Following this realisation, the number of descriptions of Precambrian fossils increased exponentially, not only in England, Namibia, and Australia, but also from subsequently discovered sites, including Russia and Ukraine, the United States, northwest Canada, and Newfoundland (eastern Canada) – although the fossils originally reported by Billings (1872) were not restudied and accepted as fossils until the very end of the 20th century (Gehling et al., 2000).
## Chapter One – Darwin’s Dilemma

<table>
<thead>
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<th>Location</th>
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Macrosopic fossils attributed to multicellular organisms have also been reported from progressively older sediments (Glaessner, 1969; Hofmann et al., 1990; Cruse and Harris, 1994; Bertrand-Sarfati et al., 1995; Rasmussen et al., 2002; Bengtson et al., 2007; Nagovitsin et al., 2008; El Albani et al., 2010; Meert et al., 2011), pushing the age of the oldest known putative non-mineralised fossils back into the Palaeoproterozoic, up to 2100 Ma (El Albani et al., 2010). The interpretation of these most ancient fossils has not always been straightforward, however. The Palaeoproterozoic structures described by El Albani et al. (2010) strongly resemble folded and deformed pyritised microbial mat fragments (Nedin, 2010, unpublished), while Matz et al. (2008) suggested that discoidal and sinuous Palaeoproterozoic structures from the Stirling Range in Australia represented not animals, but algae, based on comparison to modern algal spheroids and traces.

This was not the first time that Precambrian macroscopic fossils had been interpreted as algae. In fact, many of these specimens were originally interpreted as algal (e.g. Ford, 1958) or plant (e.g. Range, 1932) remains. Nor was it the first time that an animal interpretation of Precambrian fossils had been disputed. In fact, reinterpretation of fossil remains has been something of a constant theme to Precambrian palaeontology for several decades, due in part to the often-bizarre morphologies of the fossils concerned. Most of the known Precambrian non-mineralised fossils are simple and discoidal in shape (Gehling et al., 2000; MacGabhann, 2007a), but there is a wide range of more complex forms (see, for example, Fedonkin, 1990; Narbonne, 2005), including discoidal forms exhibiting more complex morphological features such as tentaculate protrusions (Serezhnikova, 2007) or triradial rotational symmetry (Glaessner and Dalley, 1959; Keller and Fedonkin, 1976; Fedonkin, 1984); leaflike fronds attached to the substrate by a discoidal holdfast (Laflamme et al., 2004; Laflamme and Narbonne, 2008); fractally organised organisms (Narbonne, 2004) exhibiting frondlike (Laflamme et al., 2007), bushlike (Flude and Narbonne, 2008), and spindle (Gehling and Narbonne, 2007) shapes; inverted cone shapes (Clapham et al., 2004); and bilaterally symmetrical forms, often with a segmented appearance (Sprigg, 1947, 1949; Glaessner, 1958; Runnegar, 1982b; Dzik and Ivantsov, 2002; Fedonkin, 2002; Ivantsov, 2007). Erwin et al. (2011) recently recognised ten distinct clades of Neoproterozoic forms (Fig.
1.03): Rangeomorpha, Erniettomorpha, Dickinsoniomorpha, Arboreomorpha, Triradialomorpha, Kimberellomorpha, Bilateromorpha, Tetraradialomorpha, Pentaradialomorpha, and sponges (although Tetraradialomorpha contains only one dubious genus, and is not accepted herein).

Initial descriptions of most of these fossils placed them within known animal groups; discoidal forms were often interpreted as cnidarian medusae (jellyfish) or anemones, fronds were interpreted as pennatulacean octocorallids (sea pens), and bilaterian forms were generally placed as either arthropods or annelids. Such interpretations naturally assumed that the Precambrian fossils represented ancestral forms of the Phanerozoic fossil record (and, by extension, present-day animal life); effectively, the missing stage of animal evolution alluded to by Darwin.

Others, however, disagreed. In 1984, German palaeontologist Adolf Seilacher proposed a radically different interpretation of the Precambrian fossils: that they represented an extinct Kingdom of life, separated from the Cambrian biotas by a mass extinction at the Precambrian-Cambrian boundary (Seilacher, 1984). While accepting that certain discoidal fossils represented anemones, Seilacher noted that the more complex forms were characterised by a segmented or “quilted” appearance and large surface to volume ratios, suggesting that this indicated the diffusion of nutrients and oxygen across the body wall, and placed these forms in the new, and extinct, Kingdom Vendobionta (originally termed Vendozoa) (Seilacher, 1984, 1985, 1989, 1992). This proposal attracted significant debate and attention, and led to a renewed examination of the Precambrian fossils, which were subsequently reinterpreted, either in part or as a whole group, as lichens (Retallack, 1994, 1995, 2007), protists (Zhuravlev, 1993), bacterial colonies (Grazhdankin, 2001), and fungi (Peterson et al., 2003), and commonly referred to in terms such as “a failed
evolutionary experiment” (Narbonne, 1998) or even “Alien Beings Here On Earth” (Lewin, 1984).

1.2 ‘Death Masks’ & ‘Gravity Casts’: preservation of the Precambrian fossils

Besides morphology, the other – and perhaps more significant – reason for Seilacher’s reinterpretation of the Precambrian fossils was their unusual style of preservation, as impressions (moulds and casts) in sandstones. Prior to the discovery of Precambrian remains, such a style of fossil preservation was unheard of, in sediments of any age – and it proved extremely difficult to explain.

Most of the fossils, including an overwhelming majority of the simple discoidal forms, are preserved in positive hyporelief and/or negative epirelief. However, a significant minority, including many of the more complex forms, are

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†The treatment of the Precambrian non-mineralised fossils preserved as moulds and casts as a coherent group has been the singular most detrimental feature of research into these organisms, perpetuated by the reference to these fossils collectively as the “Ediacara Biota” or “Ediacara Fauna” in most, if not all, books and papers on the subject – my own contributions included. It is likely that this collective treatment unnecessarily lengthened the debate over the affinities of these organisms, as many authors strove to include what we now know to be a highly diverse range of creatures into a single collective taxonomic group. This was, of course, an impossible task, which left obvious holes in every hypothesis. Of particular detriment is the exclusion of fossils preserved in different styles, such as those preserved as Burgess Shale-type compressions in shales, such that the term ‘Ediacara Biota’ does not include all Ediacaran fossils, thus serving to artificially separate remains preserved in different taphonomic modes. This is not to say that the original reasons for grouping the fossils together are not understandable, but we now know this not to be the case. For this reason, this footnote is the only place in this text where the term “Ediacara Biota” appears, outside of the reference list.

‡Epirelief refers to the top surface of a bed, and hyporelief to the bottom surface, and positive and negative to the sense of the impression on that surface. Thus positive hyporelief means a convex impression protruding from the base of a bed, while negative epirelief refers to a concave impression in the top surface of a bed; and vice versa. Fossils preserved within beds are said to be in endorelief.
preserved as negative hyporelief and/or positive epirelief (Fig. 1.04), and some are preserved in endorelief, within beds§.

Preservation of non-mineralised fossils as positive hyporelief casts is easily explained as the result of sediment moving downwards under gravity (hence fossils of this kind are referred to as ‘gravity casts’: MacGabhann, 2007a) to fill the space left by a decaying organism (thus the fossil was moulded by the underlying bed, with this impression cast by the sediment above), though it does require certain, quite particular conditions, as the sediment must be capable of holding the shape of the mould and cast without soft-sediment deformation or disturbance until lithification.

Preservation as positive epirelief casts, however, is emphatically not easy to explain, requiring as it does that sediment from the bed below moves upwards, against gravity, to cast a mould created in the overlying sediment. The question of quite how so many fossils of Ediacaran age were preserved as a result of sediment moving upwards against the force of gravity, holding their shape post-burial, was directly responsible for interpretation of these fossils first as vendobionts by Seilacher (1984, 1989, 1992), and later as lichens by Retallack (1994, 1995, 2007).

Mary Wade, a student of Martin Glaessner, had previously attempted to explain the preservation of the fossils at Ediacara in South Australia by grouping them into two categories:

1. non-resistant organisms, which decayed prior to the onset of diagenesis in the containing sediment, and

2. resistant organisms, which were able to support the covering sediment until cementation (Wade, 1968).

Seilacher did not accept this interpretation as a sufficient explanation, and believed that an additional non-actualistic intrinsic factor, which he proposed to be the nature

§For the sake of simplicity, only the positive aspect will be generally referred to hereafter; thus positive hyporelief should be understood to mean ‘positive hyporelief and/or negative epirelief’.

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and construction of the organisms, was necessary to explain the unusual preservation (Seilacher, 1984, 1985; Seilacher et al., 1985).

Retallack (1994) took a fundamentally different approach to this preservation puzzle, quantitatively analysing the relief on certain fossils from Ediacara, and comparing these to fossil jellyfish and plant material, concluding that if the fossils were as thick as they were wide, they had the same resistance to compaction as lepidodendrid logs – and if, as seems probable, they were thinner, a much greater resistance to compaction: far beyond the compactional resistance of taxa like jellyfish, to which they had been compared. He concluded that this could be explained by an interpretation as lichens, which contain structural chitin.

Perhaps the most perspicacious research on the preservation of the Precambrian fossils was undertaken by Norris (1989), who experimentally preserved samples of cnidarians in sand and plaster to model the taphonomy of non-mineralised organisms. He observed that even specimens preserved extremely rapidly in plaster exhibited greater deformation and irregularity than Precambrian fossil specimens, concluding that the Precambrian organisms must therefore have been substantially stiffer in composition than the modern organisms to which they had been compared.

The greatest advance in understanding, however, came from James Gehling (1999), who proposed that the preservation of these fossils was aided by microbial mats; layers of microbial biofilms which were ubiquitous on Neoproterozoic seafloors (Seilacher and Pfluger, 1994). Gehling identified several bed-surface textures common on surfaces preserving non-mineralised fossils at Ediacara in South Australia, interpreting these textures as due to microbial mats, and proposed that on burial of the microbial mat and organisms by event sedimentation, the decay of the microbial mat quickly used up the available pore-water oxygen and moved to anoxic decay, producing iron sulphides as a byproduct. These iron sulphides rapidly cemented the sole of the burying bed, creating a “Death Mask” around the fossils, enabling preservation in positive epirelief (Gehling, 1999; Gehling et al., 2005). This hypothesis gained rapid acceptance, and qualitative support (e.g. Mapstone and McIlroy, 2006).
1.3 Closure of a taphonomic window, or a mass extinction?

Gehling (1999)’s microbial mat hypothesis also served to explain one other puzzling facet of the Precambrian fossils: why none of them were found biostratigraphically above the Precambrian-Cambrian boundary. Fossils from Cambrian strata had occasionally been reported as similar to those of Ediacaran age, but few of these reports (e.g. Borovikov, 1976) were credible (see Cloud, 1973), with only rare examples of simple discoidal structures of little significance in lowermost Cambrian sediments truly having a greater resemblance to Ediacaran-aged fossils than to more familiar Phanerozoic forms (Crimes and McIlroy, 1999; Hagadorn et al., 2000).

Several possible interpretations of this observation were possible. The first, that the Ediacaran remains were ancestral to Cambrian organisms, and were thus replaced by them by gradual evolution, was an assumption inherent in the earlier work of Glaessner and colleagues (e.g. Glaessner, 1984). However, such an interpretation does not explain the sharp change from Precambrian sediments containing non-mineralised fossils preserved as moulds and casts extending right up to the Precambrian-Cambrian boundary, overlain by Cambrian trilobite-bearing strata without any impressions of non-mineralised forms.

A second potential explanation, as proposed by Seilacher (1984), was that the Precambrian-Cambrian boundary marked a mass extinction horizon, with the organisms that dominated the Ediacaran Earth wiped out, and replaced by the familiar Phanerozoic and extant animal groups.

The Gehling (1999) model of microbial mat-aided preservation introduced a third interpretation: that as the preservation of the Precambrian fossils was dependant on non-actualistic conditions – namely the presence of ubiquitous seafloor microbial mats – it was not possible for non-mineralised organisms to be preserved as moulds and casts in Cambrian and younger sediments, where such microbially bound substrates were diminished, or indeed absent. Such an interpretation relied on the premise that the terminal Neoproterozoic was a time of unique taphonomic conditions (which rapidly became known as the ‘Ediacaran taphonomic window’), and removed a key element of the argument against the
ancestral metazoan interpretation for many of the Precambrian organisms (Gehling, 1991, 1999; Gehling et al., 2005).

The increasing realisation (e.g. Seilacher and Pfluger, 1994; Gehling, 1999; McIlroy and Logan, 1999; Seilacher, 1999) that microbial mats had played a key role in Neoproterozoic palaeoecology, however, allowed a further alternative: that, rather than the closure of a unique taphonomic window, it was the demise of microbial mat-dominated ecosystems that caused the apparent change between Neoproterozoic and later fossil assemblages. While based on the same premise as the Gehling (1999) taphonomic window hypothesis above, this model implies that many forms became extinct at the Precambrian–Cambrian boundary, rather than being present in the lower Cambrian but without any fossilisation potential. One of the key differences moving across the Precambrian–Cambrian boundary is in the number and type of trace fossils, with Precambrian ichnofossils limited to simple surficial structures, with little or no evidence of significant burrowing or infaunal lifestyles (e.g. Droser et al., 2005; Jensen et al., 2005; Liu et al., 2010; Sappenfield et al., 2011). Such behaviour instead appears to have become widespread and conspicuous in Lower Cambrian sediments, a change referred to as the ‘Agronomic Revolution’ (Seilacher and Pfluger, 1994) (Fig. 1.05) or the ‘Cambrian Substrate Revolution’ (Bottjer et al., 2000). The evolution of efficient and effective bioturbation, with animals feeding on microbial mats, and burrowing within sediments such that microbial mats were destroyed or did not have time to form, largely restricted microbial mats to environments unattractive or inhospitable to widespread macroscopic life. Dzik (2005) linked this change in behaviour and the concordant evolution of mineralisation to the evolution of predatory behaviour, noting that predation would encourage the evolution of burrowing and infaunal lifestyles (for protection) and protective skeletons, which in turn would encourage the development of ‘weaponised’ skeletons and burrowing to seek infaunal prey. He referred to this as ‘Verdun Syndrome’, drawing parallels to the concordant ‘evolution’ of trenches and mechanised armour in military combat during the First World War.
1.4 Exceptional preservation of non-mineralised fossils in the Phanerozoic

One significant factor which has been overlooked in all previous discussions of the apparent biological change across the Precambrian-Cambrian boundary is the preservation of non-mineralised fossils as moulds and casts in Phanerozoic sediments. To a certain extent, this is understandable, as while non-mineralised fossils are well known from several Cambrian and younger Konservat-Lagerstätten, they are generally preserved in very different styles. For example, in the Jurassic Solnhofen lithographic limestones, non-mineralised organisms (including scyphozoan medusae, e.g. Adler and Röper, 2012) were preserved in rapidly deposited carbonate mud in hypersaline, and possibly anoxic, conditions (Barthel et al., 1990). Medusae and many other non-mineralised forms are also preserved as fossils in Carboniferous siderite concretions at Mazon Creek (Nitecki, 1979; Baird et al., 1986; Kuecher et al., 1990; Schellenberg, 2002), and pyritised within the fine-grained anoxic mudstones of the Devonian Hunsrück Slate (Briggs et al., 1996; Bartels et al., 1998; Raiswell et al., 2001). Perhaps the best known Phanerozoic Lagerstätte is the Middle Cambrian Burgess Shale of British Columbia, Canada, which preserves thousands of non-mineralised specimens as compressions in anoxic shales (Whittington, 1985; Gould, 1989; Briggs et al., 1994).

However, while preservation either within lithographic limestones or concretion, or as compressions or pyritic replacements in shales, dominates the Phanerozoic record of non-mineralised taxa, the preservation of such soft-bodied fossils as moulds and casts in sandstones is not absent. Indeed, several examples of this kind of preservation, albeit consisting of only a few specimens, were known prior to the widespread attention given to the Precambrian fossils following the discovery of the South Australian assemblages. For example, the discoidal form Discophyllum peltatum was described from the Ordovician of New York in 1847 (Hall, 1847; Walcott, 1898), Paropsonema mirabile from the Silurian of Australia in 1926 (Chapman, 1926b), and Paropsonema cryptophya from the Devonian of New York in 1900 (Clarke, 1900). Most of the Phanerozoic examples of this style of preservation are discoidal in form, but a limited number of more complex organisms are also known to be preserved in this manner, including Protonympha salicifolia, Priscapennamarina angusta, and Xenusion auerswaldae.
To date, no explanation has been proposed for how such preservation is possible in Phanerozoic sediments in the absence of microbial mats, nor how this impacts the suggestion that the apparent biological change over the Precambrian-Cambrian boundary is a taphonomic artefact resulting from the disappearance of this style of preservation.

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1.5 The Tafilalt Konservat Lagerstätte

Most of the Phanerozoic localities from which non-mineralised fossils preserved as moulds and casts have previously been described have yielded only a few specimens. To date, there has been no evidence to indicate whether this low number reflects an original low diversity of organisms at these sites, the difficulty of preserving such creatures as fossils in this style, or more simply a lack of detailed and systematic exploration. More recently, however, a potentially paradigm-shifting Konservat-Lagerstätte, preserving thousands of non-mineralised specimens as moulds and casts, was discovered by local fossil collectors in Upper Ordovician shallow marine sandstones of the Tafilalt region in southeastern Morocco (Samuelsson et al., 2001; Van Roy, 2006a).

As described in the following chapters, the fossils preserved at these sites are predominantly discoidal, but rather than the simple discs of Ediacaran-aged sediments, the most common Tafilalt fossils exhibit a complex ornamentation and limited preservation of internal structures, including part of the digestive tract. Nor are these fossils problematica: although their precise phylogenetic placement is uncertain, they belong to a widespread and long-ranging Palaeozoic group, the eldonides, with known relatives including the aforementioned Paropsonema crytophya, Discophyllum peltatum, and Paropsonema mirabile; as well as Maoyanidiscus grandis (formerly known as Rotadiscus grandis), Pararotadiscus guizhouensis, and Eldonia eumorpha from the Cambrian Chengjiang and Kaili Konservat-Lagerstätten in China; and the well-known Eldonia ludwigi from the Cambrian Burgess Shale of Canada.

1.6 Scope and aim of this project

The fact that the Tafilalt Lagerstätte in Morocco preserves thousands of non-mineralised specimens which are closely related to the well-known Eldonia ludwigi, which is preserved in a completely different style of preservation as compressions in shales in the Burgess Shale, allows a unique opportunity to evaluate the style of preservation of the Tafilalt specimens. As the biology of Eldonia ludwigi is well understood from the Burgess Shale (Friend, 1995), where it is one of the most
common fossils, the presence or absence of particular biological features in the Moroccan fossils can be understood in terms of the vagaries of the particular mode of preservation at Tafilalt, allowing an analysis of what biological features could, and more importantly could not, be preserved in this style.

Perhaps even more importantly, as the style of preservation at Tafilalt – as moulds and casts in shallow marine sandstones – is apparently similar to that of many Precambrian fossil sites, the results of the analysis of the Tafilalt taphonomic mode may be applicable to Ediacaran examples. Such a differential taphonomic analysis – involving three different fossil sites of three different ages – could have major implications for the interpretations of the biology of Ediacaran-aged fossils, and for prior explanations for the ostensibly abrupt biological change across the Precambrian-Cambrian boundary, particularly in relation to the proposed closure of the ‘Ediacaran taphonomic window’ (Gehling et al., 1998; Jensen et al., 1998; Gehling, 1999).

Most significantly, the differential taphonomic analysis of the Ediacaran-aged fossils may be able to answer the question of whether these fossils are the remains of the oldest animals, or merely the first animals to be fossilised, thus answering Darwin’s dilemma.

The null hypothesis of this thesis is in four parts:

1. That the processes involved in the preservation of the non-mineralised fossils at Tafilalt are effectively identical to those involved in the preservation of many fossils of Ediacaran age;

2. That these taphonomic processes preserve only recalcitrant, decay-resistant structures, and cannot preserve the more labile tissues preserved in Burgess Shale-type preservation;

3. That the apparent biotic change across the Precambrian-Cambrian boundary is not a taphonomic artefact;

and finally,
4. That Darwin was likely correct in his assumption of a long pre-Cambrian fossil record, as the fossils of the Ediacaran System cannot represent fossils of the oldest animals, but merely the oldest known animals to be fossilised.

This thesis will seek to falsify each part of this null hypothesis.

As part of this research, the Tafilalt sites were investigated both in terms of sedimentology and palaeontology, with particular attention paid to the taphonomy of the fossils. A re-examination of related fossils from other sites was also undertaken, and the taxonomy of the eldonide group has been completely revised as a result.

1.7 Thesis plan

This thesis is in two volumes. Volume One contains the main text, tables, and references. Volume Two comprises the figures and tables. These are referenced by chapter, as Fig./Table (chapter number).(figure number). An accompanying data DVD includes an Appendix containing additional geochemical and analytical data, a database (as an Excel spreadsheet) containing qualitative and quantitative descriptions of the Tafilalt fossils, and electronic copies of the text, figures, tables, (in PDF format) and geochemical data (as an Excel spreadsheet).

Chapter Two details the analytical methods used for both taxonomic and taphonomic study of the fossils. Chapter Three outlines the geological context of the fossil localities, both explored and unseen, and Chapter Four presents the revised systematic palaeontology of the eldonides. Chapter Five then explores the taphonomy of Eldonia from the Burgess Shale, and the Tafilalt eldonides. Finally, Chapter Six discusses the palaeoecology, mode of life, and phylogenetic placement of the eldonides; and compares the taphonomy of the Tafilalt fossils first to the Burgess Shale eldonides, and then to the fossils preserved as moulds and casts in siliciclastic sediments from five Ediacaran sites (southern Australia, central Australia, Russia, Newfoundland (eastern Canada), and Namibia), addressing the null hypothesis, along with suggestions for further work.
Analytical methods

As part of this research, fossils were examined from seven locations, including the Cambrian of British Columbia, Canada; the Ordovician of New York, USA; the Ordovician of the Tafilalt region, Morocco; the Ordovician of Co. Tyrone, Ireland; the Silurian of Victoria, Australia; the Silurian of England; and the Devonian of New York, USA. Fossils from other localities were considered primarily from the literature and previous research (MacGabhann, 2007a, and unpublished), including the Ediacaran of south and central Australia; the Ediacaran of the White Sea, Russia; the Ediacaran of Namibia; the Ediacaran of Newfoundland, Canada; the Cambrian of Siberia, Russia; the Cambrian of South China; the Cambrian of Spain; and the Ordovician of Algeria.

Extensive fieldwork was conducted only in the Ordovician of Morocco. Fossils and sediment samples were collected at outcrop from ten principal sites in the Tafilalt region (p. 34), and returned for further study in Ireland. The sedimentology of these sites was assessed by means of centimetre-scale logging of fossiliferous outcrops, with locations recorded by means of a handheld GPS, either a Garmin eTrex Summit or a Garmin eTrex Vista HCx. This was used to construct a simple map of the fossiliferous outcrops at one locality, numbered M005 (p. 40).

Fossils collected from the Ordovician of Morocco were visually examined, described, and photographed in the laboratory. Selected fossil specimens and sediment samples were subjected to further geochemical analysis for the purposes of elucidating the diagenesis of the sandstones and the taphonomy of the fossils themselves. The methods used are described below. Samples from the Ordovician of Ireland were also further analysed. Fossils from England and Australia were examined from replicas. The Australian specimens were provided by Dr. Rolf
Schmidt, Invertebrate Palaeontology Collection Manager at Museum Victoria as latex moulds, were cast in plaster to aid examination and photography. The specimen from England was provided by Ms. Jill Darrell, Curator of Cnidaria, Department of Palaeontology, Natural History Museum, as a resin mould. As no original sedimentological material was available of these specimens, no geochemical testing could be performed. Specimens from the Devonian of New York and the Burgess Shale were examined in other institutions, and so no testing of these was performed. However, previous SEM results for Burgess Shale specimens were available in the literature. Specimens from the Ordovician of New York were provided on loan by Paul Mayer, Collections Manager, Fossil Invertebrates, in the Department of Geology of the Field Museum, Chicago. As only two type specimens are available, no geochemical testing was possible.

2.1 Visual techniques and photography

All fossil specimens were initially examined and described without visual aids. Various measurements were recorded, as were the presence or absence of selected anatomical features. These measurements and observations were recorded in a database, which is provided on a data DVD accompanying this thesis.

For specimens in the Family Paropsonemidae fam. nov. (p. 94), the maximum thickness of the ‘coiled sac’ (this, along with other morphological terminology, is defined in Chapter Four) and the diameter of the specimen were the only dimensions which could be meaningfully recorded for a significant number of specimens, with both long- and short-axis diameters recorded in specimens exhibiting plastic deformation. Morphological and taphonomic characteristics also recorded included:

- whether the specimen was available as a part (mould), a counterpart (cast), or both;
- the position of the specimen with regard to the bed (top surface, bottom surface, inside the bed, or uncertain);
• the relief of the specimen (positive hyporelief and/or negative epirelief, negative hyporelief and/or positive epirelief, positive and/or negative endorelief, or uncertain);

• whether the specimen exhibited evidence for tearing, folding, stretching, or shrinkage;

• whether the sample contained multiple fossil specimens, and if so, how many, and whether or not these were overlapping;


In specimens of *Eldonia ludwigi*, the specimen diameter could not normally be reliably recorded, as most of the specimens were buried at an angle and subsequently flattened by compaction, with structural deformation further distorting the original shape. Many specimens also exhibit incomplete preservation, with the margin unclear. The size of *E. ludwigi* specimens can be better inferred from the maximum thickness of the ‘coiled sac’, which was recorded where possible, though it should also be noted that the effects of compression on the ‘coiled sac’ are unclear, and in some specimens this appears to have burst, greatly increasing its relative size. The true value of these measurements is thus not entirely apparent. The diameter of the ‘central ring’, where present, was also recorded in *E. ludwigi*, but no other useful measurements were possible. Additional morphological characters recorded included:

• the presence or absence of ‘radial fibres’;

• the presence or absence of various divisions of the ‘coiled sac’;

• the presence or absence of ‘circumoral tentacles’;

• the presence or absence of the ‘oval sacs’;

• the occurrence of radial ornamentation;

• the number of ‘bifurcating lobes’ (if any).
In specimens preserved as moulds and/or casts in sandstones, unaided visual inspection often fails to distinguish fine details of the surface ornamentation. This effect has also been commonly observed with similarly preserved Neoproterozoic fossils (e.g. Hammer et al., 2002). Low relief features can be highlighted by low-angle lighting, which casts shadows from features which are not parallel to the lighting direction. Unfortunately, those features which are parallel to the lighting direction are usually obscured. Using low-angle lighting on discoidal fossils, such as those described herein, is therefore not simple, as the complex radially-arranged ornamentation will always contain elements parallel to any possible lighting direction. Asynchronous use of lighting from various different directions is required to fully appreciate the ornamentation over the entire disc. Such photography is in fact the best way of examining these specimens: unaided visual examination often cannot properly distinguish the finest features, while examination under a microscope offers too small a field of view, and is in any case difficult to do with low-angle light. High-resolution photography offers a sufficiently large field of view with the capability of zooming in to high-magnification on selected parts of the image. The inability to vary the direction of the light source while examining the image remains a disadvantage, but can be significantly mitigated by photographing specimens from multiple angles of incident light.

All examined specimens were also photographed, using one of four different digital cameras: a Fujifilm FinePix S5700 (7.1MP), a Nikon E4500 (4MP), a Canon EOS Digital Rebel (3.4MP) SLR with an EF-S 18-55 lens and a polariser, and a Canon EOS 500D (15.1MP) SLR with an IS 18-55 lens. All photographs were taken at a low ISO (64-200) to reduce noise. The aperture was varied from f/3.5 to f/22, with large apertures used to increase image sharpness, and small apertures used when maximal depth of field was required; exposure time was varied to adjust for the aperture. Both Canon cameras were digitally controlled via USB from a laptop computer using the Canon EOS Utility Live View function.

Paropsonemid specimens were photographed using various combinations of low-angle and reflected lighting, to achieve the often-conflicting aims of illuminating the entire specimen while highlighting the low-relief surface features, with the high relief of some of the specimens further complicating matters.
The Australian paropsonemid specimens were examined as plaster casts. For the purposes of photography, these casts were painted matt black and coated with ammonium chloride sublimate to further improve the visibility of low relief surface structures. A small number of specimens from site M010, where the fossil surfaces are naturally blackened, were similarly whitened.

Specimens of *Eldonia ludwigi* at both the Royal Ontario Museum and the Smithsonian Museum of Natural History were photographed using the FinePix S5700 at ISO 64. A large aperture (f/4) was used to maximise sharpness, with the nature of the fossils as flat compressions not requiring a high depth of field. Lighting these specimens was particularly difficult: the flattened nature of the fossils required a high angle of incident light to illuminate the various features, but the extremely high reflectivity of certain structures (particularly the coiled sac) caused a large variation in light levels across the specimen, such that high shutter speeds non-reflective features were, at most, barely visible, while at low shutter speeds, the reflective features swamped the image. While increasing the distance between the light source and the specimen reduced this problem, the best results were achieved by reflecting an oblique light source onto the specimen using a semi-silvered board with an oval hole in the centre (a method developed by Chip Clarke – see Friend, 1995). This board was positioned just below the camera, such that the lens captured light through the hole, while the board diffusely reflected light onto the specimen. The diffuse nature of the reflected light significantly reduced the glare from the highly reflective features.

### 2.2 Microscopy

In order to explore the taphonomy of the fossil specimens, polished thin-sections were made through several samples from the Moroccan sites, by A. Sherlock in NUI Galway and N. Kearney in Trinity College Dublin. These were examined using a polarizing petrographic transmitted light microscope with an attached digital camera for photography. Some thin sections were further illuminated with additional incident light, directed onto the slide by fibre-optic cable, which enhanced the visibility of certain features.
Several samples were also analysed using more advanced microscopic techniques, including SEM and Laser Raman microspectroscopy.

2.2.1 SEM-EDS

Polished thin-sections and hand samples from several fossils were analysed in scanning electron microscopes in both NUI Galway, with the assistance of Dr. Éadaoin Timmins and Dr. Liam Morrison, and in Virginia Tech by Dr. James Schiffbauer. Specimens analysed in NUI Galway were coated with a 10nm gold conductive layer using an Emitech K550 sputter coater, mounted on aluminium sample stages with double-sided carbon tape, and examined in a Hitachi S-4700 SEM with an Oxford Instruments EDS and INCA software. Those analysed at Virginia Tech were coated with a 20nm gold-palladium conductive layer in a Cresington 208HR sputter coater, mounted on aluminium sample stages with double-sided carbon tape, and examined in an FEI Co. Quanta 600 ESEM at high vacuum, with a Bruker QUANTAX 400 EDS and Bruker AXS QUANTAX Esprit software.

2.2.2 Laser Raman

Laser Raman microspectroscopy (e.g. Hope et al., 2001; Pasteris and Wopenka, 2002; Schopf et al., 2002; Smith and Dent, 2005) is a technique that identifies molecules by means of inelastic scattering, or Raman scattering, of incident photons on a sample. Different chemical bonds have characteristic Raman spectra, allowing the rapid identification of minerals within samples by comparison of obtained spectra against those of known materials. Raman microspectroscopy can be used to analyse single points, and can also be programmed to analyse points in a systematic manner across a defined area on a sample. Such data can be summarised as a ‘map’ by assigning each of the three primary colours (RGB) to a particular Raman-shift values. It is also possible to produce monochromatic maps based on a single Raman shift peak, effectively mapping the distribution of particular minerals within a sample.
The advantages of Raman microspectroscopy over optical microscopy include the higher resolution, offering the ability to identify minerals at extremely small sizes; the rapid identification of rarer minerals, opaque minerals, and optically indistinguishable mineral variants; and the ability to produce accurate compositional maps. However, at a sufficiently high resolution to analyse diagenesis and taphonomy, maps take a considerable amount of time to produce: one of the maps presented herein incorporates approximately 100 hours of data collection.

Laser Raman microspectroscopy was undertaken in NUI Galway, with the assistance of Ed Lynch, on a Horiba Jobin Yvon LabRAM Raman confocal microscope with LabSpec 5 software, using a 784.34 nm laser.

Raman spectroscopy is widely used in several branches of geology, but palaeontology is not currently one of those. Previous use of Raman in palaeontology has generally been limited to mineralogical identification of structures thought to represent Archaean microbiological life (Schopf et al., 2002; see also comment by Pasteris and Wopenka, 2002).

2.3 Geochemical techniques

To supplement optical and advanced microscopy, several samples were also geochemically analysed to determine their composition. Three different analytical techniques were used.

2.3.1 XRD

X-ray diffraction is a mineral identification technique which analyses the crystal structure of a powdered sample by measuring the elastic scattering of incident X-rays. Incident X-rays are elastically scattered at angles depending on the various lattice spacings, which are randomly oriented within the powdered sample, producing a circular diffraction pattern. The patterns produced are then compared to those from known samples, allowing rapid identification of minerals. Separate diffraction patterns will be produced for all minerals in a sample. The technique may
be regarded as semi-quantitative, as the intensity of the diffraction peaks corresponds to the amount of that material in the sample.

Five samples were initially crushed in a Retsch BB1 jaw crusher and powdered in a TEMA T-100A agate mill in NUI Galway, and analysed on a Phillips PW1720 Powder X-ray Diffractometer in Trinity College Dublin by Dr. Robbie Goodhue, with the intention of exploring the mineralogy of the clays associated with fossil paropsonemids. However, the clay content was deemed too low in these samples to produce an identifiable diffraction pattern, and no further samples were thus analysed.

2.3.2 XRF

X-ray Fluorescence is a technique based on the same fundamental principles of chemistry and physics as SEM EDS, used to analyse the elemental composition of a sample by examination of secondary fluorescent X-rays. However, instead of bombardment with electrons, in this case the fluorescent X-rays are emitted by the target after bombardment with high-energy X-rays, allowing analysis of a larger sample which has been homogenised, such as to obtain compositional data for an entire sample rather than a localised area or single point.

Five samples were initially crushed in a Retsch BB1 jaw crusher, powdered in a TEMA T-100A agate mill, made into pressed pellets (10 g with 16 drops of 2% PVA solution, pressed at 10 tonnes for 5 minutes) and analysed on a Bruker S2 Ranger Energy Dispersive X-ray Fluorescence Spectrometer using a Hudson calibration for sandstones. This work was also conducted by Dr. Robbie Goodhue in Trinity College Dublin. However, a decision was subsequently made that the higher accuracy and lower detection limits of ICP-MS would be more beneficial to the interpretation of the diagenesis, and so no further samples were analysed.

2.3.3 ICP-MS

Inductively Coupled Plasma Mass Spectrometry is a high-precision method for quantitatively analysing the elemental composition of a sample, with detection limits
close to one part in one trillion. Samples are vaporised, atomised, and then ionised in a high-energy electrically-conductive argon plasma (heated to 6000°-8000° by radio frequency oscillation), which is then accelerated towards the mass spectrometer. Ions are detected and identified on the basis of their mass-to-charge ratio.

34 samples from the Ordovician of Morocco were analysed by ICP-MS at OMAC/Stewart Labs in Athenry, Galway, Ireland. Samples were initially crushed in NUI Galway in a Retsch BB1 jaw crusher, and further jaw crushed to 2mm and milled to 100μm at OMAC Labs, before fusion with lithium metaborate for the analysis. Ferrous iron was also determined by titration at OMAC in order to evaluate the ratio of ferrous to ferric iron in the samples analysed.
Geological Context of Fossil Localities

As part of this research, fossil specimens were examined from seven sites, in six countries on four continents - the Cambrian of Canada, the Ordovician of Morocco, the Ordovician and the Devonian of New York (USA), the Ordovician of Ireland, the Silurian of England, and the Silurian of Australia. The following sections consider the geological and sedimentological context of these localities. Additional material from the Ediacaran of Australia, Namibia, Russia, and Newfoundland (Canada), the Cambrian of China and Spain, and the Ordovician of Algeria, was considered primarily from the literature.

3.1 Field locations

Extensive fieldwork was conducted only in the Ordovician of Morocco, with a brief overview conducted of one site from the Ordovician of New York.

3.1.1 Morocco

The Ordovician of the Anti-Atlas region of Morocco is a predominantly siliciclastic sedimentary sequence deposited in a storm-dominated offshore shelf environment (e.g. Destombes et al., 1985; Gutiérrez-Marco et al., 2003; Bourahrouh et al., 2004; Van Roy, 2006a; Loï et al., 2010; Videt et al., 2010), and is well-exposed over an outcrop belt spanning hundreds of kilometres (Fig. 3.01). The lithostratigraphy of Destombes et al. (1985), which is still universally used with little modification, divides the sequence into four groups (Fig. 3.02): the silty-shale dominated Outer Feijas Group, which unconformably overlies Cambrian siliciclastic sediments; the sandstone dominated First Bani Group; the siltstone and mudstone dominated Ktaoua Group; and the Second Bani Group, which contains glaciomarine
diamictites associated with the Hirnantian glaciation (Destombes et al., 1985; Loi et al., 2010).

The Outer Feijas Group, at the base of the Ordovician sequence (Fig. 3.02), is subdivided into the blue-green silty mudstones and siltstones of the Lower Fezouata and Upper Fezouata formations (which are difficult to distinguish on lithological grounds in the field) and the disconformably overlying grey-white silty mudstones of the Tachilla Formation (Destombes et al., 1985; Van Roy, 2006a). Locally, the top of the Upper Fezouata Formation is replaced by sandstones of the Zini Formation. The Outer Feijas Group is exposed significantly only to the far west of the study area, but is notable for the presence of an exceptionally preserved biota in the Lower and Upper Fezouata formations in the vicinity of Zagora (Van Roy, 2006a; Botting, 2007; Vinther et al., 2008; Van Roy et al., 2010; Van Roy and Briggs, 2011; personal observations 2006, 2008, 2011).

The overlying First Bani Group (Fig. 3.02) is divided into five sandstone-dominated formations: the Taddrist, Bou-Zeroual, Guezzart, Ouine-Inirne and Izegguirene formations (Destombes et al., 1985); however, it is not possible to distinguish these formations in the Tafilalt region (Destombes et al., 1985, personal observations). Videt et al. (2010) characterised the First Bani Group sediments as representing two alternating depositional systems related to transgressive/regressive cycles, namely high-energy storm-dominated ramp systems and low-energy ramp systems dominated by geostrophic currents.

In the western end of the outcrop belt, the succeeding Ktaoua Group comprises two formations; the transgressive argillaceous Lower Ktaoua Formation (with limited coarser clastic deposits in the Middle Tiouririne member), and the Upper Tiouririne Formation, which represents much shallower proximal shelf to shoreface facies, believed to have resulted from an early glacial episode which caused a significant fall in the local sea level (Loi et al., 2010; Videt et al., 2010). To the east of Erfoud, bryozoan limestones (often referred to as the Khabt-el-Hajar limestones) form a partial lateral equivalent of the Upper Tiouririne Formation (Destombes et al., 1985). To the west of the outcrop belt, the Upper Ktaoua Formation overlies the
Upper Tiouririne Formation (Fig. 3.02), but as noted by Destombes (1985), this unit is generally absent in the Tafilalt area.

The Second Bani Group caps the Ordovician succession, and is divided into the predominantly fine-grained marine Lower Second Bani Formation, and the much coarser predominantly glacio-fluvial terrestrial Upper Second Bani Formation (Fig. 3.02).

Locally, the Ordovician sequence in southeastern Morocco can be richly fossiliferous in both macro- and microfossils, with trilobites, echinoderms, chitinozoans and acritarchs providing tight biostratigraphical control (Elaouad-Debbaj, 1984, 1986, 1988; Gutiérrez-Marco et al., 2003; Bourahrouh et al., 2004; Webby et al., 2004; Van Roy, 2006a, b; Achab and Paris, 2007; Regnault, 2007; Bruton, 2008; Hunter et al., 2010; Loi et al., 2010; Videt et al., 2010). The Lower and Upper Fezouata formations comprise the entire Lower Ordovician (Tremadocian and Floian), with the Dapingian represented only by the disconformity between the Upper Fezouata Formation and the lower Darwillian Tachilla Formation. The First Bani Group is late Darwillian to earliest Sandbian in age, with the Ktaoua Group representing the majority of the Sandbian and the entire Katian. The Hirnantian is represented solely by the Second Bani Group (Fig. 3.02).

As may be obvious from the preceding discussion, the Ordovician lithostratigraphy of Morocco requires substantial revision. Several group and formation names contravene standard practice, boundaries often cannot be distinguished in the field, and the formations of the First Bani Group are not mappable in the Tafilalt area. Further, the accuracy of existing geological maps of the area (Fetah et al., 1986, 1988) is highly questionable. For example, terrestrial fluvial sediments (which likely belong to the Upper Second Bani Formation) were observed during the course of this study in the Erfoud area, where the Upper Second Bani Formation does not feature on the geological map. For these reasons, the precise stratigraphic position of the fossil sites is often doubtful; only a complete re-mapping of the wider Tafilalt area and concordant revision of the stratigraphy could accurately place the fossils within the sequence. Unfortunately, it was not possible to undertake such an extensive enterprise during the course of this research.
3.1.1.1 Localities

This study primarily focused on exceptional fossil preservation within the First Bani Group and Ktaoua Group in the Tafilalt area, in the vicinity of the towns of Erfoud and Rissani (Fig. 3.03). Fossils were examined from nine different sites. As detailed local geographic names are either non-standardised or non-existent, each of these sites was identified with a three-digit location code, prefixed by the letter M. Codes were not assigned sequentially, to allow newly-discovered sites to receive codes adjacent to those of previously explored locations in close proximity, thus gaps exist in the sequence.

M001

Figs. 3.04–3.07

N 31° 25’ 00.5” W 004° 02’ 50.2” (±3m)**

This site is located in the desert some 18km east of the town of Erfoud (Fig. 3.04a), approximately halfway up a north-west facing hillside on the edge of a broad, shallow valley (Fig. 3.04b-c). The bedrock comprising the hill consists primarily of sandstones interbedded with sandy mudstones, with bedding (measured as 107/09°NE) dipping slightly shallower than the slope of the incline, such that the edges of successive beds are exposed in a stepwise manner over much of the surface of the hillside.

Much of the floor of the valley is covered in Quaternary wadi sediments. Where exposed, the Ordovician bedrock on the valley floor, and at the base of the hillside succession, generally comprises thin- to very thin-bedded sandy mudstones and fine sandstones, with a greenish weathering colour.

The bulk of the exposure on the hillside consists of sandy mudstones with lenses of brownish-weathering beds of medium- to coarse-grained sandstone (Fig.

** All co-ordinates are given using the WGS84 datum.
3.04b-e). The sandstones are medium- to thickly-bedded, reaching 40cm in thickness (Fig. 3.04d-e), and are generally light to white grey on fresh surfaces (Fig. 3.05a). Bedding is universally lenticular in style, and pinches out gradually over ca. 10-20m when traced laterally. Depositional sedimentary structures are limited to occasional parallel lamination; no cross-lamination was observed in the logged section (Fig. 3.04d-e), although ripples were observed approximately 10-20m stratigraphically lower (Fig. 3.05c). Most beds also display at least some evidence of horizontal bioturbation on top or bottom surfaces, and occasionally within beds, (Figs. 3.05a, 3.06) with burrows up to 12mm in width, including some backfilled burrows with a distinct branching cord-like appearance (e.g. Fig. 3.06a). Evidence for vertical bioturbation is ambiguous. Internally, the sandstones are clearly rich in quartz, but with some beds containing greater concentrations of dark brown and black grains which were unidentifiable in the field. The sandstones are interbedded with thin- to medium-bedded poorly sorted sandy mudstones, which commonly have coarser laminae developed throughout (Fig. 3.04d-e).

The hill is capped by a conspicuous and distinct unit, comprising two interbedded facies; medium-bedded red sandstones, and conglomerates (Fig. 3.07). Bedding in the conglomeratic facies is massive, with generally internally structureless beds commonly exceeding 1m in thickness (Fig. 3.07a,b), pinching out laterally over tens of metres. Bed bases are almost universally erosional. Clasts are predominantly composed of sandstone, with subrounded to rounded red sandstone pebbles and cobbles of medium to low sphericity, up to approximately 10cm in maximum dimension, and more common angular grey sandstone cobbles and boulders of low sphericity, which reach almost 1m in maximum dimension (Fig. 3.07b). Small rounded pebbles of vein quartz are also present.

The red sandstone facies comprises lenticular bedded coarse-grained sandstones exhibiting trough cross lamination (Fig. 3.07a,c), or more rarely planar lamination (Fig. 3.07a). Bed bases are generally erosional, with beds pinching out laterally over 5-10m.
The contact between these two facies and the underlying grey sandstone and sandy mudstone facies is not exposed, being covered by scree consisting primarily of large boulders which have fractured and fallen from the conglomerate outcrop.

Non-mineralised fossils are found only in a limited number of beds in a single lens approximately halfway up the hillside (Fig. 3.04b-e), in the grey sandstone and sandy mudstone facies. These are generally found within the beds, exhibiting high relief and darkening of selected structures (Fig. 3.05b), though a smaller number of tiny specimens – up to about 20mm in diameter – occur on the top surface (in negative epirelief) of at least one bed (Fig. 3.06b,c). Mineralised fossils are not common at this locality, and are principally limited to trilobite fragments, though brachiopods, gastropods, and conularids were noted to occur stratigraphically below the non-mineralised fossil horizons by Van Roy (Van Roy, 2006a, p.26: his site E-1).

Strata forming the lower part of the stratigraphic succession at M001 (comprising the valley floor and the majority of the hillside) are consistent with an interpretation as low energy shelf sediments, with increasing energy and perhaps shallowing towards the top of the succession causing the deposition of coarser, better-sorted sand beds. The occurrence of rippled surfaces in the upper part of the succession may indicate shallowing to a position in the vicinity of fair weather wave base. The lenticular nature of the sand beds is consistent with an interpretation as storm deposits, with storms likely to have been the primary control on sedimentation. The diversity of ichnofossils is too low to be a reliable palaeobathymetric indicator, but the forms present are consistent with the *Cruziana* ichnofacies and a storm-dominated shelf setting.

The overlying red sandstone and conglomerate facies differ quite significantly from these underlying strata, with the red colour indicative of a terrestrial depositional environment. The trough cross-stratified coarse-grained sandstones and thick conglomeratic beds are typical of a braided fluvial system, with the sandstone facies representing deposition on a braid bar at the channel margins, and the conglomerates representing deposition in the central part of the main channel. The
lack of muddy facies representing overbank deposits may indicate the persistence of high energy conditions in this area, with any such deposits subsequently eroded.

The nature of the contact between the terrestrial and marine strata is uncertain. Due to the marked regressive nature of the palaeoenvironmental shift, a fully conformable contact can be ruled out; further, the strata in both units are devoid of any significant structural deformation of the kind normally associated with significant faulting, making a faulted contact (such as a low angle reverse or thrust fault) unlikely. An unconformable (or disconformable) contact is thus plausible. While much of the recent cover in southeastern Morocco is fluvial and resembles braided river sediments, consisting primarily of flash-flood or seasonal, intermittent, ephemeral river deposits, these are rarely – if ever – consolidated, and certainly not to the degree observed in this particular conglomerate, nor at this topographic elevation. While Carboniferous fluvial strata are known in Morocco, in the Tafilalt area fluvial deposits are generally limited to the Upper Second Bani Formation (Fig. 3.02), of which part (Unit 3 of Loi et al., 2010) is fluvio-glacial, representing the Hirnantian (uppermost Ordovician) glaciation in Gondwana. While no direct evidence for a glacial origin was observed in this conglomerate, such evidence can be rare and difficult to observe. Fluvial conglomeratic strata related to glacial episodes may result from rapid postglacial melting or the breaching of glacial lakes, with the water released eroding and later depositing sediments and clasts which never came under direct glacial influence. Although the Second Bani Formation does not appear on the geological map of the area (Fetah et al., 1986) (Fig. 3.03), this may be the most likely stratigraphic position of these conglomeratic and sandstone facies.

The stratigraphic position of the succession on the lower part of the hillside is also unclear from the geological map (Fetah et al., 1986), which does not distinguish between the Lower Ktaoua Formation and the Upper Tiouririne Formation in the area east of Erfoud (Fig. 3.03). The exposed strata could represent either the Upper Tiouririne Formation overlying the upper part of the Lower Ktaoua Formation, or the Middle Tiouririne Member of the Lower Ktaoua Formation overlying the lower part of the Lower Ktaoua Formation (Fig. 3.02). However, Loi et al. (2010) observed the fluvial conglomeratic part of the Upper Second Bani Formation to have a sharply erosional base, eroding the entire Lower Second Bani
Formation and the top of the Upper Ktaoua Formation in the Bou Ingarf area. Destombes et al. (1985, p. 201) noted that in the Tafilalt area, the Upper Ktaoua Formation is absent, or at least very thin, thus the erosional base of the Upper Second Bani Formation would be at or around the top of the Upper Tiouririne Formation. This suggests that the hillside perhaps represents the Upper Tiouririne Formation overlying the upper part of the Lower Ktaoua Formation (Fig. 3.04a-c). The alternative stratigraphic interpretation, placing the sandstones in the Middle Tiouririne Member of the Lower Ktaoua Formation, seems unlikely, as this would require the erosion of the upper part of the Lower Ktaoua Formation as well as the entire Upper Tiouririne Formation and any part of the Upper Ktaoua Formation present in the area prior to the deposition of the Upper Second Bani Formation. Such a stratigraphic assignment is consistent with the presence of the cord-like trace fossils, which have previously been noted to be limited to the uppermost Upper Tiouririne Formation in the Erfoud area (Spjeldnaes, pers. comm. to P. Van Roy, cited in Van Roy, 2006a).

Strata at M001 thus likely represent the upper part of the Lower Ktaoua Formation on the valley floor and at the base of the hill, conformably overlain by the Upper Tiouririne Formation, which is unconformably overlain by fluvial terrestrial deposits of the Upper Second Bani Formation. The non-mineralised fossils thus occur in the Upper Tiouririne Formation, of middle Katian age (around 450 Ma).

A sample of shale for geochemical analysis was collected some 500m SW of the fossiliferous beds at W004° 03’ 3.0” N31° 24’ 48.8” (Fig. 3.05d), with the shale estimated to be around 20m stratigraphically beneath the non-mineralised fossil horizon. The sample distance from the fossil site was solely due to the lack of shales in direct proximity to the fossiliferous beds. Regional scale folding is indicated by the change in bedding orientation between the shale and fossil localities, with bedding varying from 107/09°NE at the fossil site through 078/28°N at W004° 02’ 53.1” N31° 24’ 57.5”, 048/31°NW at W004° 02’ 55.0” N31° 24’ 56.3”, 042/29°NW at W004° 02’ 58.5” N31° 24’ 52.6”, and 179/03°W at W004° 03’ 0.4” N31° 24’ 50.7”, 90m from the shale sample site.
This site is located adjacent to a *piste* (desert off-road vehicular track) on a moderately steep south-facing slope, which forms part of a ridge of hills overlooking a wide plain, some 12km east of Erfoud (Fig. 3.08a-c). The hillside exposes a sequence of medium-bedded grey-brown weathering sandstones, interbedded with light grey mudstones, which are dipping at approximately the same angle (measured as 078/24°SE) as the slope of the hillside. Large bedding surfaces are thus intermittently exposed, with variations in the slope of the hillside leading to the outcrop of successive horizons. However, much of the hillside is covered by loose blocks and desert weathering products, limiting exposure.

A narrow trench has been dug for reasons unknown immediately adjacent to the M003 fossil site, thus exposing several metres of stratigraphy (Figs. 3.08d-e, 3.10). As observed in this trench, sandstone beds are generally thinner than at M001, reaching 22cm in thickness, but are more laterally extensive. Most beds are medium- or medium to coarse-grained medium grey-brown sandstones, but at least one horizon (Bed 6 of Fig. 3.08d-e) is microconglomeratic, with mud clasts up to 3cm in width, and clasts up to 1cm (Fig. 3.11b). Towards the bottom of the measured section, finer grained units are quite poorly sorted sandy mudstones, with thin coarser laminae, sedimentologically similar to those at M001. These units exhibit considerable distortion of depositional sedimentary structures and internal lamination. Near the top of the sequence, however, the finer-grained sediments interbedded with the sandstones are generally purer shales.

Parallel lamination is quite common in both sandstone and sandy mudstone beds, and several sandstone beds exhibit unidirectional cross-lamination or bed-surface ripples (Fig. 3.11d). Flute casts were also observed on the sole of at least one bed (Fig. 3.11c).

Most of the non-mineralised fossils from M003 were found in float; however, bed thicknesses and general sedimentology indicate that most, if not all, of
the fossils are from Bed 6 of the log in Fig. 3.08d-e. The vast majority of the fossils are found preserved within this unit, rather than on bedding surfaces. Where established, it appears that all the fossils have approximately the same orientation, with none known to be orientated upside down with respect to the remainder of the specimens. Fossils from this site often have darkened rust-coloured or dark grey surfaces (e.g. Fig. 3.09).

Ichnofossils are ubiquitous throughout the M003 sequence, with horizontal burrows observed on most sandstone bed surfaces. These can be up to 13mm in width, with some displaying a cord-like appearance (Fig. 3.11a-b). Vertical bioturbation is generally limited to the mudstone and sandy mudstone units, but one burrow was measured to reach a depth of 60cm, penetrating several sandstone beds. Skeletal fossils are also common in the vicinity of the non-mineralised fossil beds, including fragmentary trilobite material and disassociated crinoid ossicles. Bryozoans, ophiuroids, orthid brachiopods, plumulitid machaeridian sclerites, and an aglaspidid (Chlupacaris) are also known from the youngest exposed beds at M003, at the base of the hillside (Van Roy, 2005; 2006a; personal observations).

The precise stratigraphic position of the M003 succession is again ambiguous, plotting within an area on the geological map (Fetah et al., 1986) where the Lower Ktaoua Formation and Upper Tiouririne Formation are not distinguished, leaving positions within both the Middle Tiouririne Member of the Lower Ktaoua Formation and the Upper Tiouririne Formation possible. Previous authors (Le Menn and Spjeldnaes, 1996; Van Roy, 2005, 2006a) have assigned this locality to the Upper Tiouririne Formation, based in part on the occurrence of the cord-like horizontal trace fossils, which, as noted for M001, appear to be limited to the Upper Tiouririne Formation in the Erfoud area. The fossils from M003, like those from M001, thus appear to be of middle Katian age, approximately 450 Ma.

A shale sample for geochemical analysis was collected from Bed 9 of the log in Fig. 3.08d-e.
This site covers the summit of a mountain, known locally as Bou Nemrou, which forms part of a range of hills in the Oued Caïd Rami area, approximately 25km west of the town of Rissani (Fig. 3.12a). The hillside rises sharply on the western flank, exposing a cross-section through the Ordovician strata, but has a much gentler slope on the eastern side, similar to the bedding orientation (Fig. 3.12b-c). The summit forms a rising ridge running from southeast to northwest, with a 400m long plateau at around 1010m altitude to the southwest followed by a short dip, then a rise over a distance of approximately 500m to the zenith of the peak at just over 1055m altitude (Figs. 3.12b-c, 3.15). Bedding orientation shows considerable variation across the site, fluctuating from 045/30°SE to 166/17°E near the summit and from 040/10°SE to 145/15°NE on the plateau. The summit thus exposes beds stratigraphically lower than those on the plateau (Fig. 3.15). Variation in strike can likely be ascribed in part to shallow dips, and to minor faulting locally; however, variation in strike between the western and eastern flanks (Fig. 3.15) hints at the presence of a fault through the valley to the west. The generally steeper dips of strata on the summit, as compared to the plateau, indicates the occurrence of gentle, regional-scale folding (Fig. 3.15).

The section exposed along the steep western flank of Bou Nemrou shows the wider succession to consist of several thick sandstone beds, laterally continuous over >1km, interbedded with thinner sandstones and finer grained beds. These overlie a thick white-grey siltstone-shale unit with thin subordinate fine sandstone horizons, which comprises the base of the topography. On the plateau and the summit, the sedimentology of the upper part of this succession is well exposed in a network of trenches constructed by local fossil collectors excavating mineralised fossils – principally trilobites – from this locality for commercial purposes (e.g. Fig. 3.12d-e). These trenches were mapped (Fig. 3.14), and logged at centimetre-scale, with logs of eight of these trenches (numbered 49, 46, 24, 22-23, 16, 8 and 42, from oldest to youngest, supplemented by logging of surface exposure on the western edge of the plateau between trenches 23 and 16/17), presented as a composite stratigraphic
section in Fig. 3.16 (see also Fig. 3.17), though a lack of trenches in certain areas, compounded by a lack of surface exposure (principally due to a high degree of desert weathering) has left a number gaps in the sequence.

The M005 succession consists largely of medium-bedded laterally persistent sandstones interbedded with poorly sorted sandy mudstones, which are often strongly oxidised and display a reddish colour in the top 2cm, principally due to shallow bioturbation. At the lowest logged parts of the sequence, the sandstone beds are up to 30cm in thickness, with grain size approximately reflecting the thickness of the beds. The thickest beds are very rich in quartz, and are often coarse- to very coarse-grained, even granular in places, with some beds containing quartz grains up to 6mm. These often have a dark red-brown colour on fresh surfaces, sometimes alternating with a light green-grey colour, and are generally internally structureless. Medium- and fine-grained sandstones are also present, often exhibiting parallel or cross-lamination; these beds are generally light green-grey in colour, although some lack the greenish tinge. The sandstone beds are interbedded with poorly sorted medium grey sandy or silty mudstones, which weather pale grey.

Higher in the succession, sandstone units become much thicker, with apparently internally structureless coarse-grained beds exceeding 1m in thickness, and parallel or cross laminated beds commonly reaching 0.7m-1m (Figs. 3.12d-e, 3.16, 3.17). Strong parallel lamination is particularly common in these younger sandstones, and is usually defined by very thin fine-grained red-brown micaceous laminae separating light greyish-green quartz-rich bands, with primary current lineation visible on exposed bed surfaces. Cross-lamination and hummocky cross stratification also occur in a small number of beds. Primary current lineation and cross-bedding indicates a palaeoflow in a NW-SE direction. These sandstones are similarly interbedded with sandy or silty mudstones, which in places (particular in the thick sandy mudstone unit in trench 24; Figs. 3.16, 3.17b) contain thin sandstone laminae.

In terms of the preservation of non-mineralised fossils, M005 is the most extensive site yet explored, with specimens occurring extensively throughout several tens of metres of stratigraphy (Fig. 3.16), and over 1km+ laterally. Fossils are found
in almost all trenches on the summit and the plateau; a single specimen has also been identified in surface exposure some 500m SW of the plateau (Fig. 3.13b-c, locality 50 in Fig. 3.15), on the western slope of Bou Nemrou. These non-mineralised fossils are generally preserved on bed surfaces in positive hyporelief/negative epirelief (e.g. Fig. 3.13a), although some are also known preserved in negative hyporelief/positive epirelief, and in endorelief within sandstone beds. Most show little or no relief, and little difference in colour from the enclosing sediment. Specimens from the lowermost parts of the stratigraphic section (preserved in coarser sandstones) are generally preserved within beds, and usually show greater relief than those from the younger units at M005, although not approaching the relief of the specimens from either M001 or M003.

In addition to the non-mineralised fossils, skeletal fossils occur ubiquitously, and are often extremely well preserved (Fig. 3.15). The biota includes complete echinoderms including eocrinoids (*Ascocystites*), crinoids, mitrate stylophorans (including *Anatifopsis, Aspidocarpus, Eumitrocystella*), ophiuroids, and edrioasteroids; conulariids; trilobites, including *Selenopeltis, Placoparia, Basilicus, Uralichus* and rarer illaenids, dalmanitids, calymenids and harpetids; arthropods, including the cheloniellid *Duslia* and eurypterids; along with more fragmentary material, including plumulitid machaeridian sclerites (Van Roy, 2006a; Bruton, 2008; Hunter et al., 2010, personal observations).

Ichnofossils are also common, with the bases of sandstone beds often highly irregular due to the presence of multiple shallow burrows. Both horizontal and vertical bioturbation are present, particularly in the sandy mudstone facies, which are commonly highly bioturbated. Individual vertical burrows were observed to reach a depth of 10cm. Identifiable forms include extremely common simple meandering burrows on sandstone bed soles which likely represent *Planolites*, U-shaped burrows likely ascribable to *Arenicola*, as well as a variety of rarer trilobite cubichnia and repichnia trace fossils including *Cruziana, Rusophycus*, and *Diplichnites*.

This ichnofossil assemblage is typical of the *Cruziana* ichnofacies, indicative of an offshore shelf setting below fair weather wave base. This is further supported by the occurrence of hummocky cross-stratification. The presence of ripple cross
lamination may indicate a position in the vicinity of fair weather wave base; however, such ripples commonly occur at the top of thick parallel-laminated beds exhibiting primary current lineation, and are thus likely to represent current rather than wave ripples in most cases. Parallel-laminated beds such as these may also be deposited by storm-generated geostrophic currents. The thickness of such units, as well as the presence of extremely thickly bedded massive sandstones indicates rapid sedimentation, and suggests proximity to a major terrestrial sediment supply. The presence of delicate mineralised fossils, including articulated crinoids with stem, calyx, and brachials, also suggests a storm-dominated environment beneath fair weather wave base, indicating both rapid burial and a low energy environment between sedimentation events. However, the metre-thick massive sandstone beds, which are observed in some cases to be laterally continuous over hundreds of metres, would be atypical for tempestite deposits. While no grading is evident, a proximal turbidite origin could be considered for these beds.

According to Fetah et al. (1986), the shales and siltstones on the valley floor form part of the Tachilla Formation, with the overlying sandstones assigned to the First Bani Group (the constituent formations of which cannot be distinguished in the broader Tafilalt area; Fig. 3.02). This is consistent with the geology and sedimentology of the area. Previous authors (B. Lefevbre in Van Roy, 2006a; Hunter et al., 2010) have noted that the echinoderm biota is indicative of an earliest Sandbian age (previously earliest Caradoc), thus assigning the site to the Izegguirene Formation, which is the only part of the First Bani Group younger than the Darwillian (Fig. 3.02). This more precise stratigraphic assignment is not followed here as the formations of the First Bani Group cannot be differentiated in the area on lithological grounds, and biostratigraphical definition of formations runs contrary to accepted standard stratigraphic practice. The non-mineralised specimens collected from M005 are therefore considered to be from the earliest Sandbian part of the First Bani Group, around 460 Ma.
M008

Figs. 3.18-3.19

W 004° 30’ 58.5” N 31° 18’ 35.7” (±2.5m)

This site occurs on the southwest facing slope of a ridge of hills some 2km southeast of M005, on the edge of a broad, shallow, northwest to southeast oriented valley, approximately 24km west of Rissani (Fig. 3.18a-c). Bedding orientation varies considerably over the area, with localised folding observed over tens of metres, but the prevailing orientation is striking roughly parallel to the ridge, at around 140, and dipping to the southwest at around 25°. The dip is slightly steeper than the slope of the hill, such that the exposed beds young to the southwest, away from the crest of the ridge.

Lithologically, the M008 section is similar to that at M005, with large, thick sandstone beds interbedded with medium-bedded parallel- and cross-laminated sandstones and sandy mudstones, with minor shales (Fig. 3.18d,e). The ridge is capped by thick coarse-grained sandstone beds, including both massive and parallel laminated units, with subordinate hummocky cross lamination and flaser bedding present. The majority of the hillside comprises very thin- to thin-bedded parallel laminated or more rarely ripple or hummocky cross laminated medium-grained sandstones, interbedded with sandy mudstones and minor shales, with occasional thick parallel-laminated or structureless sandstones (Figs. 3.18d-e, 3.19a). The youngest part of the section (at the base of the hillside and on the valley floor, where exposed) consists primarily of sandy mudstones and shales with only minor interbedded sandstones. As at M005, local fossil collectors have constructed trenches for the purposes of collecting mineralised specimens (Fig. 3.19a); however, these are all shallow, less than 1m in depth, and are not as extensive as those at M005.

Non-mineralised fossils occur over a broad area on the hillside, generally within thinly bedded parallel laminated sandstones, and are not limited to a single stratigraphic horizon. These are generally preserved as negative epirelief moulds on bed top surfaces, with corresponding positive hyporelief casts on the soles of
overlying beds, but some specimens are also known preserved within sandstone beds, or as reflective films without relief on bed surfaces.

Skeletal fossils are not as common at M008 as at M005, and include principally trilobites and cheloniellids, with some crinoids and mitrate stylophorans. Ichnofossils are also rarer, but include U-shaped burrows (*Arenicolites*) in the tops of thick sandstone beds, a structure not seen at any other locality.

Although U-shaped burrows are most associated with the shallow marine *Skolithos* ichnofacies, such ichnofossils are also common in storm-deposited sandstone beds, reflecting opportunistic colonisation. This, along with the sedimentological similarity to M005, suggests that the M008 strata similarly represent a storm-dominated shelf environment below fair weather wave base.

Approximately 600m to the southwest of M008 (W004° 30' 37.3" N31° 18' 24.0" ±3m), non-mineralised fossils were also found in a 40cm-thick parallel-laminated sandstone bed (Fig. 3.19b), which is both underlain and overlain by extremely thick generally structureless coarse sandstone beds. Large sinuous load-casting sole structures are also evident at this locality (Fig. 3.19c), consistent with rapid event sedimentation. This locality is included in M008, rather than assigning a separate locality number, due to the proximity, the sedimentological equivalence, and the low number and poor quality of non-mineralised specimens discovered at the site, none of which were collected.

According to Fetah *et al*. (1986), M008 lies within the Lower Ktaoua Formation. However, the lithological similarity to M005, particularly with regards to the presence of thick, apparently structureless sandstone beds, suggests instead that the fossiliferous section at M008 also probably lies within the First Bani Group. It is likely that M008 represents the top of the First Bani Group, with the mud-dominated sediments at the base of the hillside and on the valley floor comprising the basal part of the predominantly argillaceous Lower Ktaoua Group (Fig. 3.18a-c). Fossils from this locality are thus of early Sandbian age, around 460 Ma.
Differential taphonomy of Palaeozoic and Ediacaran non-mineralised fossils

M009

Figs. 3.20-3.21

W 004° 29’ 58.0”  N 31° 18’ 23.5”  (±3m)

This site is located approximately 2km southeast of M008, along the same ridge, approximately 22km west of Rissani (Fig. 3.20a). As at M005, local fossil collectors have dug a network of trenches on a shallow slope towards the bottom of the hill; most of these are, as yet, quite shallow and surficial, but one trench exposes just over 2m of stratigraphy (Figs. 3.20b-c, 3.21). The exposed section is sedimentologically similar to M005, but with interbedded shales, rather than sandy mudstones. Parallel- and cross-lamination is common, though some sandstone beds are internally structureless.

Non-mineralised fossils at M009 are known from at least three levels, all medium to coarse-grained parallel-laminated sandstones. Skeletal fossils at this locality are generally limited to trilobites and the cheloniellid Duslia.

As with M008, this site plots on the geological map of Fetah et al. (1986) within the Lower Ktaoua Formation, but the sedimentological similarity to M005 strongly suggests that it lies instead within the First Bani Group. It is thus likely to lie within the lowermost Sandbian, of age approximately 460 Ma.

M010

Figs. 3.22-3.23

W 004° 29’ 34.4”  N 31° 18’ 21.8”  (±4m)

This site occurs on a small plateau near the summit of a hill in the middle of the valley demarcated on one side by the ridge on which sites M008 and M009 are located, lying approximately 1.5km southeast of M009, approximately 21km west of Rissani (Figs. 3.22a, 3.23). While most of the exposure in the valley is dominated by fine-grained sediments, a greater proportion of sandstone beds, including some medium-bedded coarse-grained units, are exposed on this hill, and are likely responsible for the greater topographic relief. This site has not been exploited by
local collectors, and exposure of the stratigraphy is thus limited to heavily weathered surficial outcrop. The sedimentology of M010 is thus more poorly known than at other nearby localities.

Non-mineralised fossils were recovered from a single coarse-grained brownish-grey sandstone bed 24cm thick (Fig. 3.22b-d), along with fragmentary trilobite material. No additional fossils were recovered.

According to Fetah et al. (1986), this locality lies within the upper part of the Lower Ktaoua Formation. The site is undoubtedly higher in the stratigraphy than M008 and M009, though the lack of exposure on the plain and unknown thickness of the Lower Ktaoua Formation in the area makes the precise stratigraphic distance between these sites and M010 uncertain. While a position within the Upper Tiouririne Formation is possible, despite the inaccuracies in the geological map, there is no clear reason to contradict the placement of this site within the Lower Ktaoua Formation, likely within the Middle Tiouririne Member.

M012

Figs. 3.24-3.25

W 4° 31’ 34.3” N 31° 20’ 22.0” (±5m)

This site, some 1.5km north of M005 and 25km west of Rissani (Fig. 3.24a), was visited only briefly in 2006, at which stage only skeletal fossils, principally a diverse echinoderm biota, were known from the area. Since then, local collectors, who have again dug trenches in the area to collect mineralised fossils (Fig. 3.25), found a solitary non-mineralised specimen in float in the vicinity of the echinoderm beds. Echinoderms from the locality include the cystoid rhombiferan Homocystites, Dendrocystites–like solutes, and the mitrate Eumistrocystella; trilobites are also known, including Mucronaspis (Hunter et al., 2010).

Sedimentologically, the section is similar to M005, with medium to coarse-grained parallel-laminated sandstone beds up to 20cm thick, separated by thick sandy mudstone layers (Fig. 3.24b-c). According to Fetah et al. (1986), this site is
within the lower Lower Ktaoua Formation, while Hunter et al. (2010) assigned the site to the uppermost Lower Ktaoua Formation or lowermost Upper Tiouririne Formation. The sedimentology, however, suggests a position within the First Bani Group, of Darwillian or Sandbian age.

M020

Fig. 3.26

Several non-mineralised specimens (e.g. Fig. 3.26) have also been recovered by local fossil collectors from the Alnif area. This locality is reportedly remote and extremely inaccessible, and was not visited. While the stratigraphic position of this locality is unknown, the sediment in which the specimens are found, a reddish coarse-grained sandstone with no internal structure, strongly resembles that from the oldest exposed beds at M005 (trenches 45–49 of Fig. 3.15).

3.1.2 United States of America

Ordovician sediments in the vicinity of Troy, New York, USA, are generally deep marine shales and turbiditic sandstones and greywackes (Plesch, 1994; Kidd et al., 1995). However, Troy lies immediately beside a major thrust fault of the Champlain Thrust System, an Acadian Orogeny fault which juxtaposed the Ordovician and (formerly underlying) Cambrian sediments (Fig. 3.27). Tectonic deformation in the vicinity of this fault is extreme, and the Ordovician strata near Troy are best described as a melange, with blocks of allochthonous sandstone interspersed within fine-grained siltstones and mudstones (termed the Troy Frontal Zone, or TFZ, by Plesch, 1994). Due to the deformation, a more precise age determination is not possible.
Discophyllum peltatum was originally described by Hall (1847) from two specimens, discovered in Ordovician sediments at Troy. The fossil locality was given by Hall (1847, p. 277) as:

“near the nail factory, below Troy”.

The nail factory at Troy no longer exists, but was located on historical maps of the area (Fig. 3.28) with assistance from Ed Landing and Linda VanAller Hernick of the New York State Museum, and the locality was briefly visited (Fig. 3.29) prior to the rediscovery of the specimens. The river to which the nail factory was adjacent has changed course, cutting out a meander loop, and the area is now densely wooded and overgrown, with little exposure. Nonetheless, the foundations of the nail factory were located immediately adjacent to the present-day river, along with limited outcrop of some allochthonous fine-grained sandstone blocks within shales (Fig. 3.30). While subsequent examination of the specimens revealed that they are preserved in fine-grained silty mudstones, as the only outcrop of sandstone beds in the vicinity, this was at the time thought likely to have been the original locality from which the specimens of D. peltatum were recovered. Samples of this medium grey sandstone, which varies from medium-grained parallel-laminated to coarse-grained and internally structureless, were collected and examined for fossils, but none were found.

3.2 Geological context of additional fossil material

Previously described or collected fossils, from sites where fieldwork proved impossible due to temporal, logistical and financial constraints, were also examined in the collections of various museums. These were:

- Paropsonema cryptophya from the Upper Devonian of New York;
- Paropsonema mirabile (originally described as Discophyllum mirabile) from the Silurian of Australia;
- a specimen previously described as Pseudodiscophyllum windermereensis (here reassigned to Discophyllum peltatum) from the Silurian of England;
• previously undescribed remains from the Ordovician of Ireland;
and
• *Eldonia ludwigi* from the Cambrian of Canada.

The stratigraphic and sedimentological context of these specimens (based on a review of the available literature) are described below. Due to the historical nature of the original descriptions of *Paropsonema cryptophya*, *Paropsonema mirabile*, and *Eldonia ludwigi*, a brief history of the stratigraphical frameworks of their localities is also given, for ease of reference to older publications.

### 3.2.1 United States of America

The Upper Devonian of New York, USA (Fig. 3.31a) is a well exposed predominantly siliciclastic sequence of westwardly prograding shallower sandstone facies interrupted by transgressive black shales, termed the Catskill Delta (Rickard, 1964; Kirchgasser, 1975; L.V. Rickard, 1975; McGhee and Sutton, 1983; Woodrow and Sevon, 1985; Woodrow *et al*., 1988; House and Kirchgasser, 1993; Kirchgasser, 2000; House and Kirchgasser, 2008). The history of the stratigraphic divisions of the Devonian of New York has been somewhat complex, with the original framework of Hall (1840) based significantly on distinguishing the eastern “Chemung Fauna” and “Ithaca Fauna” from the more westerly “Portage Fauna” (later referred to by Clarke (1898) as the “Naples Fauna”). This failed to account for the lateral facies changes, and resultingly, was gradually dismantled over the following hundred years, with the seminal paper “Chemung is Portage” by Chadwick (1935a) crystallising recognition of the facies problem in New York (House and Kirchgasser, 1993). The stratigraphic framework of the succession was subsequently rebuilt around the transgressive black shales as marker horizons, with correlation of the New York sequence to standard conodont and ammonoid biozones firmly establishing a biostratigraphic framework and age range for the succession (Rickard, 1964; Kirchgasser, 1975; L.V. Rickard, 1975; House and Kirchgasser, 1993; Kirchgasser, 2000; House and Kirchgasser, 2008) (Fig. 3.32).
The first specimens of *Paropsonema cryptophya* were recorded by Clarke (1900) as having been recovered by D. Dana Luther in 1895 and 1897 from the ‘Portage Sandstone’ at Tannery Gully, just south of Naples, New York (Fig. 3.31b). Further specimens were noted by Ruedemann (1916) to have been subsequently recovered from the same horizon at West Hill near Naples (Fig. 3.31b) and ‘Johnson’s Glen’ further north at Canandaigua Lake (though no reference to a ‘Johnson’s Glen’ in this vicinity has been found on contemporaneous maps). The term ‘Portage Sandstone’ is ambiguous, having varied considerably in usage in New York stratigraphy since it was introduced by Hall (1840), referring alternatively to the ‘Portage Group’ (e.g. Clarke, 1897), or the ‘Portage Sandstone’ within this group (e.g. Merrill, 1898), which also originally included the Cashaqua Shale, Gardeau Shale and Sandstone, and Naples beds (Sutton, 1960). Subsequent to Clarke’s description of *Paropsonema*, Luther (1902) recognized that the Gardeau was not a contiguous unit and Luther (1903), Clarke (1904) and Clarke and Luther (1904) completely revised the stratigraphy accordingly, establishing in its place the Rhinestreet Shale, Hatch Shale, and Grimes Siltstone, with the Middlesex Shale underlying the Cashaqua Shale. Clarke and Luther (1904) referred to the Middlesex, Cashaqua, Rhinestreet, and Hatch formations as the ‘Portage beds’, based on faunal similarity. Chadwick (1935a, b) later formalized this definition of the ‘Portage beds’ as the Naples Group, which was retained in the synthesis of Sutton (1960), but which has since been abandoned, with the Middlesex and Cashaqua formations (and equivalents) now included in the Sonyea Group, and the Rhinestreet Shale, Hatch Shale, and Grimes Siltstone formations forming the lower part of the West Falls Group (e.g. Rickard, 1964; Kirchgasser, 1975; L.V. Rickard, 1975; McGhee and Sutton, 1983; Woodrow *et al.*, 1988; House and Kirchgasser, 2008).

Clarke (1900)’s original reference to the ‘Portage Sandstone’ as the source for *Paropsonema cryptophya* was thus unclear. Consequently Friend (1995), who briefly considered *Paropsonema* in a thesis focused on the eldoniids, mistook the stratigraphic position of the *Paropsonema* specimens, incorrectly ascribing them to the Ithaca Formation (Genesee Group), which is exposed around Canandaigua Lake, although not near the locality at the Tannery Gully, Naples (Fig. 3.31b). Friend (1995) believed that this interpretation was supported by two more recently
discovered specimen of *Paropsonema cryptophya*: USNM 62948, reported to have been recovered from the ‘Chemung Formation’ (Genesee Group) under Cornell University Library at Ithaca, New York, and PRI 42122, found in float in a field in Freeville, 8km from Ithaca, near exposure of the Genesee Group. However, Friend (1995) also noted that contradictory locality information placed USNM 62948 as having been recovered from the Nunda Formation (upper West Falls Group) at Morgan Creek, west of Lindley, near Corning, south-western New York (Fig. 3.31a), and that the West Falls Group is also exposed in the vicinity of Freeville, compromising the stratigraphic utility of these specimens.

In two papers subsequent to the original description of *Paropsonema cryptophya*, Clarke (1903) and Clarke and Luther (1904) noted that the worm-like fossil *Protonympha* (see also Conway Morris and Grazhdankin, 2005) co-occurred with *Paropsonema cryptophya* in the Tannery Gully. They ascribed these fossils first to the Hatch Sandstone Formation (Clarke, 1903) and subsequently to the immediately overlying Grimes Siltstone Formation (Clarke and Luther, 1904, pp. 35 and 63) (see Fig. 3.32), noting that the fauna of the Grimes Formation appeared to represent a westward encroachment of the eastern “Ithaca Fauna” (which may be notable in the context of potential *Paropsonema* specimens from the Ithaca area).

While both the Hatch and Grimes formations have been bereft of attention, in terms of both paleontology and stratigraphy, in recent decades, both are known to intergrade with the Rhinestreet Shale Formation (Sutton, 1960; House and Kirchgasser, 1993, 2008) (Fig. 3.32), and are currently believed to represent a lateral equivalent of the upper Rhinestreet Shale, lying within the *Palmatolespis bassi* standard conodont biozone (Conway Morris and Grazhdankin, 2005; W. T. Kirchgasser, pers. comm. 2010), the Montagne Noir conodont biozone 7 and the UD I-G (*Mesobeloceras*) standard ammonoid biozone (W.T. Kirchgasser, pers. comm. 2010), approximately 380 Ma according to the most recent Devonian timescale (House and Kirchgasser, 2004) (Fig. 3.32).

The Grimes Formation was described by Clarke and Luther (1904, p.34) as consisting of:
“compact or laminated, light bluish grey sandstones, in layers 3 inches to 4 feet thick, separated by hard, blue grey shales”.

Little has been added to this description in the past century. The samples containing *Parapsonema cryptophya* are uniformly light grey massive, laminated, or cross-laminated siltstones, which appears to accord with Clarke and Luther (1904)’s description. Notwithstanding the ambiguous (yet likely different) stratigraphic position of specimens USNM 62948 and PRI 42122, and the uncertain stratigraphic proximity of *Parapsonema cryptophya* to *Protonympha*, the Grimes Siltstone Formation is herein accepted as the stratigraphic position of the New York State Museum collection of *Parapsonema cryptophya*. The cross-laminated nature of the samples could indicate a shallow marine environment in the vicinity of wave base; however, the fine grain size may suggest instead a deeper setting, with the siltstone layers deposited by low density turbidity or contour currents. The occurrence of this formation on top of the Hatch and Rhinestreet formations, which include significant amounts of organic-rich black shale interpreted as having been deposited in a deep marine anoxic environment (e.g. Sutton, 1960) clearly supports the latter, deeper, palaeoenvironmental interpretation.

### 3.2.2 Australia

The Melbourne Trough is a fault-bounded triangular basin, widening towards the southern coast of the State of Victoria in south-eastern Australia (Fig. 3.33). The sedimentary fill of the basin consists primarily of Middle to Upper Silurian and Lower Devonian deep-marine pelagic mudstones and turbiditic siltstones and sandstones, deposited off the eastern shore of Gondwana onto a Cambrian-Ordovician basement deformed during the early Silurian Benambran Orogeny (Edwards *et al.*, 1998).

The first non-mineralised specimen found was originally described by Chapman (1926b), who noted that it had been recovered from a clay pit belonging to the Hoffman Patent Brick & Tile Company in Brunswick, north of Melbourne. These clay pits exposed at their base strata now assigned to the Melbourne
Formation (see Melbourne 1:63,360 and 1:31,680 geological maps: Geological Survey of Victoria, 1959; 1974). Additional specimens have subsequently been collected from the Dargile Formation near Panton Hill, north-east of Melbourne (Yan Yean 1:63,360 geological map: Geological Survey of Victoria, 1981), and the Hylands Member of the McIvor Formation (previously included in the Clonbinane Sandstone Member of the Humevale Formation) near Clonbinane, north of Melbourne (Kinglake 1:63,360 geological map: Geological Survey of Victoria, 1977).

Due to lithological similarities, the relationship between the Dargile and adjacent formations has been subject to several revisions, and also some controversy. This study is concentrated on a particular group of fossils, and as such, makes no inference regarding the preferred regional stratigraphic organisation. For the sake of simplicity, the use of stratigraphic names in subsequent chapters follows the widely-used scheme of Edwards et al. (1998), unless otherwise stated (Fig. 3.34). However, a brief summary of the various stratigraphic schemes is provided below, for ease of reference to publications.

The Dargile Formation, first described by Thomas (1937) as the “Dargile Beds”, conformably overlies the turbiditic Wapentake Formation. Thomas (1937) subdivided the formation into four units, based on their lithology and fossil content (Edwards et al., 1998):

<table>
<thead>
<tr>
<th>Dargile Formation</th>
<th>4</th>
<th>Encrinurus/Chonetes beds</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>3</td>
<td>Conglomerate and sandstone member</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>Graptolite beds</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>Lower mudstone member</td>
</tr>
</tbody>
</table>

VandenBerg (1971, 1973) excluded the mudstone (unit 1) from the Dargile Formation, and later reassigned rocks in the Melbourne area mapped as the Dargile Formation to the Melbourne Formation (VandenBerg, 1988), which conformably overlies the Anderson Creek Formation. Edwards et al. (1998) subsequently redefined the Dargile Formation in the Heathcote area north of Melbourne to
include only units 1 and 2 of Thomas (1937), assigning units 3 and 4 to the Hylands Member of the (conformably) overlying McIvor Sandstone. The Hylands Member was believed by Edwards et al. (1998) to be laterally equivalent to the Clonbinane Member of the Humevale Formation in the Kinglake area, which had previously been mapped as conformably overlying the Dargile and Melbourne formations (1977).

Based on palaeontological information, Rickards and Sandford (1998) identified a number of apparent stratigraphical inconsistencies, and proposed a sweeping reorganisation of the Silurian stratigraphy of the Melbourne Trough. As part of this, they abolished the Dargile Formation, assigning the strata to the Yan Yean Formation and overlying Melbourne Formation, placing these along with the underlying Anderson Creek, Bylands, Wapentake, and Costerfield formations in the Dargile Group (Fig. 3.34). However, VandenBerg (1999) disputed this reorganisation, citing biostratigraphical definitions of formations (contrary to standard practice) amongst other factors (but see Sandford and Rickards, 1999), and this revised stratigraphy has not been widely accepted (e.g. C.M. Powell et al., 2003; Cayley et al., 2008), with the stratigraphy established by Edwards et al. (1998) for the Heathcote area remaining in widespread usage beyond the study area of that work.

The mudstone-dominated Dargile Formation was interpreted by VandenBerg (1988) as a deep marine deposit, with hemipelagic mudstones interbedded with siltstones representing mass flows, and conglomerates representing debris flows. Sandstone beds within the formation were interpreted as bottom-current reworked sediments. This interpretation has generally been accepted by subsequent workers (e.g. Edwards et al., 1998; Cayley et al., 2008). The overlying Hylands Member of the McIvor Sandstone was interpreted by Edwards et al. (1998) as a storm-influenced turbiditic succession. Graptolites and other fossils indicate a Gorstian (early Ludlow) age (around 422 Ma) for the Dargile Formation, and a Ludfordian (late Ludlow) age (around 420 Ma) for the Hylands Member of the McIvor Sandstone Formation, with the Melbourne Formation straddling the boundary between these two stages (Fig. 3.34) (Edwards et al., 1998; Rickards and Sandford, 1998; Cayley et al., 2008).
3.2.3 England

The Upper Ordovician to Silurian Windermere Supergroup represents a post-volcanic succession deposited in a foreland basin likely formed by flexure resulting from the southwards progression of Laurentia ahead of the collision with Avalonia (Kneller, 1991; Kneller et al., 1993; Kneller et al., 1994; Barnes et al., 2006). The Bannisdale Formation, from which a single non-mineralised specimen was found in float near the margin of Elleray Wood in Windermere (Fryer and Stanley, 2004), lies at the base of the Kendal Group, the uppermost part of the Windermere Supergroup (Fig. 3.35), and is characterised by thin beds of siltstone or fine sandstone grading upwards to mudstone, interpreted as the deposits of dilute, deep marine, distal turbidity currents (King, 1992). Increased bioturbation is noted towards the top of the formation, approaching the transition into the overlying shallow marine Kirby Moor Formation (King, 1994).

The overall thickness of the formation is difficult to determine, due both to the complexity of deformation and the uniform nature of the lithology, which makes mapping marker horizons difficult (Barnes et al., 2006). This, allied with the fact that the single non-mineralised fossil specimen was collected in float, makes determining the precise stratigraphic position impossible.

Fossils of any kind are not common in the Bannisdale Formation, especially in the western part of the outcrop (Fryer and Stanley, 2004), with Kneller et al. (1994) reporting only brachiopods. Farther east, brachiopods are also associated with nautiloids, trilobite fragments (Fryer and Stanley, 2004), and graptolites which place the formation in the *Saetograptus leintwardinensis* biozone (Barnes et al., 2006) at the base of the Ludfordian (middle Ludlow); around 421 Ma, according to the most recent Silurian time scale (Melchin et al., 2004).

3.2.4 Ireland

The Bardahessiagh Formation of County Tyrone, Ireland, forms part of an Ordovician transgressive sedimentary sequence on the Laurentian margin of Iapetus,
which unconformably overlies the Tyrone Ophiolite, obducted during the Grampian Orogeny (Hutton et al., 1985; Candela, 2006; Graham, 2009). Cephalopods (Evans, 1994), corals (Scrutton et al., 1998) and brachiopods (Candela, 2001, 2002, 2006) have been described from the formation, and biostratigraphic control indicates that the top of the formation (Member III of Candela, 2002, 2006) straddles the boundary of the Burrellian Stage (Longvillian Substage) and Cheneyan Stage (Woolstonian Substage) of the Caradoc Series (Candela, 2002, 2006) according to the British Ordovician timescale (Fortey et al., 1995). This corresponds with the uppermost Sandbian and lowermost Katian (Sa2 and Ka1 stage slices) according to the new standard global Ordovician timescale (Gradstein et al., 2004; Bergström et al., 2009), around 455 Ma.

Several non-mineralised discoidal specimens were recovered from a temporary trench dug by the Ulster Museum in September 1992, located at 006° 52’ 41” W  54° 36’ 16” N. This site was located some 10m south from an infilled quarry, approximately 650m SSW of Craigbardahessiagh summit, near the town of Pomeroy in Co. Tyrone (Fig. 3.36). The trench exposed the top of the Bardahessiagh Formation (Member III). The non-mineralised specimens are preserved in a 50 x 40cm recovered block of medium-grained sandstone. The bed, a micaceous quartz arenite with minor chlorite and abundant iron oxides (haematite), is densely packed with skeletal remains, and several delicate fossils (e.g. asteroids, mitrate stylophorans) in the bed are preserved largely intact, although the original calcite or aragonite is often significantly or completely degraded, leaving excellent mouldic preservation. Articulation of shells is common; however, orientation is random, and no sorting is apparent. No trace fossils or evidence of bioturbation were observed in the sample, nor were any sedimentary structures. The way up of the block was unfortunately not recorded, and is unknown.

Due to the nature of the material, being loose and out of context, only a limited interpretation of the sedimentology is possible. Scrutton et al. (1998) and Candela (2006) reported that trilobite and brachiopod assemblages indicated a mid-shelf shallow water setting for most of the Bardahessiagh Formation, with differing brachiopod faunal associations and the sequential appearance of particular trilobite taxa indicating deposition in progressively deeper water. Assemblages from the top
of the formation were regarded as indicative of an upper slope setting. The articulated nature of the bivalved fossils, the lack of sorting of skeletal remains, and the undamaged detailed preservation of some extremely delicate mineralized fossils, as well as the soft-bodied remains, is indicative of fairly minimal transport distances and relatively rapid burial. This is consistent with a storm deposit interpretation, although Scrutton et al. (1998) favoured a turbiditic origin. The orientation of the non-mineralised discs subparallel to the bedding surfaces suggests that the transporting current was of low density, and that some degree of settling occurred.

3.2.5 Canada

The Burgess Shale, popularised by Stephen Jay Gould's 1989 book *Wonderful Life*, is probably the most famous and iconic fossil site in the world. Part of a Cambrian passive-margin sequence from the western margin of Laurentia, it is located on Mount Field (116° 28' W  51° 26' N) in the Canadian Rocky Mountains, in the vicinity of the town of Field, in British Columbia, Canada, near the border with Alberta (Fig. 3.37). The exceptional fossil preservation was discovered by Walcott in 1909 (Gould, 1989; Briggs et al., 1994), who had already begun to erect the regional stratigraphy (Walcott, 1908), establishing the Cathedral Formation for a platform carbonate sequence, and the Stephen Formation for the overlying shales. Walcott (1911) also coined the term “Burgess Shale” as a geographical name for the fossiliferous beds, but included them within the Stephen Formation, a stratigraphic model that was followed for decades.

Further investigations of the sedimentology and palaeoecology of the Burgess Shale, however, have revealed the stratigraphy to be much more complex than originally described. In particular, Walcott failed to recognise an abrupt lateral change in facies, and large thickness variations in his lithostratigraphic units, which were first recognised by Rasetti (1951) and Ney (1954), and brought to wider attention by Aitken and Fritz (1968) and Fritz (1971). These authors observed that the thick platform carbonates assigned to the Cathedral Formation (as defined by Walcott, 1908) were sharply juxtaposed with the ‘Stephen Formation’ shales along a near-vertical boundary, which was not tectonic in nature (Ney, 1954, p. 123-124):
"a striking change occurs at the top of the Cathedral Formation. Here there is a steep west-facing precipice of dolomite nearly 400 ft high, against which shales on the west terminate abruptly...it seems to be an original feature of deposition...".

To the western side of this near-vertical boundary, the Cathedral Formation limestones are thick, and topped by a thin shale; to the east, a thin limestone unit is topped by a thick shale sequence. Fritz (1971) retained Walcott (1908)'s lithostratigraphic names, but differentiated the facies by referring to the ‘thick Cathedral Formation’ overlain by the ‘thin Stephen Formation’, and the ‘thin Cathedral Formation’ overlain by the ‘thick Stephen Formation’ (thus many publications relating to the Burgess Shale describe the fossils as occurring within the ‘thick Stephen Formation’). The near vertical boundary between the juxtaposed facies was interpreted as an ancient submarine cliff, up to 250m in height, termed the ‘Cathedral Escarpment’ (Fig. 3.38a). Originally thought to be simply a result of vertical accretion of the carbonate reef facies (Aitken, 1971), the vertical nature of the escarpment is now thought to have resulted from marginal collapse (Stewart, 1991).

The concept of the ‘Cathedral Escarpment’ has vastly increased the palaeoecological and palaeoenvironmental understanding of the Burgess Shale and surrounding facies (e.g. Fletcher and Collins, 1998; Caron and Jackson, 2006, 2008; Collom et al., 2009) (Fig. 3.38b). Cambrian-Ordovician sequences from the western margin of Laurentia are now known to comprise three facies belts (Fletcher and Collins, 1998):

<table>
<thead>
<tr>
<th>West</th>
<th>East</th>
</tr>
</thead>
<tbody>
<tr>
<td>Outer Detrital Zone</td>
<td>Middle Carbonate Zone</td>
</tr>
<tr>
<td>Inner Detrital Zone</td>
<td>Inner Detrital Zone</td>
</tr>
</tbody>
</table>

The Middle Cambrian of the Field area is now understood to primarily comprise elements of the Outer Detrital and Middle Carbonate Zones, with minor Inner Detrital elements. At the base of the sequence, the Mount Whyte and Naiset formations were unconformably deposited on top of the Gog Group. On the platform side, the Cathedral Formation carbonates of the Middle Carbonate Zone
are topped by the shales of the Stephen Formation, now thought to be a basinwards extension of the Inner Detrital Zone (Fletcher and Collins, 1998) (Fig. 3.38).

On the basinal side, all the strata form part of the Outer Detrital Zone. The temporal equivalent of the Cathedral Formation limestones are the deep-water slope carbonates of the Takakkaw Formation, often referred to in the literature as the ‘Takakkaw Tongue’. These are overlain by the Monarch Formation, comprising calcareous shales overlain by a more carbonaceous mud-mound bearing interval (Collom et al., 2009). These mud mounds were initially thought to represent detritus from the marginal collapse of the Cathedral escarpment, but more recently have been suggested to have grown where deep-seated normal faults intersected the seafloor (see Collom et al., 2009 for further discussion). Above the Monarch Formation is the Burgess Shale Formation (Fig. 3.38), divided into ten members by Fletcher and Collins (1998), of which only five were recognised by Collom et al. (2009) (Fig. 3.39). The lowest, the Kicking Horse Shale member, contains at least one olistolith of the Cathedral Formation, approximately 40m in size (see photograph in fig. 8 of Collom et al., 2009, p. 72). This is followed by the mud mound-bearing Yoho River Limestone Member, the Campsite Cliff Shale Member, the mud mound-bearing Wash Limestone Member, and the Walcott Quarry Member, a finely laminated unit of calcareous, silty, and graphitic mudstones with a ‘stripy’ weathered appearance. Fletcher and Collins (1998) defined a further five members above the Walcott Quarry Member, namely the Raymond Quarry Shale Member, the Emerald Lake Oncoid Member, the Odaray Shale Member, the Paradox Limestone Member, and the Marpole Limestone Member. Collom et al. (2009), however, subsequently combined these as the Wapta Member. Both platform and basinal sequences are overlain by the Middle Carbonate Zone Eldon Limestone Formation.

The majority of the exceptionally preserved fossils in the Burgess Shale, including those described herein, are preserved in the Walcott Quarry Member. These are thought to have been buried in situ (or with only minimal transport) at the base of the Cathedral Escarpment, by obruption events, with storms carrying sediment over the submarine cliff edge (Caron and Jackson, 2006).
Trilobites occur throughout the succession, and allow high-precision biostratigraphical control (Fletcher and Collins, 1998; Collom et al., 2009). The Cathedral Formation was formed during the Albertella and lowermost Glossopleura biozones, in the Delmaran North American Stage, with the overlying Stephen Formation comprising the remainder of the Glossopleura biozone, and most of the Bathyuriscus biozone of the Marjuman North American Stage (Fig. 3.39). On the basinal side, the Takakkaw Formation is temporally equivalent to the Cathedral Formation, with the Monarch Formation and the lower part of the Burgess Shale Formation (up to and including the Yoho River Member) occupying the remainder of the Glossopleura biozone (and thus the Delmaran Stage). The remainder of the Burgess Shale Formation forms part of the Marjuman Stage (Bathyuriscus biozone). The Walcott Quarry Member is placed approximately in the middle of this North American stage, which roughly equates to the as yet un-named Stage 5 of the Cambrian according to the latest international Cambrian Timescale, estimated to be approximately 506-510 Ma (Babcock et al., 2007; Ogg et al., 2008).
The Class Eldoniata

The purpose of this chapter is to describe and to outline a revised classification of the eldonides, an extinct group of discoidal – but not radially symmetrical – organisms placed here in the new Order Eldonida and Class Eldoniata. To date, fossil eldonides are known only from the Palaeozoic, ranging from the Early Cambrian to the Late Devonian, apparently becoming extinct around the Frasnian/Fammenian boundary. The paucity of their post-Cambrian fossil record, however, does not allow an evaluation of whether this group was a casualty of the Frasnian/Fammenian mass extinction, or alternatively if this apparent timing is merely an artefact of a limited number of fossil specimens.

The eldonides are relatively simple creatures, with few measurable morphological characteristics consistently preserved. Potential statistical analysis is therefore difficult, and thus of extremely limited value. A particular problem lies in the nature of the group as an extinct clade, with no known extant relatives. This both precludes an unambiguous phylogenetic placement, and makes the interpretation of particular features difficult, reducing the value of such morphological features for taxonomic purposes. Differences between genera and species are therefore of necessity often subjective. This was alluded to by Caron et al. (2010, p.9), who noted with regard to the phylogenetic placement of the group that:

"the usual route of phylogenetic analysis employing cladistic analysis unfortunately remains problematic. This is on account of the relative paucity of characters [and] the assignment of morphological features that defy unambiguous interpretation".

A similar problem, enhanced by an even greater paucity of morphological characteristics, has led to significant problems with the taxonomy and interpretation of discoidal fossils of Ediacaran age, as noted by MacGabhann (2007a).
Chapter Four – The Class Eldoniata

The terminology used herein in describing the eldonides is summarised in Fig. 4.01a. The most conspicuous characteristic of the entire eldonide group is a coiled structure located near the centre of the disc, referred to as the coiled sac. The inner end of the coiled sac, closer to the centre of the disc, is referred to herein as the proximal termination, with the end closer to the disc margin referred to as the distal termination. In some specimens, the coiled sac is seen to exhibit a tripartite lengthwise division into proximal, medial, and distal portions; some specimens also show the coiled sac to contain an inner coiled tube, with both sac and tube enclosed within an outer coiled membrane.

Other internal features present on some or all eldonide fossils include tentaculate-like structures at the proximal end of the coiled sac, referred to as the circumoral tentacles; rounded structures adjacent to the outer margin of the proximal portion of the coiled sac referred to as the oval sacs; and broad radially arranged tubular internal structures running from the central part to the edge of the disc which universally bifurcate towards the margin, referred to as the internal lobes. Some specimens also preserve thin radial fibres emanating from a central ring and running towards the margin along the edge of the internal lobes. Similar structures are also occasionally seen on the internal lobes between the coiled sac and the disc margin, referred to as radial strands to distinguish them from the radial fibres.

Many specimens also show detail of ornamentation on the fossil surfaces. For ease of referring to the different surfaces of the fossils, the surface located above the coiled sac, where this is preserved coiled in a dextral direction, will be referred to as the dorsal surface, with the opposite surface referred to as the ventral surface. Although these terms imply a specific life orientation, they are not used in this sense here, and the life orientation of these fossils is still uncertain. This terminology is applied here solely to conform to previous descriptions, for the sake of simplicity.

The ventral surface, where known, is variably ornamented with radial filaments and rounded structures referred to as pores (to conform with previous descriptions). The dorsal surface ornamentation, however, varies considerably across genera and species, both in detail and in general form. Some species are simply ornamented, with the surface divided into segments referred to as bifurcated strips.
by primary radial grooves which extend from the centre of the disc to the margin, and secondary radial grooves which extend from a point at approximately half the radius of the disc to the margin. Others exhibit a more complex ornamentation, with various combinations of radial ridges, additional ridges referred to as dissepiments perpendicular to these, and concentric rings, which may take the form of ridges or grooves. In some specimens, radial ridges may be simple, running from the centre to the margin with no dissepiments, but often, several different sets of radial ridges are present. Based on their relief, length, and position, these may be differentiated into primary, secondary, and tertiary ridges. In specimens where most radial ridges have dissepiments, radial ridges without dissepiments are referred to as radial lines. In some specimens, the radial ridges broaden and increase in relief near the edge of the disc, becoming marginal lappets. Where radial ridges reach the centre of the disc, they are occasionally seen to extend from a central ring.

In some specimens, the dissepiments also show similar variation, and can be divided into primary dissepiments and secondary dissepiments. One form also exhibits an additional set of ridges perpendicular to the primary and secondary dissepiments; these are termed subdissepiments.

Often, the arrangement of the dorsal ornamentation is not uniform over the disc, with two or three concentrically-arranged zones evident on the disc surface. These are referred to as cycles, with the innermost zone being the inner cycle, and the zone adjacent to the inner cycle labelled the cardinal cycle. Where the cardinal cycle is the middle of three zones, the outer zone is termed the marginal cycle.

For fossils preserved as compressions in shale, specimens which preserve the sac coiled in a dextral orientation are referred to as the part; specimens showing a sinistral coiling direction are referred to as the counterpart (Fig. 4.01b). For specimens preserved as moulds and casts in sandstones, the mould is referred to as the part, and the cast as the counterpart. This usage reflects the taphonomic reality, whereby the mould is the original preservation of the fossil, with the casting sediment merely replicating the mould once the organism has decayed.

Symbols and annotations in synonymy lists below follow Matthews (1973). Repositories for specimens are indicated by their prefix. USNM-Smithsonian
4.1 Systematic Palaeontology

Unranked stem-group CAMBROERNIDS Caron *et al.*, 2010

*Diagnosis.*—Metazoans with prominent feeding tentacles and conspicuous gut housed in a coiled coelomic sac suspended by mesenterial elements, body form ranging from pedunculate to discoidal.

Class ELDONIATA class nov.

*Diagnosis.*—Non-mineralised discoidal, but not radially symmetrical, metazoans with the alimentary canal contained within a conspicuous internal dextrally coiled sac, suspended within a coelomic cavity; prominent branched tentacles feature at the proximal (inner) end of this sac.

*Included Orders.*—Order ELDONIDA ord. nov.
Discussion.– Dzik (1991) previously established the Class Eldonioidea for the eldonides. However, Walcott (1911) had previously established the Family Eldoniidae with *Eldonia* as the type genus, and in doing so, is deemed by ICZN Code Article 36.1†† to have simultaneously established the Superfamily Eldonioidea Walcott, 1911. Dzik (1991)’s name is therefore preoccupied, and his designation is thus invalid.

Order ELDONIDA ord. nov.

Diagnosis.– Non-mineralised discoidal organisms with branched tentacles at the proximal end of an internal dextrally coiled sac containing the alimentary canal, suspended within a coelomic cavity, and radially arranged internal bifurcating lobes.

Included Families.– Family ELDONIIDAE Walcott, 1911; Family MAOYANIDISCIDAE nom. nov.; Family PAROPSONEMIDAE fam. nov.

Discussion.–Dzik (1991) placed the entire eldonide group in the Order Vellumbrellida, which was erected based on the species *Velumbrella czarnockii*. However, this genus is poorly known, and indeed can only be tentatively referred to the eldonides. For this reason, and as the principle of taxonomic priority does not apply at ranks above Family level, this classification is not followed here. Instead, the eldonides are placed within the new Order Eldonida, with the name of the order derived from the well-known genus *Eldonia*.

††“A name established for a taxon at any rank in the family group is deemed to have been simultaneously established for nominal taxa at all other ranks in the family group; all these taxa have the same type genus, and their names are formed from the stem of the name of the type genus with appropriate change of suffix. The name has the same authorship and date at every rank” (ICZN, 1999).
Type genus.—Eldonia Walcott, 1911

Diagnosis (emended).—Unmineralised fully flexible discoidal organisms with branched tentacles at the proximal end of an internal dextrally coiled sac containing the alimentary canal, suspended within a coelomic cavity, and radially arranged internal bifurcating lobes. Dorsal surface divided into bifurcated strips by radial grooves commensurate with the internal lobes.

Genus Eldonia Walcott, 1911

non Eldonia Tanasevitch, 1995

Type species.—E. ludwigi Walcott, 1911.

Diagnosis (emended).—Non-mineralised discoidal but not radially symmetrical metazoans, with a non-mineralised fully flexible integument. Dextrally-coiled sac near the centre of the disc, divisible into three longitudinal sections. Dendritic circumoral tentacles surround the proximal opening of this coiled sac, which opens on the ventral surface, as does the distal opening. Radially arranged internal lobes, which bifurcate between the coiled sac and the margin of the disc, with associated radial fibres. Dorsal integument ornamented simply, with radial strips, which bifurcate towards the margin, running from the centre of the disc to the edge, separated by radial grooves.

Discussion.—The diagnosis is emended to account for the inclusion of E. eumorpha within the genus.
ELDONIA LUDWIGI Walcott, 1911

Figs. 4.02–4.27

v* 1911 Eldonia ludwigi Walcott, p. 41-52, pls. 8-12, text-fig. 5,
p 1912 Eldonia ludwigi Walcott; Ryan and Hallissy, p. 248-9, fig. 4,
   1912 Eldonia ludwigi Walcott; Ryan, p. 205-7,
   1912 Eldonia ludwigi Walcott; A.H. Clark, p. 723-5, 1 fig.,
p 1912 Eldonia ludwigi Walcott; H.L. Clark, p. 276-8,
p 1912 Eldonia ludwigi Walcott; Steinemmann, p. 582,
   1913 Eldonia ludwigi Walcott; A.H. Clark, p. 488-507,
p 1913 Eldonia ludwigi Walcott; Eastmann, p. 312-3, fig. 435bis,
p 1916 Eldonia ludwigi Walcott; Osborn, p. 324-5, fig. 6,
p 1928 Eldonia ludwigi Walcott; Fedotov, p. 90,
p 1932 Eldonia ludwigi Walcott; Croneis and McCormack, p. 125-7, fig. 3,
p 1948 Eldonia ludwigi Walcott; Cuénot, p. 312-4,
   1956 Eldonia ludwigi Walcott; Madsen, p. 7-14,
   1957 Eldonia ludwigi Walcott; Madsen, p. 281-2,
p 1960 Eldonia ludwigi Walcott; Lemche, p. 95,
p 1961 Eldonia ludwigi Walcott; Seilacher, p. 66-72,
   1962 Eldonia ludwigi Walcott; Madsen, p. 87-9, figs. 1-4,
p 1969 Eldonia ludwigi Walcott; Durham, p. 886-7,
   1974 Eldonia ludwigi Walcott; Durham, p. 750-5, pl. 1, text-figs. 1-2,
p 1979 Eldonia ludwigi Walcott; Scrutton, p. 166,
p 1979 Eldonia ludwigi Walcott; Conway Morris, p. 332,
p 1984 Eldonia ludwigi Walcott; Paul and Smith, p. 463,
p 1988 Eldonia ludwigi Walcott; Conway Morris and Robinson, p. 38-9, figs. 27-9,
p 1988 Eldonia ludwigi Walcott; Smith, p. 89,
p 1990 Eldonia ludwigi Walcott; Conway Morris, p. 115, fig. 4,
p 1991 Eldonia ludwigi Walcott; Dzik, p. 50-51,
p 1991 Eldonia ludwigi Walcott; Chen and Erdtmann, p. 65,
p 1992 Eldonia ludwigi Walcott; Runnegar and Fedonkin, p. 372,
p 1992 Eldonia ludwigi Walcott; Gee, p. 456, 1 fig,
Material.– Lectotype: USNM 57540 (designated by Durham, 1974).

Paralectotypes: USNM 57537, 57540 (two specimens), 57541-57545, 57546 (two specimens), 57547, 57548 (two specimens), 57549-57552, 57553 (two specimens), 57554 (four specimens), 65060, 188552, 188553, 188554 (two specimens), 188555, 188556 (counterpart is 193534), 189919-189921, 193455-193491, 193492 (three specimens), 193493, 193494, 193502-193513, 193514 (three specimens), 193515 (three specimens), 193516, 193517 (three specimens), 193518-193530, 193531 (two specimens), 193532 (two specimens), 193533, 193534-193536, 193537 (two specimens), 193538, 193539 (two specimens), 193540-193544, 193545 (two
specimens), 193546-193550, 193551 (two specimens), 193552, 193553 (two specimens), 193554, 193555, 193556 (two specimens), 193557-193564, 193565 (three specimens), 193566-193573, 193574 (two specimens), 193575, 193576 (two specimens), 193577, 193578 (two specimens), 193579 (two specimens), 193580-193613, 193614 (two specimens), 193615-193617, 193678 (two specimens), 193679-193709, 193710 (two specimens), 193711-193715, 193716 (two specimens), 193717-193727, 193728 (counterpart is 272639), 193729-193776, 193777 (two specimens), 193778 (three specimens), 193779, 193780, 193781 (two specimens), 193782 (three specimens), 193783 (three specimens), 193784, 193785, 193786 (three specimens), 193787-193791, 193792 (two specimens), 193793-193817, 193818 (two specimens), 193819-193822, 193823 (two specimens), 193824 (two specimens), 193825-193831, 193832 (two specimens), 193833-193835, 193836 (two specimens), 193837, 193838, 193839 (three specimens), 193840-193843, 193844 (two specimens), 193845, 193846 (two specimens), 193847-193875, 193876 (two specimens), 193877-193883, 193884 (four specimens), 193885, 193886 (seven specimens), 193887-193906, 201690-201692, 201693 (three specimens), 201694-201701, 201702 (two specimens), 201703, 201704 (counterpart is 356710), 201705-201716, 272639, 275690 (four specimens), 356698 (two specimens), 356699, 356700 (two specimens), 356701, 356702, 356704-356710, 356711 (two specimens), 356712-356715, 356716 (counterpart is 356717), 356717-356721, 356722 (two specimens), 356723-356732, 356733 (eighteen specimens), 356753, 202993 (two specimens), 268957 (five specimens), 467200-467205, 467206 (two specimens), 467207-467210.

Diagnosis (emended).– As for genus, with up to 30 bifurcating lobes, and short stubby dendroidal circumoral tentacles. Dorsal surface divided into (up to) 30 bifurcated strips, separated by radial grooves, congruent with the internal lobes.

Occurrence.– Burgess Shale Formation, British Columbia, Canada (Middle Cambrian); ?Duchesnay Unit, Chancellor Group, British Columbia, Canada (Middle Cambrian); Spence Shale Formation and Marjum Formation, Utah, USA (Middle Cambrian); Siligir Formation, Siberia, Russia (Middle Cambrian).

Description.– The overall body shape of *E. ludwigi* is discoidal, with numerous specimens showing evidence for flexibility, including folding near the specimen margins. However, many specimens do not preserve the full body shape. The most obvious and ubiquitously preserved morphological feature of *E. ludwigi* is a coiled structure, which occurs approximately one-third of the way from the centre of the disc to the outer margin (Figs. 4.02-4.17). When viewed from above the presumed dorsal surface, this structure coils in a dextral direction. While in most cases, this structure appears to be a single element, 258 specimens show that it is subdivided into three lateral portions. These are:

- the proximal portion, which is short, and is narrow at the proximal end but rapidly broadens;

- the medial portion, which is the thickest part; and

- the distal portion, the outer part of the coil, which is long and thinner than the medial portion (Figs. 4.02-4.12).

The boundary between the proximal and medial portions of the coiled sac is curved, and sometimes poorly defined, while that between the medial and distal portions is straight and usually quite sharp (e.g. Figs. 4.03-4.08). This structure is highly optically reflective in the Burgess Shale specimens, with the medial portion being the most reflective. The proximal and distal portions are often quite poorly reflective in
comparison to the medial portion, though not in comparison to the remainder of the preserved tissues (e.g. Fig. 4.03a).

A small number of well-preserved specimens also show this coiled structure to be a three-layered structure, with an inner coiled tube contained within a thicker coiled sac, both surrounded by a thin outer membrane (Figs. 4.02, 4.04, 4.05, 4.09-4.11). The coiled tube is observed within the coiled sac in 39 specimens. It is most commonly seen in the medial (22 specimens) and distal (27 specimens) portions, with only four specimens preserving the proximal tube (Fig. 4.09). The coiled tube was evidently free to move within the coiled sac, and can been seen preserved in different positions within this structure in different specimens (compare Fig. 4.02, 4.04, 4.09). Four specimens show an additional outline just outside the margin of the coiled sac (USNM 188556 and USNM 356726, in both cases indistinguishable in photographs, USNM 188554, Fig. 4.09a, and USNM 188553, Fig. 4.10), which is interpreted as a outer membrane surrounding both the sac and the tube.

The coiled sac is the most commonly preserved morphological feature, and in poorly preserved specimens, the medial portion of the coiled sac is commonly the only part of the organism seen (Fig. 4.08), indicating a greater degree of recalcitrance than the rest of the organism. The coiling direction of the sac, and thus the orientation of the specimen, in such poorly preserved examples can often be determined from the nature of the ends of this medial portion, which appears to taper towards the proximal end, while broadly maintaining its width towards the distal end (Fig. 4.08). In most specimens, the margins of the coiled sac are smooth; however, in a small minority of specimens, the outer margin has a corrugated appearance (e.g. Fig. 4.12a), and in a few others, the margin is highly irregular (e.g. USNM 188552, Fig. 4.12b).

The proximal portion of the coiled sac terminates in a circular aperture, which is seen clearly in three specimens – USNM 57540, USNM 201692, and ROM 95-1119b-1 (Figs. 4.02, 4.11b, 4.13). Four branches are attached to the margins of this aperture, two on each side (Fig. 4.13). These divide into a number of branchlets which are themselves further divided, terminating in dendritic structures. While these structures are observed in 121 specimens, only one or two branches are
preserved in most cases (e.g. Figs. 4.02, 4.04, 4.14), presumably due to the arrangement of two on each side, with the upper branches obscuring the lower ones. Only these three specimens show the full arrangement. These structures are often as reflective as the proximal portion of the coiled sac in Burgess Shale specimens.

The distal termination of the coiled sac is a plain circular aperture, observed in only a solitary specimen (Fig. 4.15).

Near the boundary between the proximal and medial portions of the outer side of the coiled sac, sixteen specimens preserve four small oval structures, termed oval sacs. These appear to be interconnected by small fibres, and also appear to be connected to the coiled sac. While these are only clear in a very small number of specimens, amorphous reflective features in this general area in several additional specimens provide further evidence of structures in this region. These structures are not clear in most photographs (they are, for example, present in the specimens in Figs. 4.06 and 4.11a), but can clearly be seen in one of the specimens in Fig. 4.16.

The outer part of the disc, between the coiled sac and the margin, is dominated in many specimens by a series of radially-arranged lobes, separated by much less than their width (e.g. Figs. 4.02, 4.12, 4.15, 4.17, 4.18). In most Burgess Shale specimens of Eldonia, these lobes are preserved as barely reflective structures or outlines; however, a number of specimens preserve these structures in relief from the disc (e.g. Fig. 4.18b–c). Due to the compacted nature of most specimens, the lobes often appear to radiate from the outer margin of the coiled sac. However, in a small number of specimens, these are seen to pass underneath the coiled sac (e.g. Figs. 4.15, 4.18b). This is confirmed by the Siberian specimen (Fig. 4.19), in which the lobes clearly pass over the coiled sac in ventral view. This specimen also shows the lobes to be connected to a central ring; this is not observed in the Burgess Shale specimens, in which the lobes are never recognised in the central area of the disc.

The width of the lobes increases with distance from the coiled sac, such that the spacing between adjacent lobes remains relatively constant. This varies between specimens, however, with some specimens showing the lobes to occupy most of the area of the outer part of the disc, while others exhibit significant space between
adjacent lobes. At approximately halfway between the outer margin of the coiled sac and the edge of the disc, these lobes bifurcate.

The number of lobes is uncertain, due principally to differential preservation both within and between specimens, making an accurate count impossible. Well-preserved specimens appear to have, on average, approximately 7 or 8 lobes in one quarter of the disc, or around 15 in one half of the disc, for an estimated total of 30 (60 at the margin, after bifurcation). However, it should be noted that while lobes were observed in 99 Burgess Shale specimens, two or more lobes were counted in only 52, of which only five preserved 15 or more (Fig. 4.20a). ROM specimen 95-1000-1 preserves eighteen lobes, but over approximately three-quarters of the disc, which would indicate less than thirty lobes in total (before bifurcation). However, the lobes also vary in size, with the lobes at the proximal end of the coiled sac being the thickest, decreasing in width around the disc – a feature most clearly seen in the Siberian specimen (Fig. 4.19), which preserves a complete set of 30 lobes, gradually decreasing in size in a sinistral direction from the proximal end of the coiled sac in a ventral view. This makes estimation of the total number of lobes originally present in partial specimens (though counting the lobes in one half or quadrant) inaccurate, at best. It should also be noted that larger specimens are apparently more likely to preserve these lobes than smaller specimens (Fig. 4.20b,c).

The part of the disc enclosed by the coiled sac is dominated by a series of thin, radially arranged reflective structures, termed radial fibres, which are preserved in 147 specimens (e.g. Figs. 4.02, 4.04, 4.05b, 4.07b, 4.09-4.11, 4.13, 4.14, 4.17). In 33 specimens, these are seen to connect to a central ring (e.g. Figs. 4.02, 4.04, 4.05b), of diameter 2-3mm in most cases (but reaching 5mm in one specimen, which may be due to partial decay). The fibres appear to number the same as the internal lobes, and may be connected to them. These structures are arranged in pairs which remain separate across the inner area of the disc, but coalesce at or around the inner margin of the coiled sac. Only a very small number of specimens preserve these radial fibres in the region of the coiled sac. On some specimens, a number of loops appear at the inner or outer margin of the coiled sac (e.g. Fig. 4.02), between adjacent radial fibre pairs, and appear to be connected to them.
In several of well-preserved specimens (e.g. Figs. 4.07, 4.13), it can clearly be seen that both the bifurcating internal lobes and the radial fibres are absent near, or deflected away from, the area around the proximal and distal terminations of the coiled sac, as well as the dendritic structures. This represents the ventral aperture of the organism, where the proximal and distal ends of the coiled sac protruded out of the body cavity. This suggests that the radial fibres, as well as the lobes, pass underneath the coiled sac, with both lobes and fibres deflected to allow the sac terminations to pass through the gap.

Some specimens also appear to show a number of elements similar to the radial fibres occurring on the lobes in the outer part of the disc, with three pairs apparently preserved on each lobe (Figs. 4.10, 4.11a). These structures are termed radial strands, to distinguish them from the radial fibres, as it is believed they represent different structures, although their appearance is similar.

The dorsal outer integument of the organism is seen on only a small number of mostly smaller specimens (Figs. 4.03, 4.08c-d, 4.16, 4.21, 4.22). This appears to be simply ornamented, consisting of radially-arranged strips separated by grooves. Each strip is bifurcated by additional grooves, which run from approximately halfway between the outer margin of the coiled sac and the disc margin to the edge of the disc. These strips are believed to correspond in number and location to the internal lobes, with commensurate bifurcation. In Burgess Shale specimens, this outer integument is never reflective. However, many specimens appear to have slightly increased optical reflectivity over the entire area of preservation, even where no morphological structures are observed. This general reflectivity is consistent with the presence of membrane covering the entire body, inside the integument. The ventral surface, by contrast, is never seen.

The original orientation of most Burgess Shale specimens was not recorded. Friend (1995, p. 13-14) noted that sixteen specimens of Eldonia were preserved on one block (USNM 356733), and that all of these specimens are preserved in the same orientation, indicating that the specimens were preferentially oriented on burial, with the dorsal side facing down. However, he subsequently noted that ‘virtually all specimens’ of E. ludwigi had been discovered with their ventral surface
directed towards the seafloor (Friend, 1995, p. 119-120), directly contradicting his earlier statement. The ROM material, which was collected subsequent to Friend (1995)’s work, does not appear to show a preferred orientation. As the specimens have been transported, this is unsurprising. The sixteen specimens in the same orientation may indicate a preferred orientation in that single level, which may not have been repeated throughout the Burgess Shale.

Discussion.—As part of this study, new material of *E. ludwigi* collected by the Royal Ontario Museum from the Burgess Shale in expeditions during 1995, 1997, and 1999 was examined. This material had not previously been described or considered in any previous investigation of *E. ludwigi* (Fig. 4.23), having been collected subsequent to Friend (1995)’s description (although this material was included in taphonomic and palaeoecological analysis of the Burgess Shale by Caron and Jackson, 2006, 2008). Walcott’s type collection of *E. ludwigi* in the Smithsonian Museum of Natural History in Washington DC was also re-examined. The primary focus of this investigation was to test Friend (1995)’s description and reconstruction (Fig. 4.24) on both the type collection and new material not examined as part of his work. Much of the terminology in the description above and discussion below thus follows that used by Friend (1995).

In interpreting fossils from the Burgess Shale, careful consideration must be paid to the preservation of the fossils. These are preserved as three-dimensional structures, but are highly compacted, such that the third dimension is exceedingly thin (see e.g. Briggs, 1990). The fossils are seen when the shale splits through a specimen: the level of the split controls what features may be seen, and whether observable features are seen on the part or counterpart. As demonstrated by Whittington (1975)’s work on *Opabinia*, and Conway Morris (1979a)’s work on Burgess Shale polychaetes, the level of the split through the fossil is controlled by the surface area of various structures, their thickness, and their angle to bedding. As noted above, specimens in which the coiled sac coils in a dextral direction are termed the part. In these specimens, features which are observed to overlie the coiled sac are closer to the dorsal surface of the specimen, while features lying underneath the coiled sac are closer to the ventral side. The reverse is true for counterparts. In *E. ludwigi*, this is well demonstrated by the coiled sac and radial fibres. The coiled sac
appears to be both the thickest structure and to have the largest surface area, which may explain why it is so prominently observable in many specimens. The radial fibres, which are thought to have been closer to the ventral surface than the coiled sac, are rarely preserved in the region of the coiled sac due to this level of splitting, as they are generally in a position below the coiled sac on the part, and thus are hidden. Only specimens preserved with the entire thickness of the coiled sac on the counterpart could show the radial fibres passing over this.

Another key factor is that the angle of the specimen with respect to the original bedding also controls the extent of what is observed, to a large degree. Although the specimens virtually all appear to be presently horizontal, their original orientation may have been quite different, with post-burial compaction vastly decreasing the apparent angle from horizontal. While many specimens have undoubtedly been preserved at or near an original horizontal orientation (terming dorsoventral orientation by Friend, 1995), others were evidently buried at an oblique orientation, while a minority component are lateral compressions, with the specimen buried at a near-vertical orientation. While lateral compressions can easily be recognised (e.g. Figs. 4.22b, 4.25), it is extremely difficult to distinguish slightly oblique and dorsoventral compressions, due to multiple factors including partial preservation, decay, and changing level of the split within the rock. This, unfortunately, renders most potential morphological measurements useless. The maximum thickness of the coiled sac was the only measurement recorded for most *Eldonia ludwigi* specimens (Fig. 4.20), but the overall significance of even these measurements is doubtful. At least one specimen appears to show expansion of the coiled sac due to decay (Fig. 4.12b); the effects of variable decay on the width of the coiled sac are uncertain, further reducing the value of the data collected.

The examination of these specimens confirmed that Friend (1995)’s redescription of *Eldonia* was as accurate as it was meticulous, with very few faults. The new material in the ROM conformed almost precisely to Friend (1995)’s descriptions. Importantly, no features of these specimens, or indeed the specimens in the Smithsonian, were not accounted for in his thesis. Only three features described by Friend were found to be wanting:
1. He described a marginal ring, at which the radial fibres terminated: this is thought instead to simply represent the curved nature of the dorsal surface of *E. ludwigi*, and is seen where this surface intersects with the plane of fracture through the fossil. As such, this feature provides indirect support for the presence of a membrane underneath the dorsal outer integument, as the integument itself is never seen to be reflective.

2. He suggested that the radial fibres passed over, rather than under, the coiled sac.

3. He also described concentrically-arranged fibres, similar in appearance to the radial fibres, but these are not clearly present on the specimens, and in particular are not present on several specimens which preserve the radial fibres well.

The coiled sac was proposed by Walcott (1911) to represent the alimentary tract of the animal. Walcott identified four divisions: the oral opening, oesophagus, stomach, and intestine. These correspond to the proximal aperture, proximal portion, medial portion, and distal portion of the coiled sac as described in Friend (1995) and herein. This interpretation is entirely consistent with the evidence, and is thus accepted. Friend (1995) also recognised that the coiled sac consists of three layers, where only one had been recognised before. The ‘corrugated’ appearance of the coiled sac margins in a small number of specimens is observed to coincide with the points where the radial fibres meet the coiled sac, and is interpreted as demonstrating an attachment of these fibres to the membrane surrounding the coiled sac and tube (Fig. 4.12a). The coiled sac overall is thus interpreted as an inflated three-dimensional structure suspended within a coelomic cavity. The highly irregular margin of the coiled sac in a few rare specimens is interpreted as the result of partial decay, or perhaps bursting of the sac due to compression.

The oval sacs near the junction between the proximal and medial portions of the coiled sac are of uncertain function. Friend (1995) interpreted these as potentially gonadal organs, and in defence of this interpretation, it must be noted
that no other part of Eldonia's morphology can be plausibly interpreted as having such a function, which must have existed. However, there is nothing particular in these structures to directly support such a hypothesised role. Their interpretation, therefore, must remain open to question.

The dendritic circumoral tentacles at the proximal aperture of the coiled sac (described as ‘feathery structures’ by Friend, 1995) were interpreted as feeding structures, and this interpretation is likewise maintained herein. This requires interpretation of the distal aperture of the coiled sac as the anus. In this context, it is interesting to note that both oral and anal apertures occur on the same (ventral) side of the organism. Further, as both are seen to protrude through the same gap between two internal lobes (incidentally, the largest and smallest of the lobes), both openings occur in the same general area of the body. The dendritic shape of these branching structures, in the context of food gathering, further implies that surface area was the key factor in feeding for E. ludwigi, perhaps supporting a filter-feeding mode of life. The dendritic form would also be consistent with a respiratory function, though it should be noted that respiratory and feeding functions are not mutually exclusive interpretations.

The interpretation of the internal lobes is highly problematic, as these features appear to be unique to eldonide biology. However, a key observation may lie in the fact that these lobes are preserved with relief from the otherwise flat surface in several specimens (e.g. Figs. 4.15, 4.18). This form of preservation is not seen in any other morphological structure within the E. ludwigi body, even the highly recalcitrant and obviously originally three-dimensional coiled sac. The only plausible interpretation for this observation is that these lobes were preserved by sediment infill during transport and deposition. This would imply that the lobes were, in fact, originally hollow, perhaps filled with a coelomic fluid or even seawater. Indeed, an opening to the seawater may have been the point of entry for the infilling sediment.

With such an interpretation, comparison to the water vascular hydraulic system of the Echinodermata is inevitable, at least in functional terms. In this interpretation, the central ring observed where the lobes connect in the Siberian specimen of E. ludwigi may functionally correspond to the madreporite of echinoids,
representing the point of intake of seawater. Such a comparison is not without merit. The variation in the shape and size of the lobes, with some specimens showing closely spaced thicker lobes, while others have thinner, more widely spaced lobes, may indicate the potential to alter shape by expansion and contraction (Fig. 4.26a). This may be consistent with a hydraulic function for locomotion, expanding and contracting the shape of the organism (similar, in general terms, to the peristaltic motion of a cnidarian medusa; Fig. 4.26b), although it is also possible that this could be a result, and not the cause, of such motion. A respiratory function may also be considered. If the lobes were open to the seawater, as indicated by infilling with sediment, the large internal surface area of the lobes may have been well suited as a respiratory exchange surface. However, the fluid mechanics of such an interpretation are unclear, with no obvious point (or points) of exit for de-oxygenated water.

The uncertainty over the number of lobes in a complete disc of *E. ludwigi* may suggest the possibility that the number of lobes could vary with the size of the specimen, perhaps ontogenetically. For the present, the 30 lobes present in the Siberian specimen shall be interpreted as the maximum number, as it appears to preserve a complete set. Interpreting this number as a maximum is consistent with the observations from the Burgess Shale specimens, and allows for the possibility of variation.

A reconstruction of *Eldonia ludwigi* is presented in Fig. 4.27.

**ELDONIA EUMORPHA (Sun and Hou, 1987)**

*Figs. 4.28–4.30*

1987 *Stellostomites eumorphus* Sun and Hou, p. 264-266, pl. 4:1–6, pl. 5: 1a-f, 2a,b,
1987 *Yunnanomedusa eleganta* Sun and Hou, p. 266-267, pl. 6: 1-2; text-fig. 7,
1988 *Eldonia* sp. Walcott; Conway Morris and Robinson, p. 39,
1991 *Stellostomites eumorphus* Sun and Hou; Dzik, p. 50-51,
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p 1991 *Yunnanomedusa eleganta* Sun and Hou; Dzik, p. 50-51,
p 1991 *Stellostomites eumorphus* Sun and Hou; Chen and Erdtmann, p. 65, pl. 2: 2,
p 1991 *Yunnanomedusa eleganta* Sun and Hou; Chen and Erdtmann, p. 65,
p 1992 *Eldonia ludwigi* Walcott; Runnegar and Fedonkin, p. 372,
  1995 *Eldonia eumorphus* (Sun and Hou); Friend, p. 76-91, figs. 2.6-2.9, pl. 2.1, 2.12-31,
  1995 *Eldonia eumorpha* (Sun and Hou); Chen *et al*., p. 213-244, Figs. 2-16,
  1996 *Eldonia eumorpha* (Sun and Hou); Chen *et al*., Figs. 148-154,
p 1997 *Eldonia eumorpha* (Sun and Hou); Chen and Zhou, Figs. 37-38,
p 1999 *Eldonia eumorpha* (Sun and Hou); Luo *et al*., Figs. 4–6,
p 1999 *Eldonia eumorpha* (Sun and Hou); Hou *et al*., Figs. 206–207,
  2002 *Stellostomites eumorphus* Sun and Hou; Zhu *et al*., p. 166-172, figs. 1-4,
  2004 *Eldonia eumorpha* (Sun and Hou); Hou *et al*., p. 200, figs. 20.7, 20.8,
p 2006 *Eldonia eumorpha* (Sun and Hou); Van Roy, p. 48-49, fig. 3.12,
p 2010 *Stellostomites eumorphus* Sun and Hou; Caron and Conway Morris, p. 7,

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**Diagnosis (emended).**– As for genus, with up to 44 bifurcating lobes, with associated radial fibres. Dorsal surface divided into 44 bifurcated strips, separated by radial grooves, and ventral surface with rows of pores; both congruent with the internal lobes. Circumoral tentacles long, slender, and dendritic.

**Discussion.**– Sun and Hou (1987) established four genera of supposed “medusoids” from the Chengjiang Lagerstätte, in the Lower Cambrian Maotianshan Shale of Yunnan, China. Conway Morris and Robinson (1988) proposed that two of these, *Stellostomites eumorphus* and *Yunnanomedusa eleganta* were synonymous with *Eldonia*. Friend (1995) examined both *E. ludwigi* and the Chinese specimens in detail, and concluded that they were congeneric but not conspecific, citing differences in the number of bifurcating lobes (44, compared to 30 in *E. ludwigi*) and in the oral tentacles (which were noted to be conspicuously longer and more slender, compared to the short, stubby tentacles in *E. ludwigi*, although both are dendritic in form). On this basis, he synonymised *Stellostomites eumorphus* and *Yunnanomedusa eleganta* as *Eldonia eumorphus*. Chen *et al*. (1995) likewise believed the Chengjiang specimens to be congeneric with *Eldonia*, and formally placed them in *Eldonia eumorpha*.
(grammatically correcting the species name for gender, as per the ICZN Code), citing precisely the same reasons as Friend (1995). Subsequently, however, Zhu et al. (2002) proposed that the lobes in the Chengjiang specimens did not bifurcate in the same way as those in *E. ludwigi*, but rather additional lobes were formed near the margin of the disc between adjacent lobes. On this basis, they re-established the genus *Stellostomites* for these specimens.

However, even a cursory examination of the published photographs of *E. eumorpha* (e.g. Fig. 4.28) demonstrates that Zhu et al. (2002)’s interpretation of the form of the lobes is incorrect, and that they do, in fact, bifurcate as described by Friend (1995) and Chen et al. (1995) (compare Fig. 4.29a and b). Given this, the remaining differences between *E. ludwigi* and *E. eumorpha* are not sufficient to warrant separation at the generic level. These specimens are therefore once again reassigned to *Eldonia eumorpha*.

A key observation in *E. eumorpha* is in the preserved orientation of the specimens. Zhu et al. (2002) noted that of more than two thousand known fossils, none were preserved at an interface between former bottom sediment and overlying event bed sediment with the dorsal surface facing downwards, and that 95% of specimens were preserved with the dorsal surface facing upwards.

A reconstruction of *Eldonia eumorpha* is provided in Fig. 4.30.

Family MAOYANIDISCIDAE nom. nov.

*Type genus.—*Maoyanidiscus* nom. nov.*

*Diagnosis (emended).—* Non-mineralised discoidal, but not radially symmetrical, metazoans with a conspicuously stiffened dorsal surface. Dextrally-coiled sac near the centre of the disc, divisible into three longitudinal sections. Circumoral tentacles at the proximal opening of this sac. Radially–arranged internal bifurcating lobes.

Discussion.—Dzik (1991) established the Family Rotadiscidae for Chinese specimens assigned to *Rotadiscus* Sun and Hou, 1987. However, the name *Rotadiscus* is preoccupied by *Rotadiscus* Pilsbry, 1926, and so is invalid. By ICZN Code Article 39‡‡, this also invalidates family names established on this genus. The family name is revised based on the new generic name *Maoyanidiscus*, which replaces *Rotadiscus*. Dzik (1991) did not give a diagnosis for the family: here, the stiffening of the dorsal surface, in contrast to the flexibility shown by both the Eldoniidae and Paropsonemidae, is used to distinguish members of this family of discoidal organisms.

Genus *MAOYANIDISCUS* nom. nov.

*Type species.—Rotadiscus grandis* Sun and Hou, 1987, by monotypy.

*Diagnosis (emended).—Non-mineralised discoidal, but not radially symmetrical, metazoans with a rigid dorsal surface exhibiting a conspicuous concentric ornament. Dextrally-coiled sac near the centre of the disc, divisible into three longitudinal sections. Digitate circumoral tentacles at the proximal opening of this sac. Radially-arranged internal bifurcating lobes, with associated radial fibres. Ventral surface with rows of pores and radial fibres, congruent with the internal lobes.*

*Derivation of name.—As a fitting tribute to Chinese palaeontologist Zhu Maoyan, who has been instrumental in developing our knowledge of exceptionally preserved biotas from the Cambrian of China, and particularly (in this context) the eldonides.*

*Discussion.—As noted above, the genus name *Rotadiscus* is unavailable, as it is preoccupied by *Rotadiscus* Pilsbry, 1926. The new name *Maoyanidiscus* is proposed as a replacement. The diagnosis is emended (based solely on previous descriptions) to

‡‡ “The name of a family-group taxon is invalid if the name of its type genus is a junior homonym” (ICZN, 1999).
cite the stiffening of the dorsal surface, and the digitate, rather than dendritic, form of the circumoral tentacles as diagnostic.

**MAOYANIDISCUS GRANDIS** (Sun and Hou, 1987)

*Figs. 4.31a, 4.32*

1987 *Rotadiscus grandis* Sun and Hou, p. 260-63,
1991 *Rotadiscus grandis* Sun and Hou; Dzik, p. 50-51,
1991 *Rotadiscus grandis* Sun and Hou; Chen and Erdtmann, p. 65,
1992 *Rotadiscus grandis* Sun and Hou; Runnegar and Fedonkin, p. 372,
1993 *Rotadiscus grandis* Sun and Hou; Conway Morris, 1993b, p. 596-7,
1994 *Rotadiscus grandis* Sun and Hou; Zhao and Zhu, p. 272-280
1995 *Rotadiscus grandis* Sun and Hou; Friend (unpublished), p. 60-75, figs. 2.1-2.5, pl. 2.2-2.11,
1996 *Rotadiscus grandis* Sun and Hou; Chen *et al*., Figs. 155-157,
1997 *Rotadiscus grandis* Sun and Hou; Chen and Zhou, Figs. 39-40,
2002 *Rotadiscus grandis* Sun and Hou; Zhu *et al*., p. 177-8,
2004 *Rotadiscus grandis* Sun and Hou; Hou *et al*., p. 210, Fig. 20.14,
2006 *Rotadiscus grandis* Sun and Hou; Van Roy, p. 49-50,
2010 *Rotadiscus grandis* Sun and Hou; Caron and Conway Morris, p. 7,

**Diagnosis.**– As for genus, but with up to 90 internal bifurcating lobes.

**Discussion.**– *M. grandis* (Fig. 4.31a) was originally described as *Rotadiscus grandis* by Sun and Hou (1987) from the Chengjiang Lagerstätte. A systematic re-examination of the species was later undertaken by Friend (1995), who noted that the dorsal surface (which is almost universally preserved facing upwards) was sclerotized and inflexible. Friend (1995) described the dorsal surface as being ornamented with concentric lines (interpreted as growth lines) and fine radial striae which extend from the centre to the margin. The ventral surface was described as being covered in
straight, regularly spaced radial filaments, separated by rows of circular structures termed pores, with a single row of pores from the centre to approximately half the radius, and then a double row of pores from this point to the margin. Some deformation was noted on the ventral side, indicating that this surface was flexible. The presence of a coiled sac, central ring, and bifurcating radial fibres (believed to reflect the arrangement of the internal lobes) were also noted. Only one specimen was described as preserving the internal bifurcating lobes, of which 90 were estimated. Friend (1995) was also the first to describe circumoral tentacles from this species, noting that these have a digitate form, branching only once, near the point of attachment. Zhu et al. (2002) also briefly redescribed the species, of which they noted over 50 specimens had then been found; their description corresponds almost exactly with that of Friend (1995), with the only minor difference being that they noted the number of radial fibres, rows of pores, and internal lobes as 88, not 90. Zhu et al. (2002) also observed the circumoral tentacles in *Maoyanidiscus* to exhibit an internal canal or core which is generally filled with sediment, implying that these were originally hollow, and perhaps filled with a coelomic fluid.

*Maoyanidiscus* differs from *Eldonia* in having an inflexible and concentrically ornamented dorsal surface, considerably more internal lobes, and digitate, rather than dendritic, tentacles. A reconstruction of *M. grandis* is provided in Fig. 4.32.

**MAOYANIDISCUS SP.**

*Fig. 4.31b*

1991 “Brzechowia” Czarnocki; Dzik, p. 49-50, fig. 3b,
p 1993 *Velumbrella czarnockii* Stasińska; Conway Morris, 1993b, p. 597,
p 1995 *Velumbrella czarnockii* Stasińska; Friend, p. 153,
1994 *Rotadiscus* sp. Sun and Hou; Masiak and Żylińska, 331-4, fig. 5b,6,
p 2002 *Rotadiscus* sp. Sun and Hou; Zhu et al., p. 179.
Discussion.– Dzik (1991) noted the occurrence of a concentrically-ornamented discoidal fossil in the Cambrian of the Holy Cross Mountains, Poland, along with *Velumbrella czarnockii* Stasińska 1960 (Fig. 4.31b). This had been mentioned in an unpublished manuscript by Polish palaeontologist Jan Czarnocki (Stasińska, 1960; Dzik, 1991), and referred to as *Brzechówia* sp. Dzik (1991) believed that it was related to *Velumbrella* (see p. 89 below), and hence belonged with the eldonides. Conway Morris (1993b) suggested instead that this was an integral part of *Velumbrella*, representing the other side of the organism, analogous to the concentrically-ornamented disc of *Rotadiscus*, which was followed by Friend (1995). Masiak and Żylińska (1994), however, confirmed that these were indeed separate, and assigned the specimens to *Rotadiscus* sp. One complete and four partial specimens were described by Masiak and Żylińska (1994), ranging in size from 40mm to 180mm, and are concentrically ornamented with fine radial lines. While this is certainly reminiscent of *Maoyanidiscus grandis*, the poorly preserved nature of the limited material does not allow an accurate count of the number of radial structures, nor do any specimens show either the coiled sac or circumoral tentacles. As such, an assignment to *M. grandis* cannot be upheld, and following Masiak and Żylińska (1994), the specimens are thus retained as *Maoyanidiscus* sp.

Genus PARAROTADISCUS Zhu, Zhao and Chen, 2002

*Type species.* – *P. guizhouensis* (Zhao and Zhu 1994), by monotypy.

*Diagnosis (emended).* – Non-mineralised discoidal but not radially symmetrical metazoans with a stiffened dorsal surface. Dextrally-coiled sac near the centre of the disc, divisible into three longitudinal sections. Dendritic circumoral tentacles at the proximal opening of this sac. Radially-arranged internal bifurcating lobes, with associated radial fibres. Ventral surface with rows of pores, congruent with the internal lobes; dorsal surface with both concentric and radial ornamentation.
Discussion.– The generic diagnosis is emended slightly from Zhu et al. (2002), based on their description, to consider the form of the circumoral tentacles and the hardness of the dorsal surface as generically diagnostic.

**PARAROTADISCUS GUIZHOUENSIS** (Zhao and Zhu, 1994)

*Figs. 4.33–4.34*

1994 Rotadiscus guizhouensis Zhao and Zhu, p. 272–80, pl. 1–2,
1997 Rotadiscus guizhouensis Zhao and Zhu; Dzik et al., p. 385–96, text-figs. 2–3,
p 1999 Rotadiscus guizhouensis Zhao and Zhu; Zhu et al., pl. 1–3, 5,
2002 Pararotadiscus guizhouensis (Zhao and Zhu); Zhu et al., p. 172–84, figs. 5–8,
p 2006 Rotadiscus guizhouensis (Zhao and Zhu); Van Roy, p. 49–50,
p 2010 Pararotadiscus guizhouensis (Zhao and Zhu); Caron and Conway Morris, p. 7,
p 2007 Pararotadiscus guizhouensis (Zhao and Zhu); MacGabhann and Murray, p. 6–7, fig. 7c,

Diagnosis.– As for genus, but with approximately 40 internal bifurcating lobes.

Discussion.– *Pararotadiscus guizhouensis* (Fig. 4.33) was described from the Kaili Lagerstätte (in the Middle Cambrian Kaili Formation of Guizhou Province, China), by Zhao and Zhu (1994) under the name *Rotadiscus guizhouensis*, as differing from *R. grandis* only in terms of the body size and the number of radial fibres. Zhu et al. (2002) reassigned the specimens to a new genus as *Pararotadiscus guizhouensis*, offering a redescription based on over 100 specimens, including a substantial amount of new material, again from the Kaili Lagerstätte. They described *P. guizhouensis* as having a stiff, but somewhat flexible, dorsal surface (which is always preserved facing upwards) ornamented with both concentric rings (interpreted as growth lines) and radial structures. The coiled sac was also noted to be clearly visible, although only the medial portion is preserved in many specimens. Internal lobes were described as
poorly preserved in only a few specimens, but were counted at 40 in number. Zhu et al. (2002) also described, for the first time, the circumoral tentacles, which are dendritic in form, noting that these tentacles are occasionally preserved by sediment infill. Specimen diameter ranged from 15-105mm, with most specimens around 50-60mm.

*P. guizhouensis* thus differs from *M. grandis* in having a less stiffened disc, which shows limited plastic deformation; in having fewer internal lobes, 40 compared to 88-90, and in the dendritic rather than digitate form of the circumoral tentacles, similar to those in *Eldonia*. Although not as hard as that of *M. grandis*, the stiffened nature of the disc with concentric and radial ornamentation is sufficient grounds for inclusion in the Family Maoyanidiscidae, while the differences are clearly sufficient to warrant separation from *M. grandis* at the generic level. On the basis of the dendritic form of the circumoral tentacles and the lesser degree of stiffening of the dorsal surface, however, it is likely that *P. guizhouensis* was more closely related to *Eldonia* than was *M. grandis*.

*P. guizhouensis* is also notable for a common association of shelly epibionts (Dzik et al., 1997) and the trace fossil *Gordia marina* (Wang et al., 2009)

A reconstruction of *P. guizhouensis* is provided in Fig. 4.34.

? Family MAOYANIDISCIDAE

Genus *VELUMBRELLA* Stasińska, 1960

*Type species.*– *V. czarnockii* Stasińska, 1960, by monotypy.

*Diagnosis (emended).*– Non-mineralised discoidal metazoans with a stiffened but flexible dorsal surface, divided into a small smooth inner area, and a wide outer area
with radial grooves dividing the surface into 28 segments, and fine concentric rings. A U-shaped depression near the centre of the disc may represent a coiled sac.

**Discussion.**—The generic diagnosis is heavily emended from the original, which was based on the interpretation of the fossils as cnidarian medusae, but is based solely on previous descriptions by Stasińska (1960) and Masiak and Żylińska (1994).

**VELUMBRELLA CZARNOCKII** Stasińska, 1960

*Fig. 4.35*

1960 *Velumbrella czarnockii* Stasińska, p. 337-46, fig 1, pl. 1-4, 
p 1979 *Velumbrella czarnockii* Stasińska; Scrutton, p. 165-6,
p 1982 *Velumbrella czarnockii* Stasińska; Pickerill, p. 74,
p 1986 *Velumbrella czarnockii* Stasińska; Stanley, p. 79,
p 1986 *Velumbrella czarnockii* Stasińska; Yochelson and Mason, p. 1025-8,
  1991 *Velumbrella czarnockii* Stasińska; Dzik, p. 48-50, fig. 3a,
p 1992 *Velumbrella czarnockii* Stasińska; Rozanov and Zhuravlev, p. 258, fig. 25b,
p 1993 *Velumbrella czarnockii* Stasińska; Conway Morris 1993b, p. 597,
  1994 *Velumbrella czarnockii* Stasińska; Masiak and Żylińska, p. 330-7, figs. 4-5,
p 2002 *Velumbrella czarnockii* Stasińska; Zhu *et al*., p. 179-82,
p 2007 *Velumbrella czarnockii* Stasińska; MacGabhann *et al*., p. 282,
p 2010 *Velumbrella czarnockii* Stasińska; MacGabhann and Murray, p. 5,

**Diagnosis.**—As for genus.

**Occurrence.**—Ociesęki Sandstone Formation (Lower Cambrian), Słowiec Sandstone Formation (Middle Cambrian), Holy Cross Mountains, Poland.

**Discussion.**—*Velumbrella czarnockii* (Fig. 4.35) was originally described by Polish geologist Jan Czarnocki in a manuscript from 1941 under the name ‘Brzechowia brzechowiensis’. However, this was not published, and the manuscript contained
neither descriptions nor illustrations, and as a result, this name was declared \textit{nomen nudum} by Anna Stasińska (1960), who redescribed the specimens under their current name. Conway Morris (1993b) suggested that it was related to \textit{Eldonia}, but noted that it was likely more closely related to the maoyanidiscids, citing the co-occurrence of the specimens here reassigned to \textit{Maoyanidicus} sp., and suggesting that these formed part of the same organism. Masiak and Żylińska (1994), in their redescription of \textit{Velumbrella}, disagreed with this suggestion, but did support a relationship with \textit{Eldonia}.

As noted by Zhu \textit{et al.} (2002), no author has disagreed with the suggested relationship between \textit{Velumbrella} and \textit{Eldonia}, and this is tentatively accepted herein. Following Conway Morris (1993b) and Zhu \textit{et al.} (2002), \textit{Velumbrella} is thought to be most closely related to the maoyanidiscids, with a stiffened disc exhibiting both radial and fine concentric structures, but is substantially different to all previously described genera, with radial grooves rather than ridges dividing the surface into 28 segments. \textit{Velumbrella czarnockii} is therefore tentatively referred to the Maoyanidiscidae.

Genus \textit{SEPUTUS} MacGabhann and Murray, 2010

\textit{Type species.–} \textit{S. pomeroii} MacGabhann and Murray, 2010, by original designation.

\textit{Diagnosis.–} As for species.

\textit{SEPUTUS POMEROII} MacGabhann and Murray, 2010

\textit{Figs. 4.36–4.39}

\textit{\textcopyright 2010 Seputus pomeroii} MacGabhann and Murray, p. 1-12 figs. 3-6.
Material.– Four specimens, all curated in the Ulster Museum, Belfast, BELUM K29807. Holotype shown in Fig. 4.37.

Diagnosis.– Non-mineralised ovoid disc, characterised by up to 120 radial lines extending from a central ring of diameter 2-3mm. The radial features extend out towards the margin, which is sharp and lacks any form of protrusion or extensions. A concentric ornament, of a more irregular and coarse nature, may also be present; however, this is not thought to necessarily represent the original morphology (of the living organism). The rest of the organism is unknown.

Occurrence.– Bardahessiagh Formation, County Tyrone, Ireland (uppermost Sandbian or lowermost Katian, Ordovician).

Description.– The specimens of Seputus pomeroii are discoidal impressions, preserved on a fracture surface sub-parallel to bedding, along with associated skeletal fossils (Fig. 4.36). The largest of the specimens is 70mm in diameter. Not all specimens preserve a full disc, nor are the specimens truly circular; long axes are not aligned parallel. All are noticeably darker in colour than the surrounding sediment. The uneven nature of the part impression surfaces (due to natural irregularities) appear to be exactly mirrored by the counterparts.

While preservation quality varies, some distinguishing features are visible. The disc surfaces are adorned by radial and approximately concentric features; two or three irregular approximately concentric rings are superimposed by fine unbranched straight radial lines, all of which appear to extend from the centre to the outermost sharply defined margin. The width of the radial lines is close to the grain size of the host sediment, and this (in combination with variation in the quality of preservation both within and between the specimens) makes it difficult to ascertain their number with any degree of certainty, however this is estimated at 120. A centralised structure is also present on two specimens (Figs. 4.37-4.38), 2-3mm in diameter. Importantly, the relief of the radial lines on the specimens is not the same sense on all four specimens: on the “part” block, the radial lines are grooves on three specimens, and ridges on the fourth (Fig. 4.37, the holotype), which appears to be of exactly opposite relief to the other three. An elongate area, approximately 70mm long and 30mm wide, beside the specimen in Fig. 4.39 (clearly visible in Fig. 4.36b), is rich in
mica and darkened, similar to but not as dark as the specimens themselves. This feature (taken in conjunction with the associated disc) may provide more of an indication of the original shape of the entire organism, which may suggest against a truly discoidal form. However, closely-packed tentacles or similar appendages may also have caused this feature, or alternatively it may be completely unrelated to the discs.

Deviation of the discs from a truly circular shape may be a result of the deformation of the soft body, or may be due to an original non-circular shape; tectonic deformation is ruled out as a cause by the observation that the long axes of the fossils are not aligned, and the undeformed nature of other associated fossils in the bed.

The regular and consistent nature of the radial lines is probably a reflection of the original morphology of the organism, while the irregular nature of the concentric features probably indicates that they are unrelated to morphological construction, but are more likely a result of deformation of the soft body by compaction, perhaps indicating an originally convex morphology.

Discussion.– It is believed that these fossils represent the transported remains of four examples of a non-mineralized organism with a decay-resistant discoidal structure. Without the entire organism, of course, the fossils cannot be assigned to any particular taxonomic group with any degree of confidence. However, it is thought that *S. pomeroii* is best interpreted as a maoyanidiscid.

While *S. pomeroii* differs from the previously described maoyanidiscids in both the number of radial lines and in lacking a fine concentric ornament, the similarity, particularly to *Pararotadiscus*, is striking (compare to Zhu *et al.* 2002, fig. 7a, reproduced herein as Fig. 4.33e). Moreover, it is entirely possible that the lack of fine concentric structures in *S. pomeroii* may be a taphonomic artefact due to the much coarser grain size of the host sediment, which would likely have been unable to faithfully replicate such minute details.

Although the available evidence is admittedly equivocal; based on the similarity to *Pararotadiscus* and the unlikelihood of most other potential
interpretations, *S. pomeroii* is tentatively assigned to the eldonides as the first known post-Cambrian maoyanidiscid.

The preservation of the fossils, within what is essentially a sedimentary event horizon, with different orientations and demonstrably at slightly different levels within the bed, indicates that the organisms are not preserved in situ, but have been transported. This is confirmed by reversal of the sense of relief on one of the four specimens, indicating that this specimen was preserved upside down relative to the other three. The precise matching of surface irregularities between part and counterpart, with no evidence of biomineralisation, indicates that these are true natural moulds and counterpart casts. The flat nature of the discs, meanwhile, given that they are preserved within the coarse-grained bed at different levels, suggests a strong degree of stiffness. However, the minor deviation from circularity with randomly oriented long axes also suggests that the integument of the organisms was not entirely rigid, but was at least somewhat flexible.

The tenacity of this assignment, with only on specimen potentially preserving the coiled sac, and with no circumoral tentacles or internal lobes observed, as well as the clear differences between *S. pomeroii* and the previously described maoyanidiscids, are sufficient to warrant their separation at a generic level.

**Family PAROPSONEMIDAE fam. nov.**

*Type genus.*– *Paropsonema* Clarke, 1900

*Diagnosis.*– Unmineralised discoidal organisms with a dextrally coiled sac near the centre of the disc, and radially-arranged bifurcating lobes. Conspicuous complex dorsal ornament following the structure of the internal lobes and consisting of radially-arranged ridges and dissepiments perpendicular to these.

*Other genera.*– *Discophyllum* Hall, 1847; *Praeclarus* gen. nov.

*Discussion.*– The presence of the coiled sac and internal lobes confirm that the paropsonemids lie within the Order Eldonida. The paropsonemids differ from the
eldoniids and maoyanidiscids in having a complex radial ornament on the dorsal surface; the highly flexible nature of the dorsal surface may suggest a closer relationship to the Eldoniidae than the Maoyanidiscidae.

Genus *Paropsonema* Clarke, 1900

*Diagnosis (emended).*—Unmineralised, flexible, discoidal organism, but not radially symmetrical. Dextrally coiled sac positioned approximately one-third of the radius from the centre of the disc. Radially-arranged internal hollow lobes bifurcate approximately where they cross the coiled sac. At least two cycles of alternating primary and secondary radially arranged ridges on the dorsal surface, congruent with the internal lobes; an inner cycle from the centre of the disc to the coiled sac, with an cardinal cycle beginning at the termination of the inner cycle. Secondary radial ridges of the cardinal cycle form as a continuation of the position of the primary ridges of the inner cycle, and vice versa, such that the number of ridges in both cycles is equal. Dissepiments are arranged perpendicular to these radial ridges.

*Type species.*—*Paropsonema cryptophya* Clarke, 1900

*Other species.*—*Paropsonema mirabile* (Chapman, 1926b)

*Occurrence.*—Upper Devonian of New York, USA; Upper Silurian of Melbourne, Australia.

*Paropsonema cryptophya* Clarke, 1900

*Fig. 4.40–4.52*

v* 1900 *Paropsonema cryptophya* Clarke, p. 172-8, pls. 5-9,
p 1903 *Paropsonema cryptophyum* Clarke (err. cit.); Clarke, p. 1238,
p 1904 *Paropsonema cryptophyum* Clarke (err. cit.); Clarke and Luther, p. 35, 63,
Diagnosis (emended).– Unmineralised, flexible, discoidal organism, but not radially symmetrical. Dextrally coiled sac positioned approximately one-third of the radius from the centre of the disc. Radially-arranged internal lobes bifurcate approximately where they cross the coiled sac. Three cycles of alternating primary and secondary radially arranged ridges are present on the dorsal surface, congruent with the internal lobes. Inner cycle extends from the centre of the disc to approximately the outer margin of the coiled sac, whereupon the secondary ridges terminate, and primary ridges bifurcate, with adjacent bifurcations coalescing to form primary ridges of the cardinal cycle. Secondary radial ridges of the cardinal cycle form as a continuation of the position of the primary ridges of the inner cycle, such that the number of ridges in both cycles remains equal. Alternating major and minor dissepiments are arranged perpendicular to these radial ridges; subdissepiments are also arranged perpendicular to the major and minor dissepiments. Internal lobes exhibit a second bifurcation near the margin of the disc. Primary radial ridges of the cardinal cycle follow the internal lobes in bifurcating at this point into a third marginal cycle, although unlike the bifurcation into the cardinal cycle, adjacent primary ridges do not merge, such that the number of ridges in the marginal cycle is double that of the cardinal cycle.
Dissepiments are present in the marginal cycle in the same configuration as the cardinal cycle.

**Material.**– Lectotype: NYSM 447 (Fig. 4.40), designated herein.

Paralectotypes: NYSM 445 (Fig. 4.41), 446 (Fig. 4.42), 448 (Fig. 4.43a), 449 (Fig. 4.43b), 450 (two specimens; Fig. 4.44).

Non-type: NYSM 6817 (Fig. 4.45), NYSM 6818 (Fig. 4.46); two uncatalogued specimens in the NYSM; USNM 62948; PRI 42122.

**Occurrence.**– Hatch Siltstone Formation, Naples, New York (middle Frasnian); ?Nunda Sandstone, Lindley, New York (upper Frasnian); ?Genesee Group, Ithaca, New York (Givetian-lower Frasnian); Genesee Group, Freeville, New York (Givetian-lower Frasnian).

**Description.**– The specimens of *Paropsonema* are preserved as impressions (moulds and counterpart casts) on bedding plane surfaces or inside beds, with no evidence for original mineralisation. The preserved orientation is known for only three specimens (NYSM 445, NYSM 446, and NYSM 447), where the sample contains cross-laminated siltstone. In all of these cases, it can be seen that the specimens are preserved in positive hyporelief, with the natural mould on the top surface of the underlying bed, and the counterpart cast replicating the shape of the original organisms preserved as a positive relief feature on the bed sole. The lectotype, NYSM 447 (designated herein), has a depression on the top of the counterpart cast sample, directly over the position of the fossil on the sole. This is thought to indicate the downward movement of sediment, post-deposition, to accommodate space left by the decay of the actual organism.

The specimens are discoidal to elliptical in outline, varying from 71-195mm in maximum diameter (NYSM 448, Fig. 4.43a; NYSM 445, Fig. 4.41), though several specimens are measurable along one axis only, or are not measurable at all, due to deformation or incomplete preservation. NYSM 449 (Fig. 4.43b) appears to deviate the most from circularity, at 65x92mm, while NYSM 6818 (Fig. 4.46) deviates the least, at 165x170mm. These differing degrees of variation from circularity indicate that the outer integument was evidently quite flexible, an
observation supported by the considerable non-linear deformation on a number of specimens (e.g. NYSM 446, 447, 450; Figs. 4.42, 4.40, 4.44), including one specimen which is rolled up and approaching a ‘cigar-like’ shape (NYSM 6817; Fig. 4.45). However, this flexibility was clearly reduced in the central portion of the disc, where the coiled sac apparently interfered with the flexure (Fig. 4.45). This structure coils in a dextral direction when viewed from above the dorsal surface (as is the case for all members of the Order Eldonida), and must have been relatively tougher and less flexible than the outer integument. The thickness of the coiled sac is variable along its length, being thickest in the middle. Unfortunately, it is measurable only in NYSM 6817 (Fig. 4.45), where it reaches 15mm in maximum width, and displays a crude segmentation. In other specimens examined in this study, the coiled sac is not actually clearly visible, but is represented by a depressed or raised area near the centre of the disc, with the shape, size, and precise position obscured by the surface ornament (e.g. NYSM 6818, 447; Figs. 4.46 and 4.40)§§.

Specimen PRI 42122 from the upper Givetian to lower Frasnian Genesee Group at Ithaca, New York (which was not examined, but of which a description was provided by J.W. Hagadorn, pers. comm.), preserves only a curved structure with a crude segmentation. This specimen is almost identical to the coiled sac of NYSM 6817, suggesting that it represents an isolated paropsonemid coiled sac, with the remainder of the disc unpreserved.

In his original description, Clarke (1900) described the surface ornamentation of Paropsonema cryptophya as similar to multiple pairs of cords emanating from the centre of the disc, with each cord “knotted” repeatedly along its length, and with the “knots” in any one cord fitting precisely into the space between two knots on an adjacent cord (i.e. offset). At about one third of the radius from the centre of the disc (corresponding to the distal edge of the coiled sac), these “cord pairs” taper to a point and disappear, with a new “cord pair” appearing in between

§§ This may indirectly support the interpretation of Seputus as an eldonide, in demonstrating that the coiled sac may not always be evident in specimens preserved as moulds and casts in siliciclastic sediments.
adjacent “cord pairs” of the first cycle. A third cycle of “cord pairs” appears in a similar way near the margin of the disc. This description was repeated by Friend (1995).

Close examination of the surface of NYSM 6818 would appear to confirm this as a relatively accurate description (Fig. 4.46, 4.47), at least in broad terms, with radially arranged double rows of ridges (corresponding to Clarke’s “knots”) covering the entire surface in three distinct cycles (here referred to as the inner, cardinal, and marginal). However, the ornament of other specimens (e.g. NYSM 446, Figs. 4.42, 4.48) appears to be different, and much more complex. In these specimens, radially-arranged alternating primary (thicker) and secondary (thinner) ridges of the inner cycle emanate from the centre of the disc, with the primary radial ridges bifurcating at or around the point at which they cross the distal margin of the coiled sac. Adjacent primary radial ridges intersect at their midpoint after bifurcation and merge to form primary radial ridges of the cardinal cycle (thus the number of radial ridges in the cardinal cycle remains equal to that of the inner cycle). These then bifurcate again near the margin of the disc to form primary radial ridges of the marginal cycle; however, unlike the inner bifurcation, adjacent ridges appear to remain separate and do not intersect (thus the number of ridges in the marginal cycle is double that of the cardinal cycle; e.g. Fig. 4.48).

Secondary radial ridges of the inner cycle disappear around the same point as the primary radial ridges bifurcate; secondary radial ridges of the cardinal cycle occur between the primary radial ridges of the cardinal cycle, up to the point at which the second bifurcation occurs, and secondary radial ridges of the marginal cycle again occur between primary radial ridges.

Primary and secondary dissepiments alternate along the length of the radial ridges, with up to 1-1.5mm between adjacent primary dissepiments, occupying the space between the secondary and primary radial ridges. Subdissepiments are also occasionally observed in at least the cardinal cycle, arranged in-between and perpendicular to the primary and secondary dissepiments, spaced up to 0.3-0.5mm apart. The size and spacing of the dissepiments decreases near the bifurcation points of the primary radial ridges.
The size and angular spacing of each set of ridges does not appear to be constant, but rather they decrease in thickness, length, and spacing in a dextral direction around the disc, commensurate with the distance between the outer margin of the coiled sac and the edge of the disc. Thus the sets of ornamentation are largest at the proximal end of the coiled sac, and smallest at its distal end. This is most clearly seen on NYSM 6818 (Fig. 4.46), on which the decrease in size appears sinistral, as the specimen is a mould rather than a cast. The distance of the bifurcation points from the centre increases dextrally around the disc in a similar manner.

Closer examination of the ornament of the lectotype is particularly revealing (Fig. 4.49). In the inner area of the disc, the ornament of this specimen conforms closely to Clarke (1900)'s original description. However, in the outer area of the disc, the ornament conforms instead to the more complex arrangement. Moreover, the nature of the transition between the two different styles of ornamentation on this specimen confirms that this difference is taphonomic, rather than morphological (either between specimens or between different parts of the same specimen). This observation serves as a reminder of the need to account for taphonomic effects in the interpretation of fossils of soft-bodied organisms. The more complex form of the ornament (Fig. 4.48, 4.50a) is therefore accepted to be the more faithful representation of the surface of the original organism, with the less elaborate ornamentation exhibited by NYSM 6818 (Fig. 4.46) thought to be a taphonomically-controlled simplification, with each of Clarke (1900)'s “knots” representing one set of dissepiments and subdissepiments (Fig. 4.50b).

Clarke (1900)'s observation that each “knot” lies in a position mid-way between two ridges of the adjacent “cord” is also incorrect. In fact, while many ridges do conform to Clarke (1900)'s description, others - even along the same row - do not, with many ridges observed to lie directly beside ridges of the adjacent row. This is thought perhaps to be an artefact of the increasing separation of dissepiments around the disc. As each row of dissepiments is slightly longer than one adjacent, with the dissepiments slightly more widely spaced, their positions will invariably match along the length of the row in some places, while further down the length (of the same row), their positions will become progressively more detached.
The ornament is also shown by NYSM 6818 (Fig. 4.46) to correspond to the internal structure of *Parapsonema*. This specimen, which was discovered after Clarke (1900)’s original description and was first published by Ruedemann (1916), preserves not only the outer surface of the organism, but also some of the internal structure, with internal lobes visible towards the periphery, revealed by a fracture through the fossil. These lobes, preserved by infilling with sediment, clearly bifurcate towards the margin of the disc and are seen to follow the path of the primary radial ridges (Fig. 4.50c). The bifurcation of these ridges near the margin visible in specimens NYSM 446 and 447 (Figs. 4.42, 4.40) reflects this bifurcation of the internal lobes. The inner bifurcation of the radial ridges at the outer margin of the coiled sac is therefore also thought to reflect a bifurcation of the internal lobes, although this cannot be directly confirmed, and the precise configuration of the internal lobes in the inner part of the disc remains unknown. Indeed, the configuration of the ornamentation may appear to suggest that while the lobes bifurcate at the outer margin of the coiled sac, adjacent lobes may coalesce, as is seen in the primary radial ridges.

The number of lobes, and thus the number of radial structures in the ornamentation, remains uncertain due to incomplete preservation. Clarke (1900) estimated that there were 25 pairs of ridges (corresponding to 25 primary radial ridges of the inner cycle) departing from the centre on half of the disc, and thus 50 on the full disc. Friend (1995), however, estimated that there were 15 pairs in one quarter of the disc, giving a total of 60. Examination of the lectotype (NYSM 447, Fig. 4.40) and NYSM 6818 (Fig. 4.46), which preserve the most radial structures, appears to confirm this estimate of 15 primary radial ridges of the inner cycle per quadrant. However, as the angular thickness and separation of each set of radial structures appears to decrease in a clockwise direction around the disc, the total number cannot be readily estimated with any degree of certainty, a factor which almost certainly led to Clarke’s underestimation. The total number of primary radial ridges is thus estimated to lie between 50 and 60. There are an equal number of primary radial ridges and bifurcating lobes in the cardinal cycle; the number of primary radial ridges in the marginal cycle is double this, as the lobes bifurcate near the margin of the disc, with the ornamentation following this bifurcation.
It is worth noting that the marginal cycle is observed in only three specimens (NYSM 446, 447, and 6818), each with a radius of 150mm or greater. None of the other specimens clearly preserve any ornamentation in the marginal area of the disc, due to both poor preservation and incompleteness. It is thus unclear whether the marginal cycle was a consistent element of the morphology of *P. cryptophya*, or developed during ontogeny. However, the position of the bifurcation into the marginal cycle appears to be relatively constant with respect to the radius in these three specimens:

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Disc radius (mm)</th>
<th>Radius of marginal bifurcation (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>NYSM 446</td>
<td>90</td>
<td>65</td>
</tr>
<tr>
<td>NYSM 447</td>
<td>110</td>
<td>80</td>
</tr>
<tr>
<td>NYSM 6818</td>
<td>75</td>
<td>60</td>
</tr>
</tbody>
</table>

In each case, the marginal cycle thus develops at around 70-80% of the radius of the specimen (Fig. 4.51). While the sample size is small, and measurements may be slightly inaccurate due to the flexibility and deformation of the disc surfaces, this would appear to indicate that the marginal cycle was a consistent feature of *P. cryptophya* specimens, regardless of size.

Several specimens were suggested by Friend (1995) to exhibit the reverse side of the organism, including NYSM 449 (Fig. 4.43b), and NYSM 445 (Fig. 4.41), which appears to preserve both sides of the disc. The reverse side is generally featureless, but exhibits a considerable number of disorganized and patternless wrinkles. While the origin of these structures is uncertain, their presence would seem to indicate that the reverse side was considerably thinner and much more flexible and prone to deformation than the ornamented (dorsal) surface. Their number may also indicate that the convexity of this reverse side of the animal was originally greater than that of the corresponding fossils, presumably due to compaction or post-mortem shrinkage.

Discussion.—As noted previously, a tripartite division of the coiled sac is seen in *Eldonia ludwigi*, where the sac is extremely prominent, and is often the only part of the animal preserved. While this tripartite division is not seen in *Paropsonema*, it is likely it was structured similarly to that of *Eldonia*. The presence of circumoral
tentacles, which are likewise not preserved, is also inferred based on the comparison to other eldonide species. The coiled sac of *Eldonia* has also been observed to be corrugated in some specimens (e.g. Figs. 4.09a, 4.12a), interpreted by Caron et al. (2010) as due to the presence of mesenterial elements suspending the coiled sac in an internal cavity. As noted above, this interpretation is supported herein, and is also likely to be the cause of the crude segmentation visible on the coiled sac of *Paropsonema* specimen NYSM 6817.

The distinctive dorsal ornamentation of *P. cryptophya* is unlikely to have been purely decorative; instead, degree of complexity and the form of organization (with dissepiments bridging the gaps between radial ridges, and subdissepiments ridges bridging the gaps between dissepiments, leaving the entire surface of the disc with very few gaps over 0.3mm in width), suggest that it may have served as a support structure and to increase the general rigidity of the disc. As the form of this ornamentation closely follows the internal configuration of the bifurcating lobes, it is possible that its function may have been to support these. While the nature of the ornamentation remains unknown, it may thus be possible that it was constructed from a stronger scleroprotein or other biopolymer than the rest of the integument. The degree of flexibility of the disc, however, rules out any form of biomineralisation, for which no evidence is present on any specimen.

The decrease in size of the lobes, and corresponding decrease in size and angular spacing of the ornamentation, in a dextral direction around the disc may raise questions over the mode of growth of *Paropsonema*. Two different modes of growth are suggested. The number of lobes, and thus sets of ornamentation, may have been constant with growth, indicating that the animal grew by simple inflation. In this case, the differing size of the lobes may purely be due to the concordant variation in the distance between the first bifurcation of the lobes at the outer margin of the coiled sac, and the edge of the disc. Alternatively, the number of lobes may have increased with size, with new lobes and sets of radial ornament added at the distal end of the coiled sac as the animal grew. The available material is not sufficient to conduct such an ontological analysis, and only the collection of further (well-preserved) specimens can resolve this issue. It should also be noted that the distance of the radial ridge bifurcations from the centre of the disc appears to be directly...
proportional to the specimen radius (Fig. 4.51). This suggests that *P. cryptophya* grew by inflation, not marginal accretion, and that the dorsal integument was a flexible organic structure capable of growth by expansion.

Friend (1995) noted with respect to *Eldonia* that the body of the animal was quite thin, and that the resulting high surface area to volume ratio would have been well adapted to respiration across the entire body surface. *Paropsonema* likewise clearly had a thin body, and could also have been well adapted for such a style of respiration. However, if, as suggested above, the ornament reflects a tougher biopolymer or scleroprotein, covering most of the surface with this material for support would almost certainly have prevented body surface respiration. The configuration of the ornamentation perhaps reflects a compromise between structural support and either rigidity or body mass.

The lobes of *P. cryptophya* differ from those of *Eldonia* in bifurcating twice, but they are similarly inferred to have been hollow due to the preservation by infilling with sediment. Thus the same conclusions drawn from the lobes of *E. ludwigi* (p. 81 above) also apply to *P. cryptophya*.

Friend (1995) considered *Paropsonema* to be synonymous with *Discophyllum* (see p. 121 below) at the generic level. However, the number and arrangement of radial ridges in these two genera do appear to differ considerably, with *Discophyllum peltatum* exhibiting only a single cycle of radial ridges, as compared to three in *Paropsonema cryptophya*, a distinction here regarded as significant enough to maintain the generic separation. *Praeclarus* exhibits two or three cycles of radial structures, but the form of these differs considerably from *Paropsonema*, with only simple ridges in the inner cycle, and the ridges developing into lappets at the margin of the disc. *Paropsonema cryptophya* differs from *Paropsonema mirabile* in that the latter does not have a third cycle of radial ridges.

A reconstruction of *P. cryptophya* is shown in Fig. 4.52.
PAROPSONEMA MIRABILE (Chapman, 1926b)

Figs. 4.53–4.56

1926 un-named ‘jelly-fish’, Chapman 1926a, p. 344
v* 1926 Discophyllum mirabile Chapman 1926b, p. 13-17, pls. 1-2
1965 Paropsonema mirabile (Chapman); Harrington and Moore, p. F152, fig. 121.3,
p 1986 Paropsonema mirabile (Chapman); Stanley, p. 80,
p 1993 Paropsonema mirabile (Chapman); Conway Morris 1993b, p. 598,
1995 Discophyllum mirabile Chapman; Friend, p. 98-102, pls. 3.2-3.3,
p 2002 Discophyllum mirabile Chapman; Zhu et al., 180-1,
p 2006 Discophyllum mirabile Chapman; Van Roy, 51-3,

Material.– Holotype: MV P13893 (part and counterpart) (Fig. 4.53).
Non-type: MV P26661 (pars) (Fig. 4.54), P315525 (Fig. 4.55).

Diagnosis (emended).– Unmineralised, flexible, discoidal organism, but not radially symmetrical. Dextrally coiled sac positioned approximately one-third of the radius from the centre of the disc. Two cycles of alternating primary and secondary radially arranged ridges on the dorsal surface. Inner cycle extends from the centre of the disc to approximately the outer margin of the coiled sac, whereupon the secondary ridges terminate, and primary ridges bifurcate, with adjacent bifurcations coalescing to form primary ridges of the (outer) cardinal cycle. Secondary radial ridges of the cardinal cycle form as a continuation of the position of the primary ridges of the inner cycle, such that the number of ridges in both cycles remains equal (estimated at 100-120). Dissepiments are arranged perpendicular to these radial ridges along their length.

Occurrence.– Specimen P13893 was reported by Chapman (1926b) to have been recovered from a clay pit of the Hoffman Patent Brick & Tile Company in Brunswick, north of Melbourne. Precisely which pit is unknown; however, Chapman (1926b) referred to “the clay pit”, rather than ‘a clay pit’, and it may thus be the case that the clay pit in question was the largest, the No. 1 pit. This has long been infilled.
and the site is now occupied by the M. W. Clifton Reserve (144° 57’ 10” E, 37° 46’ 02” S). In any case, all of the Hoffman pits exposed at their base the Melbourne Formation, a lateral equivalent of the Dargile Formation, of early Ludlow (Silurian) age (see Melbourne 1:63,360 and 1:31,680 geological maps: Geological Survey of Victoria, 1959; 1974).

Specimen P26661 was reported by Friend (1995) as having been recovered in a stream section immediately downstream of the bridge of the Long Gully Road over Long Gully Creek, near Panton Hill, 35 km north-east of Melbourne (37° 38’ 24.33” S, 145° 15’ 35.22” E). This outcrop is close to the boundary of the Dargile Formation with the underlying Anderson Creek Formation (Yan Yean 1:63,360 geological map: Geological Survey of Victoria, 1981), and presumably therefore lies within the lower Ludlow Dargile Formation sensu Edwards et al. (1998).

The provenance and age of specimen P315525 is unknown.

Description.— Specimen P13893B (Fig. 4.53b,c), the part mould of the holotype, is on a sample approximately 130mm long by 80mm wide, and preserves less than one-third of the disc surface. The centre of the disc is not preserved, but its position can be inferred from the radially-arranged double rows of ridges (inner cycle) which diverge from this point. These extend for approximately 30mm, before tapering to a point and disappearing. At the same point, paired rows of ridges of the cardinal cycle appear; these widen rapidly, and continue to widen to the edge of the sample (which is not thought to represent the edge of the disc). 18 pairs of rows of ridges are visible in approximately one-third of the disc; these appear to increase in size in a clockwise direction around the disc. Commensurate with this increase in size, the gaps between these paired rows of ridges appear to increase in negative relief from the surface of the disc. The area at the transition from the inner to the cardinal cycle is slightly depressed in comparison to the remainder of the specimen.

Specimen P13893A (Fig. 4.53a), the counterpart cast of the holotype, exhibits between one-third and half of the surface in terms of area, over approximately three-quarters of the disc, and is better preserved than the part. The edge of the specimen is not thought to represent the edge of the original organism, thus the full radius is not visible at any point. A crack through the sample has
removed some detail, obscuring the centre of the disc, but much of the ornamentation is clearly visible.

The reversal of relief from the part mould allows the ornamentation to be seen in greater clarity. Near the centre of the disc, two set of alternating radially-arranged ridges (thicker primary ridges and thinner secondary ridges) of the inner cycle can be observed. At approximately one-half of the visible radius, the primary ridges bifurcate, and the secondary ridges gradually fade out. Adjacent primary ridges coalesce to form primary radial ridges of the cardinal cycle, which continue from this point in a position representing a continuation of secondary inner cycle ridges; likewise, secondary cardinal cycle ridges form in a position representing a continuation of the primary inner cycle ridges. These cardinal cycle ridges continue to the edge of the preserved specimen, and appear to broaden continuously. The relief of the primary secondary ridges increases significantly in the more poorly preserved portion of the disc.

Secondary and primary radial ridges in both the inner and cardinal cycles are connected by dissepiments, of similar relief to the radial ridges. These are spaced less than 0.5mm apart near the centre of the disc, rising to 1mm apart in the inner cycle, and similarly varying from 0.5mm to 2mm spacing in the cardinal cycle. No subdissepiments are observed. The spacing of cardinal cycle primary radial ridges is slightly irregular, but can be seen to decrease slightly in a clockwise direction around the disc, varying from an angular spacing of approximately 9° in the poorly preserved lower half to 7° in the better preserved upper half. This variation makes estimating the number of ridges difficult, but based on the measured separation of the visible ridges and the variation in the spacing, a total of around 50 ridges is estimated. A curved area, corresponding to the transition between the inner and cardinal cycles, is preserved slightly raised from the disc surface.

Specimen P26661 comprises two paropsonemid specimens, partially superimposed, of which only one is assigned to *Paropsonema mirabile* (Fig. 4.54). This specimen preserves only a small portion of what appears to be quite a large disc, with wrinkling and poor presentation obscuring the ornamentation over much of the preserved surface. However, two discrete areas display the ornament remarkably
clearly. Both these areas exhibit exactly the same pattern of ornamentation, with thicker and thinner (apparently radially-arranged) ridges connected by perpendicular dissepiments. Ten primary and ten secondary ridges are visible in the cardinal cycle of the disc, with associated dissepiments spaced approx. 1mm apart. Eight primary and eight secondary ridges are preserved in the inner cycle of the disc, with dissepiments up to 0.5mm apart. The ornament on the inner cycle is of lower width and relief than that of the cardinal cycle. The edge of the disc is not preserved. The form of the area preserving the ornament in the inner cycle is of a regular curved structure, and could represent the preservation of the ornament over the coiled sac.

Specimen P315525 (Fig. 4.55) is strongly elliptical in shape, approximately 105mm long and 75mm wide. Almost the entire disc is preserved, with some damage around the edge on one side. Near the centre of the disc, the coiled sac is evident, coiling in a dextral direction. This sac is preserved in negative relief from the surface of the disc, varying in width along its length from 5mm to 9mm. Inside this structure, the surface of the disc does not exhibit any ornamentation; however, between the coiled sac and the edge of the disc the surface is adorned with primary and secondary radial ridges, with the primary radial ridges having comparatively greater width and relief from the surface.

The length of these radial ridges generally decreases in a clockwise direction around the disc, commensurate with the decrease in distance between the coiled sac and the edge of the disc; however, their length appears to be shortest where the radius of the disc is also shortest. The ridge separation also appears to be larger where the radius is shortest. The primary and secondary ridges are connected by small perpendicular dissepiments, the separation of which appears to vary systematically with the radius of the disc. The spaces framed by the ridges and orthogonally oriented dissepiments are approximately rectangular ‘pits’ of negative relief.

The number of primary radial ridges was counted at 46, but poor preservation in certain areas on the surface may have caused a slight underestimation. The elliptical shape has also distorted the angular separation of the radial ridges. The separation of the dissepiments is likewise distorted by the ellipticity; these vary from
1-1.5mm apart (with increasing distance from the centre) along the long axis, but reaching a maximum of about 0.8mm along the short axis. The radial ridges do not bifurcate as they approach the edge of the disc.

Discussion.—*P. mirabile* resembles *P. cryptophya* in almost all respects, save that the marginal (third) cycle of radial ridges is absent in the former. The holotype demonstrates the transition between the inner and cardinal cycles of radial structures to be identical to that of *P. cryptophya*. On the holotype, the raised (on the counterpart; depressed on the part) area around the transition from the inner to the cardinal cycle is believed to represent the coiled sac, which may also be preserved in P26661, represented by the curved area on which the finer ornament can be seen, and is abundantly clear on P315525 (Fig. 4.55). The internal lobes are not directly preserved, but as the ornamentation of *P. cryptophya* has been shown to follow the structure of these lobes, it may be inferred that the increased relief on some parts of the radial ornament is due to the presence of the internal lobes beneath.

This thus also suggests that a terminal (second) bifurcation of these lobes was not a feature of *P. mirabile*. While the absence of this third cycle may reflect poor preservation in the holotype (P13893) and specimen P26661, the clear absence of a terminal bifurcation in well-preserved parts of P315525 indicates that this is not likely to be a taphonomic artefact. The specimens of *P. mirabile* appear to be smaller than the specimens of *P. cryptophya* in which the marginal cycle is present, and it is possible that the absence merely reflects ontogenetic variation. However, the observation that three specimens of *Paropsonema cryptophya* of different sizes exhibit the terminal bifurcation at approximately the same point, proportional to the radius of the disc, appears to indicate that the marginal cycle does not develop during ontogeny. Given this, and the difference in age (with *P. cryptophya* known only from the Late Devonian, and *P. mirabile* from the Silurian) it may be premature at this point to synonymise the two species. *P. mirabile* is therefore retained as a separate form.

Specimen P315525 (Fig. 4.55) appears to differ considerably from the other two specimens. The number of radial structures (estimated at 46 primary and 46 secondary, for a total of 92) is slightly low compared to both the holotype and also
*Paropsonema cryptophya* (with both estimated to have 50-60 primary and an equal number of secondary ridges, for a total of 100-120). This difference could be due to underestimation caused by poor preservation of the radial structures, or ontogenetic variation in the number of radial ridges. Further, the absence of radial structures in the inner cycle in this specimen, and greater relief on the radial ridges than is usual in *Paropsonema*, could be purely taphonomic differences. There is thus no firm evidence to suggest that this specimen does not belong in *P. mirabile*.

Chapman (1926b) described the holotype as having 56 radial elements, as did Friend (1995), slightly higher than the estimate provided herein. Only a complete well-preserved specimen could confirm the number of radial elements precisely. Both Chapman (1926b) and Friend (1995) also noted the occurrence of an ‘apical spot’ of diameter 4mm on the part (mould) of the holotype, and possibly carbonaceous stains on the counterpart. Neither are clear, particularly the ‘apical spot’. However, this re-examination of the specimens was conducted primarily on plaster casts made from latex moulds, which could not preserve such carbonaceous stains. Chapman (1926b) believed these to represent tentacles, while Friend (1995) regarded them as remnants of internal lobes. Chapman (1926b) also described ‘*four gastro-genital pouches arranged in a cruciform manner*’. There is no evidence or indication of any such structure.

A reconstruction of *P. mirabile* is shown in Fig. 4.56.

**Genus Praeclarus** gen. nov.

*Type species.*– *P. vanrooi* sp. nov.

*Diagnosis.–* Unmineralised flexible discoidal, but not radially symmetrical, metazoan. Dextrally coiled sac present in the inner third of the disc. Thin radial lines extend from a central ring to the outer edge of the coiled sac before losing their relief. Between the coiled sac and the outer margin of the disc, three series of radial ridges are present. Broad primary radial ridges extend from the outer margin of the coiled sac to the edge of the disc. Secondary ridges, of similar size, are not present in the
vicinity of the coiled sac, but appear midway between the primary ridges at a point approximately half the radius from the centre of the disc. Thin tertiary ridges are also present to either side of the primary ridges along their length. Orthogonal dissepiments connect these tertiary ridges to both primary and secondary radial ridges. At approximately two-thirds of the radius from the centre of the disc, the primary and secondary ridges broaden into raised ovoid lappets, which widen rapidly, before tapering towards the periphery.

*Derivation of name.*—A Latin word meaning “excellent”, “beautiful”, “striking” or “very clear”, which seems an eminently suitable name for such a beautiful set of fossils.

**PRAECLARUS VANROII** sp. nov.

*Figs. 4.57–4.63*

*Material.*—Holotype: M010-0026 (Fig. 4.57).

Paratypes: M010-0008, M010-0010, M010-0012, M010-0023, M010-0025, and M010-0029 (Figs. 4.58–4.61).

Non-type: 23 specimens in the collections of the National University of Ireland, Galway.

*Diagnosis.*—As for genus, but with additional tertiary lappets developed at the outer margins between the primary and secondary lappets. The number of radial lines in the inner part of the disc is estimated at 26–30, with an equal number of both primary and secondary radial ridges and lappets, and with double this number of tertiary ridges and lappets.

*Derivation of name.*—For Peter Van Roy, who introduced me to the Moroccan paropsonemids, and who assisted me in the field for almost all of my time there.
Occurrence.— Middle Tiouririne Member of the Lower Ktaoua Formation, Tafilalt, Morocco (field locality M010).

Description.— The specimens of *Praeclarus vanrooi* are preserved as impressions (moulds and counterpart casts) within a single coarse-grained sandstone bed, with no evidence for original biomineralisation. The fossil surfaces are significantly darkened in comparison to the enclosing sediment due to a coating of manganese and iron oxides and oxy-hydroxides (see Chapter Five). Limited plastic deformation is apparent in several specimens, particularly in the central region of the disc.

The specimens are discoidal to elliptical in outline, varying from 35mm to 110mm in radius. Most are partial, and only two specimens preserve the entire known surface, neither of which clearly preserve a full set of ornamentation. The number of primary radial ridges is estimated to be between 26 and 30 based on their angular separation. This uncertainty is due in part to the deviation of several specimens from true circularity, potentially distorting the angular relationships, but also due to an apparent subtle decrease in angular separation and size in a dextral direction around the disc.

The central part of the disc is dominated by the dextrally coiled sac, generally preserved in negative relief from counterpart casts of the disc surface (Figs. 4.57, 4.59a, 4.60, 4.61), although occasionally, it is preserved as a positive relief structure on the cast and a negative relief structure on the mould (e.g. Fig. 4.58). Deformation of the surface around the coiled sac is also occasionally visible (e.g. Figs. 4.57, 4.58).

Radial structures within the area of the disc enclosed by the coiled sac (inner cycle) are preserved only in a few specimens (e.g. Fig. 4.57, 4.58, 4.61). These are simple, unbranched thin ridges, around 0.4mm in width, which extend from a faintly visible central ring, of diameter up to 5mm, towards the inner margin of the coiled sac. Lack of preservation of these structures where the inner part of the disc is preserved is likely a taphonomic artefact, rather than an indication of actual absence.

Radially-arranged structures in the depression representing the coiled sac are clearly visible on two specimens - the holotype (M010-0026, Fig. 4.57), and M010-0025 (Fig. 4.61) – and faintly visible on a third, M010-0029 (Fig. 4.58). These
represent a continuation of the position of the radial lines from the central (inner cycle) part of the disc, but are noticeably broader, and widen somewhat towards the outer margin of the coiled sac. Small dissepiments can be seen on both sides of these radial structures (on both specimens where these are well-preserved), spaced 0.3-0.4mm apart, and extending 0.3-0.4mm from the radial structures (Figs. 4.57b and 4.61b).

Radial ridges are clearly visible on the outer area of the disc in the holotype (Fig. 4.57) and all the paratypes (Figs. 4.58-4.61). These may be distinguished into primary, secondary, and tertiary radial ridges. Primary ridges, which are broad, and of relief similar in magnitude to their width, extend from the outer margin of the coiled sac. Secondary ridges, by contrast, are not present in the vicinity of the coiled sac, but rather appear midway between the primary ridges at approximately half the radius from the centre of the disc. These are of approximately the same width and relief as the primary ridges. Tertiary ridges, which are thinner and of lower relief than the primary and secondary ridges, occur adjacent and parallel to the primary ridges along their length.

The tertiary ridges are connected to the primary and secondary ridges by orthogonal dissepiments, spaced approximately 1mm apart (Fig. 4.57, 4.58, 4.60). No dissepiments are present in the areas between the outer margin of the coiled sac, and the appearance of the secondary radial ridges (e.g. Fig. 4.57b).

These radial ridges and dissepiments are consistent in form in all specimens on which they are preserved.

At approximately two-thirds of the radius from the centre of the disc, the tertiary radial ridges are observed to gradually terminate, and the primary and secondary radial ridges broaden out to form elongated oval lappets, which extend to the margin of the disc, tapering towards the periphery (Fig. 4.57, 4.60).

Near the margin of the disc, a set of smaller tertiary lappets develops between the primary and secondary lappets (Figs. 4.57, 4.58, 4.59c). These broaden, commensurate with the tapering of the primary and secondary lappets, before likewise tapering slightly towards the periphery. All lappets appear to extend slightly,
but perceptibly, beyond the margin of the disc, giving the edge a somewhat scalloped appearance (e.g. Fig. 4.57).

The primary and secondary lappets are clearly visible on all 28 specimens which preserve the radial ridges, although where the primary and tertiary radial ridges are not visible or not preserved, it is difficult to differentiate primary from secondary lappets (e.g. Fig. 4.59c). The tertiary lappets, by contrast, are clearly visible in only a few specimens (e.g. Fig. 4.57, 4.59c). Closer examination, however, shows that they are in fact preserved on all 23 specimens in which both radial structures and the outer margin of the disc are preserved (the five remaining specimens which preserve radial ornamentation are broken around the entire margin, such that any evidence of their presence, or absence, is missing).

The distance between the centre of the disc and the appearance of the tertiary lappets was measured and compared with the specimen radius, for all specimens on which both were measurable. The results (Fig. 4.62a) indicate a directly proportional relationship with a coefficient of 0.91 ($R^2=0.9957$).

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Disc radius (mm)</th>
<th>Radius of tertiary lappets (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>M010-0006</td>
<td>110</td>
<td>100</td>
</tr>
<tr>
<td>M010-0013</td>
<td>110</td>
<td>100</td>
</tr>
<tr>
<td>M010-0026</td>
<td>87.5</td>
<td>80</td>
</tr>
<tr>
<td>M010-0022</td>
<td>70</td>
<td>62</td>
</tr>
<tr>
<td>M010-0029</td>
<td>70</td>
<td>63</td>
</tr>
<tr>
<td>M010-0008</td>
<td>65</td>
<td>60</td>
</tr>
<tr>
<td>M010-0012a</td>
<td>65</td>
<td>62</td>
</tr>
<tr>
<td>M010-0015</td>
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<td>58</td>
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<td>60</td>
<td>55</td>
</tr>
<tr>
<td>M010-0007</td>
<td>55</td>
<td>51</td>
</tr>
<tr>
<td>M010-0025</td>
<td>55</td>
<td>50</td>
</tr>
</tbody>
</table>

None of the specimens preserves the opposite (‘ventral’) surface or any internal structures except the coiled sac, which may indicate a taphonomic bias towards the preservation of this particular surface. The opposite side and most internal structures are therefore unknown.
Discussion.—The coiled sac in these specimens is clearly analogous to that of *Eldonia*, confirming the relationship of these specimens with the eldonides. The complex surface ornamentation clearly allies the specimens with the paropsonemids.

The simple radial lines emanating from a central ring in the inner part of the disc are likely to be analogous to the central ring and radial fibres of *E. ludwigi*; the resolution of the preservation of these specimens is insufficient to determine whether these are paired here, as in *Eldonia*.

The radial structures preserved across the coiled sac (e.g. Fig. 4.57b), arranged between the primary radial ridges, are interpreted as continuations of internal lobes (like those of *Eldonia* and *Paropsonema*). Such an interpretation is consistent with the position of the lobes beneath the coiled sac. The short, thin perpendicular disseipments extending from these may be interpreted as possibly representing the attachment of internal fibres to the lobes, suspending them within the coelomic cavity.

As is the case for *Paropsonema cryptophya*, the radial ornamentation in the outer area of *Praeclarus vanrooi* is thought to partly correspond to the form of the internal bifurcating lobes. A postulated position for these lobes directly underneath each of the radial ridges and lappets would suggest that the lobes did not bifurcate, but that instead additional partial lobes were inserted between adjacent lobes, with no apparent interconnection. As this arrangement is quite inconsistent with the form of the lobes as observed in other eldonide species (particularly *Eldonia ludwigi* and *Paropsonema cryptophya*), such an interpretation is likely to be untenable. The general form of eldonide internal lobes could, therefore, only be consistent with a position underneath the spaces between adjacent radial ridges and lappets (Fig. 4.62b). This would indicate a bifurcation of the lobes at approximately half the radius from the centre of the disc (where the secondary radial ridges develop), and a second bifurcation towards the outer margin of the disc (where the tertiary lappets develop). This is consistent with the interpretation of the radial structures across the coiled sac (see above; Fig. 5.47) as part of the internal lobes beneath (Fig. 4.62b).

The consistency in form, both within and between multiple specimens, confirms that the lappets are indeed a morphological feature, and not merely a
taphonomic artefact caused by the presence of the lobes underneath the radial structures. This interpretation is supported by the inferred position of the internal lobes underneath the gaps between the radial ridges, rather than the ridges themselves (Fig. 4.62b,c).

The directly proportional relationship between the specimen radius and the distance between the centre of the disc and the tertiary lappets (Fig. 4.62a) indicates that these were not a feature which appeared later on during ontogeny, but were a consistent part of the morphology of *Praeclarus vanroii*. Further, this also indicates that *Praeclarus vanroii* likely grew by inflation, and not marginal accretion.

While some plastic deformation is clearly visible in several specimens (e.g. M010-0026, Fig. 4.57, and M010-0025, Fig. 4.61), the limited extent of this may suggest a degree of inelasticity, particularly given the coarse nature of the enclosing sandstone bed. This contrasts with the apparent preservation of internal structures, which indicates that the outer integument was sufficiently flexible to allow the impression of fine details (such as the dissepiments under the coiled sac) through the surface. The rigidity may thus have been imparted by the radial ridges and dissepiments, rather than the integument itself; indeed, this may have been the primary function of the ornamentation.

The surface ornamentation of *Praeclarus vanroii* differs significantly in form to all previously described paropsonemids in lacking the complex ornament in the inner cycle of the disc, and in the radial ridges developing into lappets at the outer disc margin. These differences are deemed sufficient to warrant the erection of a new genus and species for these specimens.

A reconstruction of *Praeclarus vanroii* is shown in Fig. 4.63.
PRAECLARUS SP.

Figs. 4.64–4.67

p 1995 Discophyllum mirabile Chapman; Friend, p. 98-102, pl. 3.3,
p 2010 Paropsonema mirabile (Chapman); MacGabhann and Murray, fig. 7b.

Material.– MV P30713 (part and counterpart) (Fig. 4.64–4.65), MV P26661 (pars) (Fig. 4.66).

Occurrence.– Specimen P26661 occurs within the Lower Ludlow (Silurian) Dargile Formation near Panton Hill, as described above (p. 106). Specimen P30713 was noted by Friend (1995) to have been recovered from a quarry 1.9 km SE of Walls Crossing on the Spur Road, near Clonbinane (37° 17’ 24.39” S, 145° 04’ 45.57” E), approximately 80 km north of Melbourne, exposing the top of the Clonbinane Sandstone Member of the Humevale Formation (Kinglake 1:63,360 geological map: Geological Survey of Victoria, 1977). As discussed in Chapter 3.2.2 (p. 54), this member was subsumed by Edwards et al. (1998) into the Hynlands Member of the McIvor Sandstone Formation, of late Ludlow age.

Description.– Specimen P30713 (Fig. 4.64–4.65), of which both the part mould and counterpart cast are available, is an elliptical disc, varying from 90mm to 100mm in diameter, which is slightly folded along the long axis. The counterpart comprises only the disc, while the part is in the centre of a slightly larger block, with the matrix (a greenish medium- to coarse-grained sandstone) visible around the specimen. Approximately half of the disc is stained red-brown, fading towards the other side; from the part mould, it is clear that this discolouration is limited to the surface of the disc. The specimen is revealed by a fracture through the rock matrix, which is clearly not concordant with a bedding plane, indicating that the specimen was preserved within a sandstone bed.

The central part of the disc is dominated by an elongate curved area of greenish matrix, seen in positive relief on the counterpart, and negative relief on the part. This is believed to represent the medial portion of the coiled sac, infilled with
sediment. From one end of this, a long, thin, curved tube-like structure emerges, seen in negative relief on the counterpart and positive relief on the part. This is thought to represent the distal portion of the coiled sac.

Between the coiled sac and the centre of the disc, only a small number of fine radial ridges are preserved, of sub-millimetric thickness and relief. The outer part of the disc is covered by a complex ornament, consisting of radial ridges and dissepiments, in a configuration similar (but not identical) to that of *Praeclarus vanroii*.

Three series of radial ridges are preserved. Primary ridges extend from the outer margin of the coiled sac, while secondary radial ridges appear between the primary ridges at approximately half the radius of the disc from the centre. As in *P. vanroii*, significantly thinner tertiary ridges are preserved to either side of the primary ridges. Orthogonal dissepiments connect the tertiary ridges to both primary and secondary radial ridges.

The gap between the outer margin of the coiled sac and the appearance of the tertiary ridges is obscured around the medial portion of the coiled sac, where the sediment infill appears to have expanded to partially cover the outer area of the disc.

Towards the margin of the disc, the broadening primary and secondary radial ridges develop into rounded lappets, which narrow slightly towards the periphery. At approximately 10mm from the margin of the disc, the tertiary radial ridges and dissepiments disappear; only the primary and secondary lappets reach the periphery. These give the margin of the disc a slightly scalloped appearance.

The number of primary radial ridges is estimated at approximately 26, based on their angular separation, with the uncertainty due to both incomplete preservation and plastic deformation.

Only the counterpart cast of specimen P26661 is preserved (Fig. 4.66). This specimen comprises two fossils (Fig. 4.66a): a large specimen of *Paropsonema mirabile*, with a smaller specimen of *Praeclarus sp.*, and clearly demonstrates the differences between these two forms. The specimen of *Praeclarus sp.* comprises just under half of a discoidal specimen, with an estimated diameter of 80mm. The central
area of the disc, estimated at 25mm in diameter, is featureless, but is surrounded by a curved depression around 6.5mm wide, representing the coiled sac, inside which positive radial ridges are visible. The outer part of the disc, from the coiled sac to the margin, is covered by radial structures and dissepiments in exactly the same configuration as the holotype. Based on their angular separation, a total of between 22-26 primary radial ridges is estimated, but this is again uncertain due to incomplete preservation and the dextral decrease in the angular spacing of the radial ridges. The margin of the disc is not preserved.

Discussion.– These specimens preserve almost exactly the same features as *Praeclarus vanroii*. The coiled sac, primary, secondary and tertiary radial ridges, primary and secondary lappets, dissepiments, and inner radial ridges, are all observed a similar configuration to those of *Praeclarus vanroii*, and are interpreted in the same way. This arrangement confirms that these specimens belong in the genus *Praeclarus*, differing in only three respects from the type species:

1. The radial structures observed in the coiled sac of specimen P26661 are aligned with the primary ridges, instead of the secondary radial ridges as in *P. vanroii*.

This is likely to be a taphonomic artefact.

2. The number of radial ridges is also estimated to be slightly lower than that of *Praeclarus vanroii*.

This may be due to natural variation between two species, ontogenetic variation (with the number of lobes increasing with the age, and thus size, of a specimen), or simply uncertainty in the estimations; but most likely the latter.

3. Tertiary lappets are not observed at the disc margin.

This is thought to reflect the form of the internal lobes, which may thus interpreted to have only one bifurcation, around the appearance of the secondary radial ridges, instead of the two inferred for *Praeclarus vanroii*. While only one of these specimens, MV P30713 (Fig. 4.64-4.65), preserves the outer margin of the disc, there are clearly no tertiary lappets present. Moreover, similarly sized specimens of *Praeclarus vanroii*,
e.g. M010-0007, M010-0010, and M010-0025, do preserve the tertiary lappets, which were also shown above to be consistently present on *Praeclarus vanrooi* specimens of all sizes, and thus not an ontogenetic feature (Fig. 4.62a).

The lack of tertiary lappets in the Silurian specimens *may* be a morphological character worthy of distinction at the specific level. As such, these specimens cannot be assigned at present to *Praeclarus vanrooi*. However, as only one of the two specimens preserves part of the outer disc margin, it would be premature to erect a new species on this basis alone. These specimens are thus placed in open nomenclature as *Praeclarus* sp.

Plastic deformation in specimen MV P30713 (Fig. 4.64-4.65) also confirms the flexibility of the surface. However, the small number of specimens again precludes any estimation or precisely how flexible this surface was.

The co-occurrence of specimens of *Praeclarus* sp. and *Paropsonema mirabile* on a single sample (Fig. 4.66a) is particularly important, as it is the only known example of the preservation of two adjoining different kinds of paropsonemid, and confirms that different genera and species could co-exist in the same area. However, the details of this co-existence are not yet clear. Did the two genera have subtly different habitats, with the specimens transported and preserved together post-mortem? Did the two genera occupy different ecological niches? Unfortunately, more specimens collected over a broader area and range of environments in Victoria would be required to elucidate more details about this co-existence.

A reconstruction of *Praeclarus* sp., assuming the absence of the tertiary lappets is real and not an artefact, is provided in Fig. 4.67.
Genus DISCOPHYLLUM Hall, 1847

_Type species._– _D. peltatum_ Hall, 1847

_Diagnosis._– Unmineralised, flexible discoidal metazoan, not radially symmetrical. Dextrally coiled sac present in the inner third of the disc. Radial ridges, divisible into more prominent primary and less prominent secondary ridges, extend continuously in a single cycle from the centre of the disc to the margin, laterally connected by orthogonal dissepiments.

_Discussion._– Barrois (1891) believed _Actinophyllum_ Phillips, 1848 was a junior synonym of _Discophyllum_ Hall, 1847, and reassigned _A. plicatum_ Phillips, 1848 (in Phillips and Salter, 1848) as a second species of _Discophyllum_, describing specimens from Northern France under this name. However, the genus _Actinophyllum_ was restored by Straw (1926), who regarded the French specimens as distinct from _A. plicatum_. Harrington and Moore (1956b) did not believe the French specimens to belong in either _Discophyllum_ or _Actinophyllum_, and regarded them as _incertae sedis_, though possibly medusoid. Further investigation of these specimens is required to determine their taxonomic affinity, but there appears little _a priori_ reason to suggest a relationship between the illustrated specimens and _Discophyllum_.

Specimens from Ethiopia were attributed by Saxena and Assefa (1983) to _Discophyllum cf. peltatum_, who accordingly proposed that the host sediments were Ordovician, based on the known age of the type specimens of _D. peltatum_. However, their specimens are extremely similar to specimens described under the generic name ‘Rutgersella’ by Johnson and Fox (1968), which were convincingly shown to be pyrite rosettes by Cloud (1973). There is little doubt that the Ethiopian specimens should be interpreted in the same way, and are thus of no biostratigraphic significance.
Chapter Four – The Class Eldoniata

**DISCOPHYLLUM PELTATUM** Hall, 1847

*Figs. 4.68–4.109*

\[\text{v}^*\] 1847 *Discophyllum peltatum* Hall, p. 277, pl. LXXV fig. 3,
\[\text{v}\] 1898 *Discophyllum peltatum* Hall; Walcott, p. 101, pl. XLVII,
\[\text{p}\] 1900 *Discophyllum peltatum* Hall; Clarke, p. 178,
\[\text{p}\] 1916 *Discophyllum peltatum* Hall; Ruedemann, p. 26,
\[\text{p}\] 1956 *Discophyllum peltatum* Hall; Harrington and Moore, p. F150, fig. 120,1a–b,
\[\text{p}\] 1986 *Discophyllum peltatum* Hall; Stanley, p. 79,
\[\text{p}\] 1993 *Discophyllum peltatum* Hall; Conway Morris, 1993b, p. 598,
\[\text{p}\] 1995 *Discophyllum peltatum* Hall; Friend, p. 92-4, pl. 3.1,
\[\text{v}\] 2001 un-named paropsonemid, Samuellson et al., p. 367, fig. 2,
\[\text{p}\] 2002 *Discophyllum peltatum* Hall (err. cit.); Zhu et al., p. 180-1,
\[\text{.}\] 2003 *Eldonia berbera* Alessandrello and Bracchi, p. 337–58, fig. 4–8,
\[\text{.}\] 2004 *Pseudodiscophyllum windermerensis* Fryer and Stanley, p. 1112-8, pl. 1, text-figs. 2–4,
\[\text{p}\] 2006 *Pseudodiscophyllum windermerensis* Fryer and Stanley; Van Roy, p. 52-4,
\[\text{p}\] 2006 *Discophyllum peltatum* Hall; Van Roy, p. 51-3,
\[\text{v}\] 2006 *?Discophyllum berberum* (Alessandrello and Bracchi); Van Roy, p. 52-7, fig. 3.14-3.15.

**Material.**—Lectotype: UC 12517 (designated herein) (Fig. 4.68)

Paralectotype: UC 60886 (Fig. 4.69)

Non-type: 231 specimens in the collections of the National University of Ireland, Galway; 2 specimens in the collections of the Yale Peabody Museum; BMNH R 54916 (Natural History Museum, London).

**A note on the type specimens.**—Hall (1847) described *Discophyllum peltatum* from two specimens, illustrating one. Walcott (1898) repeated Hall’s description with some additional details, and figured both specimens. With the exception of Harrington and Moore (1956b), who reproduced Walcott’s illustrations, this was the last time
Both Hall and Walcott listed the repositories of the specimens as being the Cabinet of Troy Lyceum and the Cabinet of Professor Cook. Walcott (1898) also noted that he had examined the specimens courtesy of Professor J.M. Clarke, then at the Rensselaer Polytechnic Institute (RPI); later the Director of the New York State Museum. The Troy Lyceum of Natural History no longer exists: its collections were transferred to the RPI. Professor George H. Cook was, in 1847, a Senior Professor at the RPI. Unfortunately, the RPI moved its collections several years ago, but as they had no invertebrate palaeontologist on staff, left this collection packed in storage, and it is thus inaccessible (Dr. Jon Price, pers. comm., 24 June 2009); the current RPI staff were therefore unable to search their collections for these fossils.

Prof. Cook had subsequently become Professor of Chemistry and Natural History at Rutgers University, New Jersey, and was appointed State Geologist of New Jersey in 1864. However, neither specimen moved to New Jersey with Prof. Cook.

Ruedemann (1916) seems likely to have examined the specimens. At this time, John M. Clarke was then Director of the NYSM (having succeeded Frederick Merrill, who had in turn replaced James Hall), while maintaining his Professorship at the RPI; the specimens could, at this time, have been in either the collections of the NYSM. However, the NYSM has no record of the specimens.

James Hall, during his life, sold part of his collections to the American Museum of Natural History in New York City. After his death, a further part of his collections was sold. Part was bought from his estate in 1907 by Mr. J.D. Rockefeller, and donated to the University of Chicago (University of Chicago, 1907), where, as the James Hall Collection, it formed the core of the palaeontological collections of the Walker Museum. The Walker Museum’s collections were transferred to the Field Museum, Chicago, Illinois, in 1965.

The chance discovery of a list of type specimens of Coelenterata in the Field Museum, Chicago (Forney et al., 1977), revealed that to be the current repository of
the specimen figured by Hall (1847), on permanent loan from the Walker Museum of the University of Chicago. Forney et al. (1977) noted the whereabouts of the second specimen to be unknown; however, this specimen was also subsequently discovered in the Field Museum, where a label records it was rediscovered by Eric Slusser while washing Devonian fossils. It is also on permanent loan from the Walker Museum.

The descriptions and figures of these specimens herein are thus the first in over one hundred years, and significantly add to our knowledge of this genus and species.

Walcott referred to both specimens as the “type specimens” (Walcott, 1898, p. 101). Harrington and Moore (1956b), however, listed the specimen originally figured by Hall as the holotype of *D. peltatum*, and the second as the paratype.

This was incorrect, as no such designation was made by Hall (1847), and accordingly, both specimens should have been considered syntypes. Article 74.5** of the ICZN Code on Zoological Nomenclature clearly states that where a taxon is established on the basis of more than one specimen, a subsequent referral to one of the specimens as the holotype does not constitute the valid designation of that specimen as the lectotype. To ensure full compliance with the ICZN Code, therefore, specimen UC 12517 (Fig. 4.68), originally figured by Hall (1847), and referred to as the holotype by Harrington and Moore (1956b), is hereby designated as the lectotype of *D. peltatum*. UC 60886 (Fig. 4.69) is therefore the paralectotype.

*Diagnosis.*—As for genus.

*Occurrence.*—First Bani Group, Tafilalt, Morocco (Sandbian, Ordovician); Upper Tiouririne Formation, Ktaoua Group, Tafilalt, Morocco (Katian, Ordovician); Troy

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** “When the original work reveals that the taxon had been based on more than one specimen, a subsequent use of the term “holotype” does not constitute a valid lectotype designation unless the author, when wrongly using that term, explicitly indicated that he or she was selecting from the type series that particular specimen to serve as the name-bearing type” (ICZN, 1999).
Frontal Zone, Troy, New York, USA (Ordovician); Bannisdale Formation, Windermere Supergroup, Windermere, England (Ludfordian, Silurian).

Description.– The lectotype of *D. peltatum*, UC 12517, is an oval disc, approximately 85mm along the long axis, and an estimated 65mm along the short axis (Fig. 4.68). The disc is virtually complete, with minor damage removing the margin along one long side of the specimen, but it is poorly preserved. Nonetheless, radial structures are observed over much of the surface, running from near the centre to the margin. It is unclear whether the failure of these radial structures to reach the centre is a faithful representation of the original morphology, or a taphonomic artefact caused by the poorer preservation of thinner radial structures in that part of the disc. However, some approach the centre closer than others, suggesting a taphonomic artefact.

The radial structures can be divided into two kinds. Most of the ridges are large and broad, widening towards the periphery. However, small, thin ridges of approximately constant width (<1mm) are observed in places between the larger ridges towards the periphery. The spacing of the ridges is clearly not constant, with those on one side of the specimen noticeably more closely spaced than those on the other side; however, due to the plastic deformation (elongation) and relatively poor preservation, it is impossible to define this variation more precisely. This also makes evaluating the number of radial structures difficult. Nonetheless, a total of 80-90 (and likely on the smaller end) of thicker radial structures is estimated, with an equal number of thinner ridges.

The surface of the specimen is otherwise not entirely smooth, with a raised curved area in the inner third of the disc.

The paralectotype, UC 60886, is much better preserved and less deformed than the lectotype, but preserves far less of the specimen (Fig. 4.69). The diameter of this specimen is estimated at 130mm, twice the long axis of the lectotype. Radial structures again cover much of the preserved surface, and are much clearer than on the lectotype, with three, rather than two, types of radial ridges distinctly visible. The broader, widening ridges visible on the lectotype are here seen to in fact form two distinct sets of ridges: primary radial ridges, which extend uninterrupted from the margin almost to the centre of the disc, and secondary radial ridges, which extend
from the margin to approximately one-third of the radius from the centre of the disc. These are extremely similar in form in the outer part of the disc, and cannot be distinguished where the difference in length cannot be seen. Tertiary ridges, which are thin, and do not broaden towards the margin, are seen in the outermost part of the disc, between primary and secondary radial ridges. Orthogonal dissepiments occur between all of the radial ridges over the entire disc.

As in the lectotype, the angular spacing between the radial ridges is clearly not equal, with the ridges in the section close to the preserved margin of the disc clearly spaced wider than those on the opposite side of the disc. Eighteen primary ridges were measured, with radial separation varying from 6.5° to 13°. Using an average value for the angular separation, it is estimated that there were originally around 40 primary radial ridges, with an equal number of secondary radial ridges, and 80 tertiary radial ridges. The large variation in angular spacing makes such an estimation inaccurate, particularly as the exact nature of the variation is uncertain, due to the mechanical damage to the disc, and thus partial preservation. However, this corresponds closely with the estimate for the lectotype.

There is again a distinct raised area in the centre of the disc which may represent the coiled sac, but due to the incomplete preservation, the precise form of this cannot be distinguished. The margin of the disc, where preserved, is sharp and clear.

231 discoidal specimens collected from field localities M001, M003, M005, M008, M009, M012, and M020 in the Ordovician of Morocco, were identified as paropsonemid, by the presence of either the coiled sac or the distinctive radial ornamentation (not including the 30 specimens from site M010 described above as the new genus and species *Praeclarus vanrooi*, this species is not known from any of the other localities). These were examined in the collections of the National University of Ireland, Galway, and the Yale Peabody Museum. 14 of these specimens preserve sufficient diagnostic features to be unequivocally identified as *D. peltatum*: specimens M001-0021 (Fig. 4.70), M003-0004 (Fig. 4.71), M003-0015 (Fig. 4.72), M003-0025 (Fig. 4.73), M003-0026 (Fig. 4.74), M005-0001 (Fig. 4.75), M005-0033 (Fig. 4.76), M005-0034 (Fig. 4.77), M005-0042 (Fig. 4.78),
Differential taphonomy of Palaeozoic and Ediacaran non-mineralised fossils

M005-0106 (Fig. 4.79), M005-0165 (Fig. 4.80), M008-0046a (Fig. 4.81), YPM 226462 (Fig. 4.82), and YPM 226468 (Fig. 4.83). The remaining 217 paropsonemid specimens are tentatively assigned to *D. peltatum*, on the basis that their morphology is fully consistent with *D. peltatum*, and no other paropsonemid species are known from these particular localities. Several of these specimens show most of the diagnostic features, save that the radial ridges are not seen to extend uninterrupted from the centre of the disc to the margin (e.g. specimens M005-0090 and M005-0096a, Figs. 4.84-86). This is primarily due to the poor preservation in the inner area of the disc.

The quality of preservation across these specimens is quite variable. However, taken together, these specimens exhibit not only all of the diagnostic features observed in the type material, but significant new morphological details, considerably enhancing our knowledge of this genus and species.

The coiled sac, not clearly observed in the type material, is preserved in 184 of the Moroccan *Discophyllum* specimens, and is always dextrally coiled on counterpart casts and sinistrally coiled on part moulds (Fig. 4.87). Generally, this is preserved in negative relief on casts and in positive relief on moulds, but this is not universally the case, with 18 specimens (specimens M005-0010b, M005-0017, M005-0042, M005-0043, M005-0048, M005-0054, M005-0065b, M005-0086, M005-0087, M005-0088a, M005-0119, M005-0128, M005-0133a, M005-0145, M005-0149, M005-0163, M005-0171, and M005-0191) preserving the sac as either a positive relief structure on a cast or as a negative relief structure on a mould. This is particularly clear on specimen M005-0042 (Fig. 4.78), a counterpart cast, which preserves a substantial part of the coiled sac in significant positive relief from the surface.

Twenty-eight specimens also preserve the coiled sac with little or no relief from the surface. In these specimens, the sac is preserved with slightly increased lustre (or optical reflectivity) in comparison to the remainder of the surface, likely due to the concentration of aluminosilicate minerals in this area (e.g. M005-0035, Fig. 4.87e). Such an increase in surface lustre is also notable on some specimens.
which do preserve the coiled sac in relief, for example specimens M005-0033 (Fig. 4.76) and M005-0034 (Fig. 4.77).

The shape of the coiled sac is relatively consistent, broadening slightly from the proximal end, reaching the maximum thickness at approximately one-third of its length, then tapering to become narrower (than the proximal end) until approximately two-thirds of the length, and then maintaining a similar width from this point to the distal termination. However, the shape and flexibility of the sac makes morphological measurements difficult; even the maximum thickness of the coiled sac may not be a useful measurement in all cases, due to the potential for variation in shape due to differential compaction or plastic deformation. Nevertheless, this was recorded for all possible specimens (n=161) for comparison to *E. ludwigi*. (Fig. 4.88a). To analyse the utility of these measurements, this was compared to the size distribution determined from the direct measurement of the long axis diameter of every measurable specimen (n=177), which shows a similar distribution (Fig. 4.88b), albeit with a more pronounced trough in the middle of the peak region (this double-peak distribution may indicate a difference in the size distribution of specimens from different levels; the more pronounced trough between peaks may also reflect the decrease in margin of error for measurements of 120-150mm, as compared to those in the region of 12-15mm). For 146 specimens, both the maximum width of the coiled sac and the disc long axis diameter were measurable. Plotting the coiled sac maximum width as a function of the disc long axis diameter for these specimens confirms that these are approximately directly proportional (Fig. 4.88c), with the coiled sac maximum width approximately 10% of the disc diameter. This suggests that the maximum width of the coiled sac may be a relatively valid proxy for the disc diameter in specimens for which the diameter is not measurable (and may validate the such use of this measurement for *Eldonia ludwigi*; p. 75, Fig. 4.20).

A structure is preserved at the proximal termination of the coiled sac in 27 specimens (M001-0011, M005-0011, M005-0021, M005-0033, M005-0034, M005-0038, M005-0057, M005-0090, M005-0096a, M005-0100b, M005-0102a, M005-0103, M005-0104, M005-0106, M005-0126, M005-0138, M005-0165, M005-0174, M005-0183a, M005-0192a, M005-0194, M008-0030, M008-0046a,
YPM 226462, and YPM 226468). This is generally preserved on counterpart casts as a thick ridge or bar-like structure irregularly preserved in positive relief, slightly wider that the sac termination. This is also preserved in negative relief on part moulds (Fig. 4.89).

Occasionally, as in M005-0034 (Figs. 4.77 and 4.89e), irregular structures extend to either side of the proximal termination of the coiled sac. An approximately circular depression is observed at the distal termination of the coiled sac (Fig. 4.90) in 12 specimens (M001-0020, M003-0015, M003-0027a, M005-0033, M005-0090, M005-0096a, M005-0104, M005-0134, M005-0157, M005-0183a, YPM 226462, and YPM 226468). Only 8 specimens preserve structures at both proximal and distal terminations (M005-0033, M005-0090, M005-0096, M005-0104, M005-0157, M005-0183a, YPM 226462, and YPM 226468).

Radial ridges are preserved in 177 specimens. These are preserved in the inner area of the disc only in the fourteen specimens noted above to preserve sufficient diagnostic features to be unequivocally assigned to *D. peltatum*: M001-0021 (Fig. 4.70), M003-0004 (Fig. 4.71), M003-0015 (Fig. 4.72), M003-0025 (Fig. 4.73), M003-0026 (Fig. 4.74), M005-0001 (Fig. 4.75), M005-0033 (Fig. 4.76), M005-0034 (Fig. 4.77), M005-0042 (Fig. 4.78), M005-0106 (Fig. 4.79), M005-0165 (Fig. 4.80), M008-0046a (Fig. 4.81), YPM 226462 (Fig. 4.82), and YPM 226468 (Fig. 4.83). Importantly, one of these specimens shows these radial ridges to extend from a central ring (YPM 226468, Fig. 4.83). The remaining 163 specimens exhibit radial ridges only on the outer part of the disc.

In 79 specimens, primary and secondary radial ridges can be distinguished (e.g. Figs. 4.70-4.80 and 4.82-4.86). The primary radial ridges in these specimens are more prominent, especially towards the inner part of the disc, being of greater width and relief than the secondary ridges. Both primary and secondary radial ridges broaden towards the periphery, with the secondary ridges broadening closer to the margin than the primaries. The secondary radial ridges appear in some specimens to be shorter than the primaries, and in particular are often not visible in the region immediately outside the outer margin of the coiled sac. This is the case, for example, in specimens M001-0021 (Fig. 4.70) and M003-0026 (Fig. 4.74). However, the
presence of the secondary radial ridges over the coiled sac in both of these specimens shows that this absence is merely a taphonomic artefact, and does not reflect the original morphology.

Dissepiments are seen in 21 specimens, and are of marginally lower relief than the radial ridges. These extend to either side of each primary radial ridge from the central ring (or inner part of the disc) to the margin. For the inner two-thirds of the disc, these dissepiments extend to the secondary radial ridges. However, in the outer third of the disc, as shown clearly by specimens M005-0042 (Fig. 4.78) and YPM 226468 (Fig. 4.83), dissepiments also extend from the secondary radial ridges. Over this area, where the dissepiments from adjacent primary and secondary radial meet, thin tertiary ridges can be observed (Figs. 4.91 and 4.92). These tertiary radial ridges detach from the secondaries where dissepiments start to extend from the latter. The tertiary ridges are thinner than the dissepiments, and do not widen towards the disc margin in the same manner as the primary and secondary radial ridges.

Both the length and width of the dissepiments increases towards the outer margin, commensurate with the increase in size of and space between the radial ridges. The distance between two adjacent dissepiments is approximately the same as their width. The net effect of these ridges is to define a set of approximately rectangular pits (of negative relief from the disc surface) at either side of each radial ridge (Fig. 4.91).

Where dissepiments from adjacent radial ridges meet, they are sometimes aligned, creating the appearance of one continuous dissepiment joining adjacent radial ridges. However, this is not always the case, and they are often offset, such that one dissepiment is aligned with the gap between two dissepiments from the adjacent radial ridge. This often changes radially along a single set, such that at one point between a pair of adjacent radial ridges, the dissepiments are aligned, but closer to the margin and/or the centre of the disc, they are offset (see e.g. Fig. 4.91, YPM 226468).

A small number of specimens (M005-0076, M005-0083, M005-0092, M005-0181, and M020-0006) exhibit the radial structures as a series of thin,
unbranched dark red-purple lines of constant width (e.g. Fig. 4.93). These lines may represent the gaps between the radial ridges, rather than the ridges themselves, as indicated by two specimens which preserves both relief and darkened lines (M005-0076 and M005-0083).

Due to variations in completeness and quality of preservation, most specimens preserve only a small number of radial ridges. However, five specimens:

- M005-0042 (Fig. 4.78),
- M005-0090 (Fig. 4.84),
- M005-0096a (Figs. 4.85 and 4.86),
- M005-0106 (Fig. 4.79), and
- M005-0165 (Fig. 4.80),

preserve the radial ridges over the entire surface of the disc. Each of these specimens preserves the same number of ridges, with 50 primary and 50 secondary radial ridges observed.

These specimens also demonstrate that the size and angular spacing of the radial ridges is not equal, but decreases in a dextral direction around the disc, with the largest spacing at the proximal termination of the coiled sac. A similar size variation was also noted in many additional specimens which do not preserve the full set of primary radial ridges, including M001-0021 (Fig. 4.70), M003-0026 (Fig. 4.74), and M005-0033 (Fig. 4.76).

To analyse this apparent dextral decrease in angular spacing, the primary radial ridges on specimen photographs were marked with lines running from the centre to the edge of the disc in Adobe Illustrator, with the angular spacings between the marked lines measured in the image analysis program ImageJ Freeware; available from http://rsbweb.nih.gov/ij/†††. The angles were sequentially measured to an accuracy of 0.01°; the main source of error in this process

†††Freeware; available from http://rsbweb.nih.gov/ij/
was thus the placement of the lines on the radial ridges, and such errors were compensated for by adjacent measurements (as indicated by the sum of measured angles totalling almost precisely 360° in complete specimens).

This was done for the five specimens (noted above) preserving a complete set of primary radial ridges, and 7 specimens preserving only a partial set, namely M005-0010a, M005-0020, M005-0024b, M005-0038, M005-0150, M005-0157, and M005-0178 (Figs. 4.94-4.96). These specimens were chosen as they clearly preserved more than ten primary radial ridges, and appear to be only minimally deformed from an originally circular outline. The full dataset is presented in the Appendix, as an Excel spreadsheet, in the data DVD accompanying this thesis.

In the case of M005-0020, the evidence for a decrease in size is questionable; although a regression line through the points has a negative slope, the decrease is low. However, the other eleven specimens all appear to show a dextral decrease in angular spacing. Interestingly, the 5 complete specimens (Fig. 4.94) demonstrate that this size decrease is concentrated around the proximal and distal ends of the coiled sac, with the largest spacing between ridges at the proximal end of the sac reaching around 9°-10°, and the smallest spacing at the distal end falling to around 5°-6°. The ridge spacing across the middle part of the coiled sac appears to be relatively constant, falling between 6°-8°. though all of these specimens exhibit some variation between these values. Perhaps more importantly, the nature of this variation is not constant between specimens. This may indicate that the position of the radial ridges was not fixed, due to the flexibility of the integument or just natural variation. Further, this may also suggest that the spacing decreases seen in partial specimens (with only ridges over the middle part of the sac preserved) could be a result of unrecognised deformation, or of such natural variation.

For the specimens which do not preserve radial ridges around the complete disc (Fig. 4.96), the equation of a regression line through the collected data for each individual specimen was used to estimate the original number of primary radial ridges on the complete disc. In each of these cases, the estimated number was in the vicinity of 50. This may be interesting in the context of the size of the specimens so analysed, ranging from a diameter of 90mm for M005-0020 to 195mm in M005-
However, M005-0020 is an outlier, with the next smallest analysed specimen, M005-0178, having a diameter of 145mm.

Concentric rings are observed on the surface of the disc in 49 specimens (e.g. Figs. 4.76, 4.80, 4.85, 4.86, 4.89a, 4.89c, and 4.97). These appear to be fairly consistent in their relative position with respect to the radius of the disc. They most commonly occur at approximately half the radius (15 specimens), two-thirds of the disc radius (10 specimens), and near the margin of the disc, at approximately five-sixths of the radius (38 specimens). These are generally preserved as thin, shallow grooves on counterpart casts, and as thin ridges on part moulds, but reversal of this relief is also known. In some specimens, these are not discrete ridges, but are closer in appearance to irregular annular bands on the surface – best seen in M005-0011 (Fig. 4.89c), M005-0096a (Figs. 4.85 and 4.86), and M005-0138 (Fig. 4.97b). Only one specimen (M003-0003, Fig. 4.97a) preserves concentric rings in the inner part of the disc.

Tubular structures in strong positive relief are observed on two specimens, M012-0001 and M005-0102b, both counterpart casts preserved in endorelief (Fig. 4.98). These are seen to bifurcate at approximately two-thirds of the radius from the centre of the disc. While the form of the radial ornament on part moulds occasionally reflects these tubular structures, with the space between two primary radial grooves “bifurcated” by the broadening secondary radial grooves, this is due to the reversed relief of part moulds, and the radial ornamentation is never seen to take this form on counterpart casts, nor to be preserved with such strong relief. These structures strongly resemble the internal lobes seen in *Parapsonema cryptophya* specimen NYSM 6818 (Fig. 4.46).

Taphonomic effects and variations are also observed in multiple specimens of *Discophyllum peltatum* from Morocco. For example, on specimen M005-0001 (Fig. 4.75), a reticulate texture is observed on the bed surface, surrounding the fossil. Interestingly, a triangulate area with sharply defined curved margins within the boundary of the specimen also shows a continuation of this surface texture. This may
be interpreted as evidence of tearing. Specimen M005-0023 also appears to exhibit evidence of tearing (Fig. 4.99).

49 specimens are seen to be significantly folded (e.g. Fig. 4.100), including two which are rolled-up into a ‘cigar-like’ shape (M005-0048 and M005-0181, Fig. 4.101). Minor folding, surface irregularities, and plastic deformation are observed in numerous other examples. 24 specimens also exhibit plastic deformation in the form of stretching, taking a more elliptical form. Several specimens from sites M001 and M003, meanwhile, show a change in relief across the disc, with area inside the outer margin of the coiled sac raised with respect to the outer area (e.g. M001-0021, Fig. 4.70).

11 specimens are observed to have evidence of possible post-mortem shrinkage. This is particularly strong in specimen M005-0043 (Fig. 4.102), where the ornamentation can be seen to stop at an inner margin, while a broader outer outline indicates the original size. Other specimens generally display only a few millimetres of shrinkage, commonly expressed by a ridge surrounding the counterpart cast in positive hyporelief (e.g. M005-0033, Fig. 4.76, and M005-0042, Fig. 4.78).

In 13 cases (comprising 27 specimens), discs are preserved overlapping, often as far as the coiled sac (Fig. 4.103); one extraordinary example (M005-0002, Fig. 4.104) comprises three discs of different sizes stacked on top of each other, such that only a small part of the margins of the second and third discs are observed.

Three specimens appear to show evidence of post-mortem scavenging. Specimens M001-0021 (Fig. 4.70) and M003-0025 (Fig. 4.73) both exhibit irregular or meandering tube-like structures, while irregular curved pairs of ridges, separated by a furrow, are present near the distal end of the coiled sac and also on the outer part of the disc, adjacent to the medial portion of the coiled sac, on M005-0042 (Fig. 4.78). These do not correspond at all to any morphological structure of the specimens, and clearly resemble ichnofossils.

Most specimens at the sites are preserved as positive hyporelief casts and/or negative epirelief moulds (including 82 collected specimens). A plurality of the
collected material (112 specimens), however, are preserved in endorelief, within beds. Five specimens are preserved as positive epirelief moulds and/or negative hyporelief casts (specimens M005-0020, M005-0034, M005-0035, M005-0183a, and M005-0183b). It should be noted that several specimens were found in float, or were initially recovered by local workers who did not record any orientation or positional data (32 specimens). In these cases, the original orientation and relief relative to bedding geometry is unknown.

In several specimens (e.g. M005-0034), a depression is present on the top surface of the bed, with the low point corresponding to the centre of a parapsonemid specimen preserved on the bed sole (or inside the bed) beneath. This likely represents sediment moving downwards under the force of gravity to fill the space vacated by decaying organic tissues.

No matter the orientation of preservation, only the described dorsal surface is known: no specimen preserves the ventral surface. Specimens preserved in positive hyporelief/negative epirelief are universally preserved with the dorsal surface facing downwards, as are the majority of specimens in endorelief. Specimens preserved in positive epirelief/negative hyporelief, along with a minority of endorelief specimens, are always preserved with the dorsal side facing upwards.

One additional specimen which should be assigned to D. peltatum was described by Fryer and Stanley (2004) as a new genus and species Pseudodiscophyllum windermerensis. This specimen (Fig. 4.105), preserved in endorelief within a fine mudstone, is slightly oval, varying from 117mm along the long axis to 107mm on the short axis. The specimen was collected in float, thus the original orientation is unknown.

The disc is dominated by a dextrally coiled raised area, representing the coiled sac, which varies from one-third to one-half of the distance from the centre to the margin. A distinct radial ornament is clear over most, but not all, of the surface, with alternating primary and secondary radial ridges. These are identical in form to those seen in well-preserved Moroccan specimens and the paralectotype, save that the secondary radial ridges are more prominent in the inner part of the disc, inside the coiled sac. 38 primary and 38 secondary ridges are visible on the surface, with an
average spacing of 6.4°, suggesting an original total of 56 of each on the complete surface. However, the spacing varies in a non-linear fashion around the disc, suggesting that the angles have been somewhat distorted by deformation, which is supported by the non-circular shape of the fossil. The true number of each is thus uncertain, but is likely to have been around 50.

Towards the edge of the disc, tertiary ridges can also be seen in well-preserved areas. These are not strictly radial, but appear to diverge from the secondary radial ridges, and continue at an angle at approximately 6° from the secondary ridges until they reach a point approximately midway between the primary and secondary radial ridges, at which point they straighten and continue as radial ridges towards the margin. These ridges are thin, and of constant width.

Dissepiments are present on the surface in the same configuration as M005-0042 and YPM 226468, branching from primary radial ridges over their entire length, and from the secondary radial ridges where the tertiary ridges are present. Unlike other specimens, however, the dissepiments are not strictly perpendicular to the radial ridges, but are somewhat oblique, angled slightly towards the disc margin.

A concentric ridge is visible around most of the disc, at approximately five-sixths of the radius from the centre. The margin of the disc is sharp and smooth, surrounded by a distinct groove.

Discussion.–The occurrence of the Tafilalt specimens was first noted by Samuellson et al. (2001), who noted the occurrence of parops onemids at one of the Erfoud sites (M003). They figured a single specimen, in a paper concentrating on the micropalaeontology of the site. Subsequently, Alessandrello and Bracchi (2003) described 71 specimens from this site as ‘Eldonia berbera’, a new species. Van Roy (2006a), in a thesis focusing primarily on non-trilobite arthropods from the Ordovician of Morocco, noted the occurrence of the paropsonemids at M005 and M001 as well as M003 (his KR-1, E-1, and E-3 respectively), offering a brief description and figuring several specimens. While this was primarily in the context of these being associated fossils with exceptionally-preserved arthropods, he provided a
detailed criticism of Alessandrello and Bracchi (2003)’s description. This need not be repeated in full here, but significantly, he correctly noted that Alessandrello and Bracchi

“overloaded their paper on the Moroccan paropsonemids with an incomprehensible number of errors and misconceptions” (p. 56)

including describing the orientation of the fossils as the reverse of their actual orientation, stating that the ornamentation occurred only on the coiled sac even though this was clearly not the case on their figured specimens, suggesting that the organism had a mineralised exoskeleton despite the plastic deformation, and assigning them to the very different genus *Eldonia*.

The radial ridges and dissepiments observed on both the lectotype and paralectotype are immediately reminiscent of those of the other described paropsonemid species, and confirm that *Discophyllum* is, indeed, a paropsonemid. While no coiled sac is directly observed in either specimen, the raised area towards the centre of both may represent the position of this structure below the integument. Both specimens are regarded as external casts of the dorsal surface.

The Tafilalt specimens are clearly assignable to *D. peltatum* based on the remarkable degree of similarity to the type series. Well-preserved Tafilalt specimens show the same arrangement of radial ridges as the paralectotype, with more prominent primary radial ridges, less prominent secondary radial ridges, and accessory tertiary radial ridges, which appear to diverge from the secondary radial ridges at approximately two-thirds of the disc radius. The size and angular spacing of the radial ridges is not constant in either set, with some clearly larger and more widely spaced than others. The total number of radial structures does appear to differ slightly, with the type series estimated to have around 40 primaries, and the Tafilalt specimens observed (or estimated) to have 50. This apparent discrepancy is likely due to incomplete preservation in the type specimens. Both also exhibit dissepiments. The margin of both sets of specimens is smooth and sharp.

As may be expected from the large volume of material, the Tafilalt specimens preserve several features not seen in the type material. Significantly, all of these features are also known in other eldonides.
Specimen YPM 226468 (Fig. 4.83) confirms that the primary and secondary radial ridges connect to and extend outwards from a central ring. The radial fibres and internal lobes of *Eldonia ludwigi* are also seen to be connected to a central ring, as are the radial fibres in *Maoyanidiscus grandis*, and the radial ridges in *Sepatus pomeroii* and *Praeclarus vanroii*. This central ring structure is thus likely a universal feature of eldonide biology.

No pattern in the variation in width and angular separation of the radial ridges can be distinguished in the type specimens, due to poor and partial preservation, although such variation is particularly clear on the paralectotype. This is not the case for the Tafilalt specimens, in which at least 29 specimens demonstrate that the radial ridges decrease in both size and separation in a dextral direction around the disc (in dorsal view). This same trend is also identified here for *Eldonia ludwigi* (p. 75), *Paropsonema cryptophya* (p. 100), *Paropsonema mirabile* (p. 107), *Praeclarus vanroii* (p. 112), and *Praeclarus sp.* (p. 119), and thus appears be another universal feature of eldonide biology (with the maoyanidiscids the only group in which this has not been observed). The Tafilalt specimens also show that the radial ridges with the largest size and angular spacing occur at the proximal end of the coiled sac, with the smallest at the distal end, or as close as possible in specimens in which the distal end overlaps the proximal end. This feature could not be revealed in the type series, as the coiled sac is not clearly preserved in either the lectotype or paralectotype.

The Tafilalt specimens, on the other hand, show the coiled sac extremely clearly (Figs. 4.70-4.74, 4.77-4.80, 4.82-4.87). This is generally preserved as a depression on counterpart casts, and correspondingly in positive relief from the surface of moulds, although it is occasionally preserved as a positive relief structure on casts, as negative relief structure on both mould and cast, or with no relief, but as an area which is slightly more lustrous than the remainder of the disc.

It can likely be assumed, from the almost identical shape, that the coiled sac of *D. peltatum* is structurally, functionally, and morphologically indistinguishable from the coiled sac of *Eldonia ludwigi*. However, neither the three-layered structure of the coiled sac of *E. ludwigi*, nor the tripartite division of the coiled sac into
proximal, medial, and distal portions, is seen in *D. peltatum*, save perhaps for specimen M005-0042 (Fig. 4.78), which preserves the proximal and distal portions as tubular areas of raised relief. These can plausibly be interpreted as the result of infilling of the coiled sac by the enclosing sediment during transport and deposition.

The branched tentacles at the proximal end of the coiled sac are not clearly present in any of the *D. peltatum* specimens, although irregular structures are occasionally seen in a corresponding position (e.g. Figs. 4.77 and 4.89). Most often a raised bar on counterpart casts, or depression on moulds, of length slightly greater than the width of the sac, is observed at the proximal end of the coiled sac. This may be taken to indicate the possible presence of such structures here, but as the tentacles in *Eldonia* are seen to extend to either side of the opening of the coiled sac, such a bar is evidently not in the correct position to represent this feature. Much more likely is the interpretation that this represents instead a taphonomic artefact caused by the sediment-casting process. Amorphous irregular structures are, however, observed to either side of the proximal end of the sac in four specimens (M001-0011, Fig. 4.89c-d, M005-0034, Fig. 4.89e, M005-0038, Fig. 4.89a-b, and M005-0096a, Figs. 4.85-4.86). These cannot be ruled out as representing the circumoral tentacles, though little can be discerned from these structures, which would likely be accorded no significance whatsoever if such features were not well-known from other eldonides.

The rounded depression (on counterpart casts) occasionally observed at or towards the distal end of the coiled sac (Fig. 4.90) is also thought to be taphonomic artefacts of the casting process. As in *E. ludwigi*, the evidence in *D. peltatum* indicates that the apertures of the coiled sac opened on the ventral side of the organism, as shown by specimens in which the ornamentation continues undisturbed over the entire coiled sac. The deflation of the coiled sac would thus have a greater effect at either end, where it connected to the ventral side of the animal, rather than in the medial portion, where it remained near the dorsal surface.

Evidence from other eldonides (principally *E. eumorpha* and *Paropsonema cryptophya*) has also been taken to indicate the presence of a central cavity, in which the coiled sac was suspended by mesenterial elements (Friend, 1995; Zhu *et al.*, 2002). The presence of a central cavity in *D. peltatum* is supported by two
observations. The occasional deflection of primary and secondary ridges from a strictly geometric radial pattern in the central area of the disc of certain flattened specimens (e.g. YPM 226468, Fig. 4.83) is consistent with deformation of this part of the disc due to the compression of an underlying cavity. The raised inner area of certain specimens preserved in endorelief (particularly those from M001 and M003, e.g. Fig. 4.70), with the central area containing the coiled sac showing greater relief than the outer part of the disc, is also consistent with the interpretation that the sac was contained within such a cavity.

Both of the specimens which appear to preserve the internal lobes are counterpart casts, with the lobes preserved in raised relief. These are thought to have been preserved by sediment infill, similarly to the comparable preservation of the lobes in *Paropsonema cryptophya*, and those specimens of *Eldonia ludwigi* which preserve the lobes in relief. This further supports both the interpreted hollow nature of the lobes, and the interpretation of their function in *Eldonia ludwigi* (p. 81).

In *Paropsonema cryptophya*, the internal lobes are seen to follow the form of the radial ridges on the disc surface, with bifurcations in the ridges representing the bifurcation of the underlying lobes. This is not directly observed in *D. peltatum*, but can reasonably be inferred. The lobes in *D. peltatum* are therefore interpreted to be positioned underneath the secondary radial ridges in the inner part of the disc, and to bifurcate at the point where the secondary ridges begin to broaden and tertiary ridges develop (Fig. 4.106). The lobes are inferred to follow the path of the tertiary ridges from this point to the margin of the disc. The number of lobes is thus estimated to be equal to the number of secondary radial ridges.

As noted above, 5 specimens were observed to have a total of 50 primary radial ridges (and an equal number of secondary ridges) over the complete surface, with 7 additional specimens estimated to have a similar number, based on the angular separation of the ridges. 11 of these specimens have a diameter between 145mm and 195mm, but with the remaining specimen (M005-0020) having a diameter of only 90mm. This suggests that the number of ridges and internal lobes was constant, with 50 primary and 50 secondary radial ridges, and 100 tertiary ridges, on the surface, and 50 bifurcating lobes. However, the number of ridges on
M005-0020 was estimated based on the spacing of 14 primary radial ridges, and thus further data would be required to rule out ontogenetic variation in the number of ridges and lobes.

The form of the dissepiments suggests that their purpose may have been simply to increase the number of ridges on the disc surface, thus strengthening the integument in a manner allowing the minimal reduction in flexibility.

Concentric rings such as occur in *D. peltatum* have been observed in other eldonides. *Maoyanidiscus grandis* and *Pararotadiscus guizhouensis*, for example, both have fine concentric lines covering the disc surface, previously interpreted as growth lines (e.g. Zhu *et al.*, 2002). This could be a plausible interpretation the concentric structures observed on *D. peltatum*. However, the consistent positions of these concentric structures and other morphological features relative to the disc radius, regardless of size, as well as the consistency of the distance between adjacent dissepiments (around 1mm, regardless of the size of the disc, with more dissepiments present in larger specimens) indicate that *D. peltatum* grew by inflation, and not by marginal accretion. No growth lines should thus be present on the surface. Zhu *et al.* (2002) also considered concentric structures on *E. eumorpha* as growth lines, but this interpretation is also thought to be unlikely for the same reasons.

Both Chen *et al.* (1995) and Friend (1995) interpreted the concentric features in *Eldonia eumorpha* as muscle bands. These were broad annular bands a few millimetres in width, situated approximately halfway between the outer margin of the coiled sac and the edge of the disc, quite similar in appearance to the concentric structures on certain Tafilalt specimens (e.g. M005-0011, Fig. 4.89c, M005-0096a, Figs. 4.85-4.86, M005-0138, Fig. 4.97b, M005-0065a, Fig. 4.97b, and M009-0001, Fig. 4.97d). The similarity of the concentric structures in *E. eumorpha* and *D. peltatum* certainly suggests that they were functionally and morphologically identical; a muscular interpretation may be plausible, but it is admittedly equivocal.

A concentric structure is also present in the English Silurian specimen, at the same position relative to the radius as observed in many Tafilalt Ordovician specimens. Fryer and Stanley (2004) interpreted this as a circular rib; however, this
interpretation was in the context of considering this specimen as a porpitid, and so should be considered suspect.

No evidence for mineralisation of the surface is observed in any specimen: indeed, the specimens which are folded, stretched, and displaying irregularities in the surface demonstrate beyond reasonable doubt that the organism was flexible. The overlapping specimens provide compelling evidence of transport prior to deposition, as do the specimens preserved within beds, indicating entrainment within sediment-carrying currents. The fact that only two specimens show potential evidence for tearing, despite both the implied current strength and the fact that many of the specimens are preserved within beds, indicates that the integument was cohesive and strong.

Two remaining taphonomic observations may be of particular significance. First, the fact that only one surface is ever preserved, even in specimens preserved within beds, despite the large volume of material, and even where specimens are preserved upside-down with respect to the majority of the fossils, strongly indicates a taphonomic bias towards the preservation of that particular surface. This suggests that there was something compositionally different about this surface which facilitated its preservation, regardless of orientation. Softer structures are known only from their modification of the topography of this surface, or by infilling with sediment.

Second, virtually all the specimens, even those preserved within beds, are preserved in the same orientation: with the dorsal side facing down. While this may be taken to indicate a mode of life in this orientation, the fact that this observation applies to specimens which were unequivocally transported prior to burial, suggests that a taphonomic factor may instead be the cause. It is likely that the centre of gravity of *D. peltatum* was closer to the dorsal surface, perhaps due to the mass of the dorsal integument itself, or the presence of the coiled sac. Such an interpretation is supported by the fact that all other paropsonemid specimens for which the orientation is known are likewise preserved with the dorsal surface facing downwards (although it is curious to note, in this context, that most known eldoniids and
maoyanidiscids are preserved in the reverse orientation, with the dorsal side facing upwards).

The specimen from England was found in float in a dry stone wall (sourced from a local historical quarry). It was described, under the name *Pseudodiscophyllum windermerensis*, by Fryer and Stanley (2004) as a porpitid hydrozoan. However, the dextrally-coiled raised area on the disc clearly corresponds to the coiled sac of the eldonides. The presence of this coiled sac and the similarity of the surface ornamentation to *Discophyllum* confirm that this species also belongs with the eldonides, as noted by Van Roy (2006a). Fryer and Stanley (2004) chose to assign the specimen to a new genus, noting the similarity to *D. peltatum*, but considering this to be superficial, stating that

"differences far outweigh similarities" (p. 117).

Their cited differences include that *Discophyllum* is oval, has a lesser number of about 80 radial ridges in a single cycle, and displays a series of close-set concentric rings. None of these statements are true: the oval shape of the lectotype is a taphonomic artefact, and the number and arrangement of radial ridges is extremely similar in the type specimens, the Tafilalt material, and the English specimen, with around 50 primary and 50 secondary radial ridges. Nor does any specimen of *D. peltatum* exhibit a series of close-set concentric ridges. Fryer and Stanley (2004) also described the secondary radial ridges as bifurcating at the circular rib, providing magnified photographs of one side of the fossil to show evidence of this bifurcation. This is not the case, and their figures in this regard (reproduced in Fig. 4.107) can only be described as highly misleading. In fact, on the specimen (Fig. 4.105), the secondary radial ridges are clearly visible after the point of “bifurcation” in their figured area, and the opposite side of the fossil – which they did not figure at all – clearly shows both primary and secondary ridges to continue to the margin, with no indication of any bifurcation. The ridges that they interpreted as bifurcated secondary ridges are, in fact, the tertiary ridges.

Some morphological differences do exist, however:
• the secondary ridges are more prominent in the central area of the English specimen, where these are clearly secondary to the primary ridges in the type and Tafilalt material;

• the dissepiments of the English specimen are often oblique to the radial ridges, rather than perpendicular to them.

Both of these characteristics could be taphonomic, rather than biological. Notwithstanding the age difference, therefore, this specimen is also assigned to *D. peltatum*.

This Silurian specimen adds little to our knowledge of the morphology or biology of the species, but is significant for the extension of the temporal range of *D. peltatum* to the Ludfordian. However, given the small size of the specimen, with a maximum diameter of 117mm, it is of interest to note that the similarity in the number of radial ridges to the Ordovician specimens. This may lend additional support to the interpretation that the number of ridges, and thus the number of internal lobes, is constant, and does not vary ontogenetically.

Given the wide separation of Tafilalt (then on the margin of Gondwana, near the south pole) and New York (on the Taconic margin of Laurentia, in the southern tropics) in the late Ordovician (Fig. 4.108), and the time difference between the Sandbian and Ludfordian, the similarity between the specimens from these three different locations is highly significant, indicating:

1. The widespread distribution of paropsonemids, in general, in Palaeozoic oceans;

2. The widespread occurrence of *D. peltatum*, in specific, in the Late Ordovician, indicating that at least one life stage of this organism was pelagic, and capable of intercontinental movement;

3. The wide environmental tolerances of the species, occurring in both polar and tropical seas; and

4. The highly conservative nature of the species in evolutionary terms.
It is worth noting, however, that this evolutionary conservatism may in part be an artefact of the lack of preservation of the more labile morphological components seen, for example, in *Eldonia ludwigi*, such as the circumoral tentacles and radial fibres (i.e. ‘Volkswagen Syndrome’, sensu Schopf et al., 1983).

A reconstruction of *D. peltatum* is presented in Fig. 4.109.

4.2 Other potential eldonides

Several other fossils have been described which have been, or may be, suggested to be related to the eldonides (Fig. 4.110, 4.111). It is worth briefly considering these.

4.2.1 *Eomedusa datsenkoi* (Popov, 1967)

*Eomedusa datsenkoi* (Fig. 4.110a) was described from two specimens from the Upper Cambrian of Siberia under the name *Camptostroma datsenkoi* by Popov (1967), as a scyphozoan. However, *Camptostroma roddyi*, the type species of the genus (Ruedemann, 1933a), was known, even then, to be an echinoderm (Durham, 1966), and the specimens were reassigned to the new genus *Eomedusa* by Datsenko et al. (1968).

Rozanov and Zhuravlev (1992) reconstructed *Eomedusa* as a tripartite structure, with a central smooth circular area, subcentral ring of broad lappets, and an outer ring again with broad lappets. The published illustrations, however, are unclear as to the precise form of their subcentral ring, which may represent the coiled sac of the eldonides. It is also notable that the number of lappets in the outer zone appears to be double that of those in the subcentral ring, suggesting that these bifurcated at the outer margin of the latter feature. The outer part of the disc also appears, in places, to have ridges perpendicular to the radially-arranged lappets. Such an organisation would clearly suggest an eldonide affinity, based on comparison to *Eldonia* and the paropsonemids. A re-examination of the specimens would be required to confirm this hypothesis, but an eldonide interpretation appears likely.
4.2.2 *Sinoflabrum antiquum* Zhang and Babcock, 2001

*Sinoflabrum antiquum*, from the Lower Cambrian of China, was described from a single specimen (Fig. 4.110c) by Zhang and Babcock (2001), who tentatively considered it as a poriferan. It has not previously been considered as a potential eldonide.

The specimen is ovoid in outline, except for a 120° segment: it is unclear whether this segment is missing, or was not originally present. The surface is covered in irregular branching lobes which extend from the centre to the periphery. These are covered in small pustules. Larger pustules occur in a concentrically-arranged pattern over the surface.

The form of the lobes is somewhat reminiscent of the lobes of eldonides; some are extremely similar, bifurcating towards the margin. However, others do not appear as simple, and seem to bifurcate several times, in an irregular pattern. There is no indication of a coiled sac, and the pustules have no analog in known eldonide biology. It therefore seems unlikely that *Sinoflabrum* is closely related to any known eldonide. However, given that the eldonide lobes are a virtually unique feature, the similarity is striking, and a more distant relationship may be considered, and cannot be ruled out. However, the single available specimen is insufficient to confirm any such relationship.

4.2.3 ‘Trace fossils’ from Algeria

Le Heron (2010) described several discoidal structures preserved in negative relief on a glacially striated pavement from the uppermost Ordovician of Algeria as cnidarian resting trace fossils. These are discoidal forms, 50-60mm in diameter (e.g. Fig. 4.111). Le Heron described them as consisting of three concentrically-arranged cycles, with the inner cycle showing the greatest negative relief, and the outer cycle exhibiting “thumb-shaped” pits or depressions. The taphonomic model presented suggested that ice sheets striated soft sediment, and following the glacial retreat, the sediment was colonised by cnidarians, which were subsequently preserved.
This proposed taphonomic model is completely untenable. Glacial striations result from the frictional contact between glaciers and underlying lithified strata. Unconsolidated sediments would not be striated: they would simply deform under the pressure of the overlying ice-sheet mass, and following deglaciation, any regular features which might have formed on the surface would certainly have been destroyed by soft-sediment deformation due to the lifting of the glacial overburden pressure. Glacial outflow would almost certainly have removed such unconsolidated sediments.

A much more likely interpretation is that these are discoidal organisms preserved in endorelief within a rapidly lithified sandstone bed, which was subsequently glacially striated.

Given the close geographic and temporal association of these fossils with the Tafilalt paropsonemids, such an interpretation must be considered. The single specimen figured in detail (Fig. 4.111b) is somewhat suggestive of the paropsonemids, with the 'middle cycle' of Le Heron (2010) potentially representing a coiled sac. The peripheral structures could represent paropsonemid marginal lappets. Unfortunately, this specimen is not well-preserved, and other specimens are figured only at outcrop scale. A re-examination of the specimens would be required to elucidate the possibility of a relationship with the eldonides. It may also be possible that these structures are instead related to other discoidal forms known from Tafilalt; however, only the paropsonemids show peripheral structures in any way similar to those in the Algerian specimens. Notwithstanding the biological ambiguity, however, these specimens are almost certainly pre-glacial discoidal organisms preserved in endorelief, and not post-glacial cnidarian trace fossils.

4.2.4 *Astropolichnus hispanicus* Crimes *et al.*, 1977

Structures from the Cambrian of Spain were briefly described as scyphomedusae by Van der Meer Mohr and Okulitch (1967). These are discoidal structures consisting of a smooth inner area, and an outer area covered in lappets (e.g. Fig. 110b). Friend *et al.* (2002) and Ivantsov *et al.* (2005) both considered these fossils as *Eldonia*. 
However, these structures were unequivocally reinterpreted as trace fossils by Crimes et al. (1977), under the name *Astropolichnus hispanicus*, an interpretation which was fully supported by Pemberton et al. (1988). Interpreted as cnidarian resting/feeding traces, these fossils show marginal ‘lappets’ around a central axial cylinder, and have been observed to show vertical repetition in form. A relationship with the eldonides is thus not thought to be likely, and *Astropolichnus* should thus be removed from any discussion of the eldonides.

4.3 General remarks

4.3.1 Eldonide phylogeny

The Class Eldoniata, as described herein, contains three families, eight genera, and at least ten species. The eldonides are clearly a very conservative group, with a very consistent biology from the Early Cambrian to the Late Devonian. All members of the Class Eldoniata apparently possessed a dextrally coiled sac with circumoral tentacles, and bifurcating internal lobes. The key differences between different genera, species, and families lie in the nature of the dorsal integument, the number of lobes, and, where preserved, the form of the circumoral tentacles (Fig. 4.112). In the Family Eldoniidae, the dorsal integument is simple, with bifurcated radially-arranged strips running from the centre to the margin. The Family Maoyanidiscidae differ in having a harder surface covered in a fine concentric ornament, previously interpreted as growth lines, while the dorsal surface of the Family Paropsonemidae is covered by a complex ornamentation consisting of various radially arranged ridges with dissepiments.

The differences in this dorsal surface may highlight differences in the mode of growth of the organisms: evidence in the paropsonemids indicates that these grew by inflation (see pp. 103, 116, 141), while growth lines on the maoyanidiscids could indicate growth by marginal accretion (there is little evidence to indicate the mode of growth of the eldoniids). However, this has not been unequivocally demonstrated,
and it is unlikely that such closely related organisms had such contrasting modes of growth. Due to the clear evidence for growth by inflation in the paropsonemids, this is thus presumed to be the mode of growth for all eldoniids.

Both maoyanidiscids and paropsonemids appear to possess more autapomorphic characters (e.g. the radial ridges and dissepiments in the case of the paropsonemids, and the hardened dorsal integument in the case of the maoyanidiscids), and the eldoniids are therefore presumed to be the most plesiomorphic family.

Within families, the key differences between genera and species are in the arrangement of internal lobes (and the concordant dorsal ornamentation in the case of the paropsonemids), and the form of the circumoral tentacles, where these are observed. The form of the circumoral tentacles is interpreted to reflect different feeding strategies, which is regarded as sufficient to warrant generic separation. The significance in the number of lobes is uncertain, and is thus accepted as diagnostic only at the specific level. For this reason, the number of internal lobes is omitted from generic diagnoses, even where genera are monospecific.

_Eldonia eumorpha_ and _Eldonia ludwigi_ both possess dendroidal circumoral tentacles, and are therefore maintained within the same genus, though those of _E. eumorpha_ are longer and more slender than those of _E. ludwigi_; _E. eumorpha_ also has 44 internal lobes, as compared to 30 in _E. ludwigi_. These differences are sufficient to warrant separation at the specific level.

In the maoyanidiscids, _Maoyanidiscus grandis_ has 90 lobes and digitate tentacles, as compared to 40 lobes and dendroidal tentacles in _Pararotadiscus guizhouensis_. The difference in the form of the tentacles is sufficient to warrant separation at the generic, as well as the specific level.

In the paropsonemids, the circumoral tentacles are never observed. Instead, the arrangement of the dorsal ornamentation is accepted as generically diagnostic. _Discophyllum_ exhibits a single cycle of radial ridges extending from the centre of the disc to the margin. _Paropsonema_, by contrast, has two (_Paropsonema mirabile_) or three (_Paropsonema cryptophya_) cycles of radial ridges, with dissepiments occurring on all
radial ridges. *Praeclarus* may also have two (*Praeclarus sp.*) or three (*Praeclarus vanroii*) cycles of radial structures, but the inner cycle consists of simple, thin ridges with no dissepiments; the second cycle develop into marginal lappets, and the third cycle, where present, is only present as marginal lappets. Thus the departure from a single cycle of ridges is generically diagnostic, while the development of a marginal third cycle, indicating a second bifurcation of the internal lobes, is diagnostic only at the specific level. This may seem counterintuitive; however, the morphology of both *Paropsonema* and *Praeclarus* is more different from each other than from *Discophyllum*, suggesting that *Discophyllum* is perhaps the more plesiomorphic form.

The positions of *Sepatus* and *Velumbrella* within the Maoyanidiscidae are both somewhat tentative, and due to a lack of diagnostic features, it is not clear exactly where within the phylogeny of the eldonides they should be placed.

These three families are all included in the Order Eldonida, characteristic of which are the dextrally coiled sac with circumoral tentacles, internal lobes, and discoidal morphology. However, Caron *et al.* (2010) recently described a new genus and species, *Herpogaster collinsi*, from the Burgess Shale, which features a coiled sac with circumoral tentacles, but neither discoidal shape nor internal lobes. This species was placed with the eldonides in the unranked stem-group Cambroernids. As such, both the discoidal shape and lobes must represent synapomorphic characters of the eldonides, but not the Cambroernids. The possibility must be considered, therefore, that discoidal forms without internal lobes may have existed. Both the lobes and discoidal shape are thus included in the diagnosis of the Order Eldonida, containing the Families Eldoniidae, Paropsonemidae, and Rotadiscidae, but excluded from the diagnosis of the Class Eldoniata. The discoidal shape is included in the Class diagnosis.

A proposed phylogeny for the Class Eldoniata is presented in Fig. 4.113.
4.3.2 Palaeoenvironmental tolerance of the eldonides

As noted for *Discophyllum peltatum*, the eldonides occur in a strata formed in a wide range of palaeoenvironments, from above fair-weather wave base to deep marine shales, and from arctic to tropical palaeolatitudes. While many of the fossils have undergone some form of transport prior to deposition, it seems likely that this reflects to at least some extent their original range of habitats. The eldonides are therefore not particularly useful as palaeoenvironmental indicators. Such a wide range of environmental tolerances may indicate a lifestyle or life cycle which was cosmopolitan, perhaps in part either pelagic or perhaps even nektic, rather than purely benthic. This is also supported by the wide geographic distribution of *D. peltatum*.

4.3.3 Stratigraphic range of the eldonides

The biostratigraphic value of the fossils is also limited. In particular *D. peltatum*, with a range from the upper Middle Ordovician (~460 Ma) to the upper Silurian (420 Ma), indicates the conservative nature of the group; the genera *Paropsonema* (460-420 Ma) and *Praeclarus* (420-380 Ma) also have extended ranges. This, admittedly, is likely a function of both the simple morphology and non-mineralised nature of the organisms, with the preservation of more labile tissues subject to taphonomic control.

The overlapping stratigraphic ranges of the paropsonemids, and the co-occurrence of *Discophyllum peltatum* and *Praeclarus vanroii* in the same palaeogeographical area in Tafilalt, and of *Praeclarus sp.* and *Paropsonema mirabile* on the same rock sample in Victoria (Fig. 4.66a), indicates that different species of eldonide co-existed during the Palaeozoic.

One conclusion which can be reached, however, is that the eldonides were a significant part of Palaeozoic ecosystems, from the Early Cambrian to the Late Devonian. *Eldonia eumorpha* is among the most common fossils in Chengjiang, as is *Pararotadiscus guizhouensis* in Kaili, and *Eldonia ludwigi* in the Burgess Shale. *Discophyllum peltatum* is by far the most abundant fossil in the Tafilalt Konservat-
Lagerstätte, indicating that these organisms were gregarious and also occurred in huge numbers in the Ordovician. Indeed, the small number of post-Ordovician eldonide fossils is likely to be an artefact of taphonomy, with soft-bodied preservation limiting their fossilisation, and small collections in areas where such fossilisation occurred. That many more paropsonemid specimens occur in both the Silurian of Victoria and the Devonian of New York is extremely likely. No systematic excavations or collecting have been conducted in these areas, and it can reasonably be expected that if such excavations were carried out, many more specimens would be recovered.

The small number of described eldonides and lack of post-Ordovician specimens almost certainly also results from a simple lack of knowledge about the group. The fact that even within the last decade, over one hundred and fifty years after the description of the first paropsonemid, *D. peltatum*, a new specimen – of the same species! – could be described as a porpitid hydrozoan (Fryer and Stanley, 2004) illustrates the total lack of general knowledge of this group with acute clarity.

This can, however, be viewed in a positive light. That many future discoveries will be made, and previously collected specimens rediscovered, is highly probable. Other specimens not previously connected to the eldonides may be realised to be related. It is likely that the coming years will see a vast increase in our knowledge and understanding of what may accurately be described as the least-well-known major group of Palaeozoic organisms.
Taphonomy

The science of palaeontology differs from zoology in one fundamental respect. Not only does it attempt to interpret the biology of whatever fossil organisms are under consideration, but it first must assess which geological processes have affected the remains of these organisms over the often many millions of years since their death. Taphonomic processes - for example transport, disarticulation, abrasion, scavenging, decay, dissolution, diagenesis (including chemical alteration and authigenic mineralisation), compression, and lithification – and metamorphic processes (including heating, recrystallization, and deformation) can take place over a variety of timescales, from hours to millions of years, and may not only control which organisms are preserved as fossils, but may also substantially change the preserved remains from their original form. Identifying which processes have acted upon any particular fossil, and accounting for any potential alteration or modification, is thus necessary before considering the original biology.

Nowhere is this more true than for non-mineralised organisms, such as those preserved as compressions in shales, or as moulds and casts in sandstones, particularly when such fossils represent groups which are now extinct. With no modern analogues to clarify the biology and ecology of these vanished creatures, understanding the taphonomy of such specimens becomes even more crucial in determining what parts and characteristics of the animal are preserved, and more importantly not preserved, in the fossil record. Such fossils are crucial for our understanding of almost all aspects of palaeontology, from the early evolution of life to the palaeoecology of marine communities: the first animals to evolve must have been non-mineralised, and non-mineralised organisms can account for around two-thirds of animal communities (e.g. Schopf, 1978).
Not all of the post-mortem processes noted above apply in the case of non-mineralised fossils. Dissolution, for example, applies only to skeletal remains. Similarly, disarticulation and abrasion, normally associated with transport, are not significant factors with non-mineralised fossils. As a result, transport is a much less significant factor in the taphonomy of soft-bodied fossils, with state of decay the main control in the completeness of such specimens (Allison, 1986).

Other factors are arguably more important in the case of non-mineralised fossils. With no mineralised skeleton for protection, such organisms would often have been more prone to scavenging (post-mortem predation by macroscopic organisms). Similarly, without a mineralised skeleton to maintain the shape and form of the body, non-mineralised organisms would have been more susceptible to pre-lithification folding, deformation, and compression. As such, early diagenesis and the timing of lithification may be crucial to whether or not non-mineralised organisms are preserved as fossils. Deformation and compression post-lithification, however, may affect all fossils equally, regardless of whether or not they were originally mineralised. Similarly, the processes of decay – the utilisation of a carcass as a food source by microbiological organisms – affect all organisms.

It is also important to note that not all of these post-mortem processes may have affected particular specimens. In some cases, this is a trivial point – many geographic areas have never experienced metamorphism, for example. Likewise, autochthonous specimens (buried in situ) will not have been affected by transport. In other cases, however, the lack of a particular factor may be crucial in controlling whether or not an individual organism is preserved as a fossil.

As decay is such an important process, it is useful to examine it in more detail. Three factors control decay (e.g. Allison, 1990):

1. The supply of oxygen, and other electron acceptors (including NO$_3^-$, MnO$_2$, Fe (III), and SO$_4^{2-}$);

2. Environmental factors including pH (acidity), Eh (reduction potential), temperature, and sedimentary mineralogy and geochemistry;

3. The nature of the organic material which is undergoing decay.
In aerobic environments, organic matter is broken down with oxygen as the primary electron acceptor (Allison, 1988a; 1991; Emerson and Hedges, 2003) (all equations using the Redfield ratios for organic matter):

\[
(CH_2O)_{106}(NH_3)_{16}H_3PO_4 + 106O_2 \\
\rightarrow 106CO_2 + 106H_2O + 16NH_3 + H_3PO_4
\]

However, the oxygen requirements for aerobic decay are high: the aerobic decay of 1g of organic carbon requires 671cm\(^3\) of oxygen (Allison, 1988a, 1990; 1991). If the demand for oxygen exceeds supply, anoxia results, with decay proceeding using an alternative electron acceptor. In an idealised situation, the particular acceptor used depends on the free energy released by the reaction (e.g. Allison, 1988a, 1990; 1991; Emerson and Hedges, 2003), with \(NO_3^-\) providing the highest yield:

\[
5(CH_2O)_{106}(NH_3)_{16}H_3PO_4 + 424NO_3^- \\
\rightarrow 36CO_2 + 494HCO_3^- + 212N_2 + 245H_2O + 80NH_4^+ + 5HPO_4^{2-}
\]

followed by \(MnO_2\):

\[
(CH_2O)_{106}(NH_3)_{16}H_3PO_4 + 212MnO_2 + 332CO_2 + 120H_2O \\
\rightarrow 212Mn^{2+} + 438HCO_3^- + 16NH_4^+ + HPO_4^{2-}
\]

then \(Fe\) (III):

\[
(CH_2O)_{106}(NH_3)_{16}H_3PO_4 + 424Fe(OH)_3 + 756 CO_2 \\
\rightarrow 862HCO_3^- + 424Fe^{2+} + 304H_2O + 16NH_4^+ + HPO_4^{2-}
\]
and SO$_4^{2-}$:

\[ 2(\text{CH}_2\text{O})_{106}(\text{NH}_3)_{16}\text{H}_3\text{PO}_4 + 106\text{SO}_4^{2-} \]

\[ \rightarrow 106\text{H}_2\text{S} + 182\text{HCO}_3^- + 30\text{CO}_2 + 30\text{H}_2\text{O} + 32\text{NH}_4^+ + 2\text{HPO}_4^{2-} \]

Once these receptors have been consumed, decay proceeds by reduction of the organic matter itself, producing methane:

\[ (\text{CH}_2\text{O})_{106}(\text{NH}_3)_{16}\text{H}_3\text{PO}_4 + 14\text{H}_2\text{O} \]

\[ \rightarrow 53\text{CH}_4 + 14\text{HCO}_3^- + 39\text{CO}_2 + 16\text{NH}_4^+ + \text{HPO}_4^{2-} \]

Under ideal conditions, these reactions would occur in layers within substrates, with aerobic decay near the sediment-water interface, and each subsequent reaction occurring at a progressively deeper level. In practice, this sequence varies, depending on the local (palaeo)environmental conditions, including pH, Eh, temperature, and on the availability of particular ions and electron acceptors in either the pore water or detrital minerals in the sediment. For example, nitrate reduction is important in freshwater environments, but is insignificant in marine sediments (e.g. Allison, 1988b), while sulphate reduction dominates in marine settings, but is insignificant in freshwater, where the availability of sulphate ions is considerably reduced.

The nature of the decaying organic matter is also a significant influence, both in terms of its form and its composition. Dispersed particulate organic matter will decay more or less as outlined above, with reduction zones layered in the subsurface. Where localised concentrations of organic matter occur, however, such as a decaying macroscopic organism, the decrease in the surface-to-mass ratio of the organic matter tends to inhibit the supply of oxygen (and other electron receptors). This leads to the occurrence of the reactions described above in localised zones around the organic matter in question (Allison, 1988a, 1990). Anoxic decay can thus occur locally, even in well-oxygenated sediments. Such an effect was noted in decay experiments conducted by Allison (1988a) and Briggs and Kear (1993), who observed that the decay of non-mineralised invertebrate taxa rapidly became...
anaerobic even when the sediment and water were oxygenated. Localised sulphate reduction was also observed in micro-niches around burrows by Bertics and Ziebis (2010). In fact, Jørgenson (1977) had previously demonstrated that even in oxygen-saturated seawater, particles of organic matter greater than only 2mm in diameter will decay anaerobically at the centre. As noted by Allison and Briggs (1991), therefore,

"given size/surface area constraints on oxygen diffusion, it is obvious that any large carcass must decompose essentially anaerobically" (p.35).

Different types of organic matter also decay at different rates (e.g. Logan et al., 1991). Nucleic acids, DNA and RNA, decay extremely rapidly, as do labile tissues like muscular proteins, and simpler carbohydrates, including glucose, starch, and glycogen. Structural proteins such as collagen and structural polysaccharide carbohydrates such as chitin and cellulose are more recalcitrant, as are lipids (fatty acids). Some biopolymers are extremely recalcitrant, and are often quite readily preserved, such as lignin and sporopollenin. This sequence is not consistent, however, and may depend on other factors. Briggs and Kear (1993) observed that the initial stage of decay of the polychaete worm *Nereis* in taphonomic experiments involved the decline of lipids and nonsclerotised cuticle collagen, followed by the rapid degradation of muscular proteins, carbohydrates, and continued decline of the cuticle and lipids. Within 30 days, only sclerotized structural tissues (chitin and collagen) remained. In terms of fossilisation potential, the muscles decayed first, followed by the gut, the cuticle, and the jaws and setae. This was shown by Briggs and Kear (1993) to correspond to the fossil record.

One potential contributory factor to this departure from the theoretical stability sequence may be the complexity and form of the particular biomolecules included in the various tissues. Jørgenson (1982, 1983) suggested that anaerobic bacteria are less efficient biodegraders, and thus the complete degradation of more refractory organic biomolecules may require the successive action of a range of anaerobic bacteria, with initial action breaking the complex molecules down into a form more readily utilisable by successive bacteria. This was supported by Allison (1988b).
In fact, a key step in the breakdown of complex organic biopolymers (for example cellulose, collagen, or chitin) is enzymatic degradation. Most organic matter consists of polymeric compounds that cannot be directly assimilated by bacteria (Chróst, 1991; Hoppe, 1991). Extracellular enzymes, consisting of free extracellular exoenzymes in the surrounding water, and ectoenzymes adhering to microbial cell walls, are required to break down these compounds into smaller molecules capable of transportation across the cellular membrane. This requires the active sites on the enzymes to achieve a precise co-ordination with particular bonds in the organic matter, which are then hydrolysed, with the products being taken into cells for further degradation. Due to the precise co-ordination required between organic matter and enzymes, particular compounds require specific enzymes to degrade them.

Oxygen is an important factor in the rate of enzymatic degradation of organic biopolymers. Previous studies have demonstrated that certain refractory organic compounds, such as lignin, require oxygen for enzymatic decay (Hedges et al., 1985; Emerson and Hedges, 2003). In contrast, the breakdown of polysaccharides (including chitin and cellulose) and proteins (including collagens) is not dependent on the presence of oxygen, and enzymatic degradation is efficient under anoxic conditions. However, anoxia has been shown to slow the rate of such decay (e.g. Harvey et al., 1995; Emerson and Hedges, 2003).

Previously, it was believed that anoxia was the most significant factor in the inhibition of decay, and therefore in the fossilisation of soft tissues (e.g. Seilacher, 1970; Seilacher et al., 1985). More recently, decay experiments such as those of Plotnick (1986), Allison (1988a), and Briggs and Kear (1993) have demonstrated that anaerobic decay proceeds quite rapidly. Briggs and Kear (1993) did note that in the complete absence of oxygen, decay of the polychaete *Nereis* was slowed, particularly for the most volatile tissues in the first 10 days, indicating that an initial stage of aerobic decay may be disadvantageous to fossilisation, especially for the most labile tissues. The subsequent rapidity of the anaerobic decay processes, however, nonetheless indicates the ineffectiveness of anoxia in the preservation of soft-tissues. Instead, the key factor in such preservation is early diagenic mineralisation (Allison, 1988a, b, 1990; Allison and Briggs, 1991). The form of early diagenic mineralisation...
in fossil preservation varies considerably, depending on the nature of the sediment, the particular mode of decay, and other factors. Examples include:

- Three-dimensional preservation of extremely labile tissues (for example the Upper Cambrian phosphatic ‘Orsten’ deposits of north-eastern Europe: Müller, 1990);

- Mineral coating of non-mineralised tissues (for example the pyritised olenid trilobite Triarthrus from Beecher’s Trilobite Bed and other localities in the Devonian of New York, USA: Farrell et al., 2009; 2011);

- Moulding of organisms by mineralisation (such as in the Carboniferous Mazon Creek shales of Illinois, USA: Nitecki, 1979; Schellenberg, 2002).

Mineralisation results from the reaction of decay byproducts (such as Mn$^{2+}$, H$_2$S, HCO$_3^-$) with seawater or sedimentary ions (most commonly Ca$^{2+}$ and Fe$^{3+}$), producing authigenic minerals including calcite, siderite, and pyrite.

While anoxia is not a significant inhibitor of decay on the timescales necessary for the primary preservation of organic material, decay must have been inhibited in the case of any example of organic carbon preservation, whether in the form of exceptional fossils or fossil fuels. This usually involves either extreme conditions inhospitable even to specialised micro-organisms or the effective sealing of organic matter from such microbes. For example, decay may be inhibited by the adsorption of clay minerals or ions onto the biological molecules, restricting access to the reactive sites. This process can, and does, result in the preservation of original carbon, which is commonly later kerogenised by late diagenic and subsequent geological processes. Such processes are primarily responsible for the preservation of organic matter in black shales, and significantly contributed to the preservation of fossil fuels in the subsurface (Kennedy et al., 2002), as well as macrofossil preservation (Butterfield, 1990).
5.1 Taphonomy of the Burgess Shale and *Eldonia ludwigi*

5.1.1 Previous Research

The taphonomy of the exceptionally preserved non-mineralised and lightly mineralised fossils of the Burgess Shale, including *Eldonia ludwigi* (see Chapter Four, p. 69), has been disputed in the literature. However, the initial stage of the taphonomic process – transport – and the contemporaneous redox conditions have lately been clarified. While the majority of the fossils are believed to have been transported (e.g. Conway Morris, 1979b, 1990a; Allison and Brett, 1995), and are preserved within event beds, more recent work has suggested that the Burgess Shale represents a series of para-autochthonous burial assemblages with relatively minimal transport (Caron and Jackson, 2006). The lack of fugichnia (escape trace fossils) has been taken to indicate that most of the fossils were essentially dead on burial (Conway Morris, 1990a), though again, some recent work has demonstrated that some fugichnia are indeed present (Caron and Jackson, 2006). The limited number of these fugichnia, and of trace fossils in general, has been viewed as supportive of geochemical data indicating that while the Burgess Shale bottom waters were oxygenated, the sediment pore waters beneath were actually anoxic (W.G. Powell *et al.*, 2003; Caron and Jackson, 2006).

The fossils, including *Eldonia ludwigi*, are preserved as darkened but reflective films on fracture planes within the shale. Some sponge spicules have retained their original siliceous composition, while phosphatic shells (principally inarticulate brachiopods) are preserved as apatite (Conway Morris, 1990a). Framboidal pyrite is also associated with some fossils, sometimes as a coating, but also partially replacing some sponge spicules and the exoskeleton of some echinoderms, trilobites, and problematic fossils (e.g. Conway Morris, 1977b; Briggs, 1981; 1985a, b, 1986). Reddish coatings on many specimens (e.g. Conway Morris, 1985b), including some specimens of *Eldonia* (e.g. Figs. 4.04, 4.09a, 4.10), may represent iron oxides resulting from weathering of original pyrite. Some skeletal material is also replaced by aluminosilicates (Conway Morris and Pye in Conway Morris, 1986; Butterfield *et al.*, 2007). Initially, the presence of aluminosilicates in
the fossils was believed to be highly taphonomically significant. The fossils were thus thought to have been preserved solely by aluminosilicate replacement of the original organic structures (Whittington, 1971; Conway Morris, 1977b, 1985b, 1986, 1990a). This was supported by Auger electron spectroscopic analysis of the priapulid *Ottoia* (Conway Morris, 1977b) and electron microprobe analysis of *Eldonia* (Conway Morris and Pye in Conway Morris, 1990a) (Fig. 5.01a), both demonstrating the presence of aluminosilicate films (interpreted as potassium mica) over the fossil surface.

Butterfield (1990, 1995) was the first to recognise that the highly reflective parts of the Burgess Shale fossils were preserved original organic carbon remnants. Maceration of Burgess Shale samples in hydrofluoric acid yielded mm-sized organic carbon fragments of *Marrella*, *Marpolia*, and *Ottoia*, as well as *Wiwaxia* and *Canadia* sclerites/setae, and various unidentified fragments and abundant acritarchs. Butterfield (1990, 1995) proposed that decay of the organic matter was inhibited by the adsorption of extracellular bacterial enzymes onto the surfaces of aluminosilicate clay minerals in the enclosing sediment matrix, which deactivated the enzymes, thus restricting decomposition. He further suggested that the temporal restriction and non-uniform geographical distribution of Burgess Shale-type preservation was due to the temporal and regional variations in average clay mineralogy (a consequence of natural changes in weathering and provenance) and ocean chemistry. Four factors were cited as key to such preservation:

1. **Clay mineralogy** – expandable clays, such as smectites, have a far greater surface area and cation exchange potential than either illite or kaolinite, with iron-rich smectites being the most reactive;

2. **The valency of the exchange cations** – divalent ions, such as Ca$^{2+}$ increase the stability of adsorbed organic matter, but monovalent ions such as Na$^+$ increase the interlayer spacings in the clay minerals, allowing larger molecules to penetrate this space, and effectively increasing the available surface area;

3. **pH** – most organic matter and some clays have a pH-dependant surface charge, with a pH below the isoelectric point (the value at which the charge changes from negative to positive) enhancing adsorption;
4. **Total organic carbon content (TOC)** – if the TOC is high, clay mineral surfaces could potentially become saturated with organic matter, effectively lowering the clay mineral surface area available for the adsorption of enzymes.

Towe (1996) disagreed with this assessment, arguing that organic preservation in the Burgess Shale fossils was extremely limited. However, this suggestion was falsified by analysis of the coiled sac of a more poorly preserved specimen of *Eldonia* (Butterfield, 1996). EDS elemental analysis both prior and subsequent to removal of the coiled sac from the matrix by maceration in hydrofluoric acid and subsequent Auger spectroscopic analysis all confirmed a high carbon content, with X-ray photoelectron spectroscopy confirming a high graphite content (Fig. 5.01b; Tables 5.01 and 5.02).

While it is thus undoubtedly true that many specimens – including *Eldonia* – are preserved with original organic carbon, Orr *et al.* (1998) demonstrated that not only are many specimens coated with aluminosilicates, but that the particular chemical composition of the aluminosilicates varies both within specimens and from the surrounding shale matrix (Fig. 5.02). Although they did not dispute the organic preservation of certain structures, they proposed that replication by either early diagenic or detrital clay minerals thus accounted for the preservation of the most labile tissues, with different tissues replicated by different minerals. Orr *et al.* (1998) also argued that the differences in composition between aluminosilicates on the fossils and in the shale matrix (in which the fossils occur) indicated that these could not have been introduced during burial. Aluminosilicates within fossil body cavities were suggested to have been introduced after burial, but before compaction, necessitating an early diagenic origin. The chemistry of the clay minerals on the exterior of the organisms was suggested to have been controlled either directly by the composition of the organic matter, or indirectly by the stepwise authigenesis or adsorption of clay minerals depending on the lability of the tissues.

Petrovich (2001) agreed with Butterfield (1990, 1995, 1996) that the original preservation was primarily organic, and that free extracellular enzymes would be adsorbed onto clay mineral surfaces, but disagreed that this was the cause of decay inhibition. Noting that Chróst (1991) had considered ectoenzymes to be
considerably more important than free extracellular exoenzymes, due to the fact that ectoenzymes produce food that only the host bacterium can exploit, and that the activity of exoenzymes cannot be regulated by bacteria, Petrovich (2001) suggested that it was unlikely that ectoenzymes would be easily deactivated by adsorption onto clay mineral surfaces, as this would be a considerable disadvantage in a marine environment with abundant clay minerals. He instead proposed that the adsorption of Fe$^{2+}$ ions onto the organic tissues of the fossils inhibited enzymatic degradation, followed by the nucleation of authigenic iron aluminosilicate minerals (smectites) around the adsorbed ions. In defence of this hypothesis, Petrovich (2001) noted that previous laboratory experiments on the preservation of the bacteria *Bacillus subtilis* had shown that exposure to Fe$^{2+}$ greatly increased the preservation potential by exactly this process (Ferris *et al.*, 1988; Urrutia Mera and Beveridge, 1993, 1994).

In fact, it has also been previously demonstrated that certain organic biopolymers, including cellulose, collagen, and particularly chitin, have a strong tendency to adsorb heavy metal ions, especially Fe$^{2+}$ (Muzzarelli and Tubertini, 1969; Hawke *et al.*, 1991). Indeed, this effect is extremely well known in the environmental science literature, with chitin having even been used to clean waste mine water of metal ions (Daubert and Brennan, 2007; Bhatnagar and Sillanpää, 2009; Morris and Sneddon, 2011).

Adsorption of Fe$^{2+}$ (or other) ions onto biopolymers blocks the functional groups of enzymes from achieving the requisite co-ordination with the biopolymers necessary to break them down, preventing enzymatic degradation. Petrovich (2001) proposed that Fe$^{2+}$ produced by bacterial reduction of Fe(III) thus prevented the decay of the complex biopolymers in the Burgess Shale fossils, now primarily preserved as graphite and kerogens (Butterfield, 1990, 1995, 1996), and that the nucleation of iron rich clay minerals around the adsorbed Fe$^{2+}$ ions caused the growth of the aluminosilicate films identified by Orr *et al.* (1998).

Butterfield *et al.* (2007) disagreed with this contention, arguing that the aluminosilicate minerals were late diagenic, citing the partial replacement of trilobite shell and vein carbonate by such minerals. They proposed that although the fossils are currently preserved replicated in aluminosilicate minerals, the original
preservation was organic, via decay inhibition. Page et al. (2008) supported the Butterfield et al. (2007) hypothesis, demonstrating that aluminosilicate films were commonly associated with organic graptolite periderm in Palaeozoic shales, and suggested that these films were late diagenic, based on alignment with cleavage and Kubler crystallinity data. They proposed that progressive mineralisation with stepwise maturation of the various component tissues was responsible for the compositional variation depending on the nature of the original organic materials. However, an early authigenic origin for these clay minerals, with subsequent recrystallization during maturation, would produce a similar result.

Anderson et al. (2011) recently demonstrated that aluminosilicate films on carbonaceous compressions of the Ediacaran acritarch Chuaria from the Doushantuo Formation, China, were undoubtedly ultimately authigenic (formed in early diagenesis). This strongly suggests that the aluminosilicates outlining the Burgess Shale fossils were also originally early diagenic, although subsequently altered during later diagenesis, with additional late diagenic clay minerals also present (as demonstrated by Butterfield et al., 2007). Anderson et al. (2011) also identified pyrite enveloping, and sometimes within, Ediacaran carbonaceous compressions, suggesting that in these specimens, the decay of more labile organic tissues by sulphate reduction produced pyrite which moulded the specimens. However, not all specimens were pyritised to the same degree; the curtailment of sulphate reduction due to limited sulphate availability was suggested as an explanation. Importantly, pyritisation corresponded with reduced preservation of carbonaceous material. Petrovich (2001) had previously considered that the pyritisation in the Burgess Shale was a result of the depletion of reactive Fe$^{3+}$, promoting further decay by sulphate reduction, with the H$_2$S produced reacting with adsorbed Fe$^{2+}$ to form pyrite on the organic biopolymers. In particular, Petrovich (2001) noted that reaction of adsorbed Fe$^{2+}$ with sulphate would desorb it from active sites on the organic molecules, removing their decay protection. He suggested that the curtailment of the sulphate supply was thus a necessary condition of Burgess Shale-type preservation, as extensive sulphate reduction and pyritisation would result in the complete degradation of the organic matter. This hypothesis is entirely consistent with the
observations made by Anderson et al. (2011), suggesting that Petrovich (2001)’s model is, at least in part, correct.

Three additional factors also support Petrovich (2001)’s model.

1. As noted above, the adsorption of metal ions onto complex organic biopolymers, most significantly chitin and collagen, is a well-known and well-studied effect. It is not simply that such a process might have occurred: it should be expected to have occurred. In the absence of any evidence to the contrary, it should be presumed that dissolved metal ions would be adsorbed onto the anionic sites of organic biopolymers. Such adsorption would retard, and could even prevent, enzymatic degradation.

2. As noted by several previous authors (e.g. Conway Morris, 1977b; Briggs, 1981; 1985a, b, 1986; Butterfield, 1990; Conway Morris, 1990a; Petrovich, 2001; Page et al., 2008), pyritisation is extremely limited in the Burgess Shale, suggesting that anoxic decay proceeded primarily by Fe(III) reduction, with, as noted above, a premature curtailment of sulphate reduction. Fe²⁺ ions would therefore have been present in the pore waters.

3. As noted by Petrovich (2001), the preservation of organic matter by the attachment of pre-existing clay minerals is unlikely. To be protected, the entire complex molecule would need to be attached to the clay mineral surface at numerous functional groups. While this is easily attainable in the case of authigenic clay minerals overgrowing an organic surface, the probability of a pre-existing clay mineral surface having both the correct surface configuration, and attaching to the organic biopolymer in the correct orientation, is extremely low. Where organic carbon is preserved with aluminosilicate film, therefore, a different process must be responsible for the preservation of the organic matter.

However, this does not necessarily indicate that adsorption of pre-existing clays onto organic biopolymers did not occur. Indeed, the occurrence of fossils preserved partly or primarily as aluminosilicate films (with no original organic carbon present) is entirely consistent with this process, as the end result would be the replication of
organic structures by aluminosilicates with no organic matter preserved. It is entirely possible, and (based on the known attraction between organic biopolymers and clay minerals) even likely, that this process also occurred. Indeed, as the adsorption of metal ions onto more labile tissues has not been demonstrated in previous taphonomic experiments, it is highly plausible that it was the adsorption of detrital aluminosilicate particles which is responsible for the preservation of the more labile tissues observed in many of the fossils.

It must also be noted that the adsorption of exoenzymes onto detrital clay minerals, as proposed by Butterfield (1990, 1995), should be expected to have occurred. This must have been a key factor in slowing the decay process, as ectoenzymatic degradation requires direct contact between the microbial cell and the organic matter in question. Further research is required to explore the possibility of ectoenzyme deactivation by adsorption onto detrital clays.

The preservation of the Burgess Shale fossils is thus likely to have been a complex combination of several factors:

1. Low supply of O$_2$ prevented significant initial aerobic decay.


3. Adsorption of detrital aluminosilicate particles onto some organic tissues replicated them, but did not ultimately prevent their subsequent decay.

4. Decay of dissolved organic matter, particulate organic matter, and extremely labile tissues in the fossils, proceeded by the reduction of reactive Fe(III), produced a high pore-water concentration of Fe$^{2+}$ in the immediate vicinity of the fossils.

5. These Fe$^{2+}$ ions were then adsorbed onto the active sites of organic molecules, preventing degradation by ectoenzymes.

6. Depletion of reactive Fe(III) promoted further decay by sulphate reduction, producing H$_2$S.
7. Reaction of this H₂S with adsorbed Fe²⁺ produced metastable iron monosulphides (which later transformed to pyrite) on the organic tissues, removing their decay protection.

8. Curtailment of the sulphate supply blocked further sulphate reduction.

9. Growth of authigenic aluminosilicate minerals around the adsorbed Fe²⁺ ions on the organic matter, which replicated the tissues in clays.

10. Subsequent diagenesis and alteration of clay minerals occurred, along with the kerogenisation of the preserved organic carbon.

It is possible, as Page et al. (2008) suggested, that differential maturation of the organic material caused the tissue-dependant variation in clay mineral chemistry observed by Orr et al. (1998). An original compositional variation in the authigenic clays depending on the tissue itself cannot be ruled out. However, if, as suggested above, some tissues were replicated by authigenic clays, while others were replicated by detrital clays, compositional differences would almost certainly have resulted. Further research is required to clarify this step, with a combination of multiple factors again a distinct possibility. In particular, examination of multiple specimens of the same species could help to ascertain whether particular tissue types are consistently preserved with the same aluminosilicate mineralogy. If this is the case, analysis of the clay mineralogy of specimens with no modern analogues could even allow us to potentially estimate the composition of their various component tissues.

One additional point which must be noted is that, regardless of which process or processes were active in decay retardation in particular specimens, at least some decay is almost certain to have occurred in all specimens.

5.1.2 Taphonomy of Eldonia ludwigi from the Burgess Shale

Specimens of *Eldonia ludwigi* are preserved in various orientations within the enclosing shale matrix, indicative of at least some degree of pre- or post-mortem transport, but there are no indications of how far they have been carried from their life position. The specimens are now preserved as a combination of kerogenised and
graphitic organic carbon (generally limited to the coiled sac) and aluminosilicate films. It is also clear that the specimens are preserved in variable states of decay, with some showing most of the known anatomy (e.g. Figs. 4.02, 4.03, 4.09, 4.10, 4.11, 4.13), whilst others preserve only the medial portion of the coiled sac (e.g. Fig. 4.08). As the state of decay would have been dependant on multiple factors, including availability of oxygen, clay mineralogy, local Fe\textsuperscript{2+} concentration in the pore waters, and microorganism and enzyme concentrations, such preservational variation is expected.

The medial portion of the coiled sac is preserved organically, as demonstrated by Butterfield (1996). The proximal and distal portions, and the circumoral tentacles, also appear to be organically preserved, based on their reflectivity (e.g. Figs. 4.02, 4.11, 4.14a). It is not clear whether any organic carbon remains in any other parts of the internal anatomy, which appear to be primarily replicated by aluminosilicates. The dorsal integument (e.g. Fig. 4.21) is never reflective, and is often conspicuously darker than the surrounding matrix; this may be preserved as non-reflective organic carbon.

It is notable that specimens with a reddish coating (presumably of iron oxides) appear to preserve less reflective carbon than other specimens (e.g. Figs. 4.04, 4.09a). This may be viewed as supportive of the hypothesis that sulphate reduction led to a loss of organic preservation by desorbing Fe\textsuperscript{2+} ions from organic compounds, assuming the iron oxides are produced by the weathering and oxidation of pyrite. However, in some cases, this red coating is constrained between veins (e.g. 4.09a – vein visible beside the scale bar at the left of the image). No pyrite is visible on the specimens outside these veins. The source of the iron may thus have been clay minerals, with the lower level of organic preservation perhaps due to later diagenic alteration. No pyrite was directly observed associated with any specimen of *E. ludwigi*, supporting the role of iron, rather than sulphate reduction, as the mode of anoxic decay in these specimens.

In the *Eldonia ludwigi* coiled sac sample separated from the shale matrix by HF maceration (see p. 162 above) by Butterfield (1996), two layers were identified:

- An inner highly reflective layer, and
An outer, conspicuously non-reflective layer, which was the part of the coiled sac in contact with the sediment (Fig. 5.01b).

The reflective layer in *Eldonia ludwigi* comprises the coiled sac *sensu stricto*, and the identification of an outer layer provides conclusive evidence that this structure was enclosed by an outer membrane (see p. 73). Petrovich (2001, p. 689) incorrectly speculated, based on this analysis, that *Eldonia* might actually be an annelid, with the outer non-reflective layer representing the originally collagenous body wall, and with the inner reflective layer representing the chitinous gut wall. While the taxonomic suggestion is obviously erroneous, the tissue identification – based primarily on the greater capacity of chitin for the adsorption of metal ions, as compared to collagen – is worthy of consideration. An extension of this hypothesis could also consider the non-reflective outer integument to have had a collagenous (or similar) composition.

The remainder of the organs of *Eldonia ludwigi* appear to be preserved as aluminosilicate films, identified by electron microprobe in one specimen as potassium mica (Conway Morris and Pye in Conway Morris, 1990a). The original composition of these tissues remains unknown, and as noted above, the precise mechanism which led to their replication by clay minerals is yet to be fully determined. It is clear, however, that some of these tissues were very labile, at least in comparison to the coiled sac. The lack of clear evidence for musculature and other very labile tissues, however, strongly suggests that the most labile tissues decayed early in the taphonomic process.

### 5.2 Taphonomy of the Tafilalt paropsonemids

In contrast to *Eldonia ludwigi*, the taphonomy of paropsonemid specimens preserved as moulds and casts in sandstones, from any of the known sites worldwide, has not previously been considered. However, some previous work has examined the taphonomy of other kinds of non-mineralised fossils preserved as moulds and casts in sandstones.

Experimental studies using cnidarians (Norris, 1989; Bruton, 1991) have demonstrated that once decay has started, fine details of truly soft-bodied organisms
cannot be preserved. In laboratory experiments, subtle features, analogous to the fine surface ornamentation preserved in the paropsonemids, could only be preserved by the rapid application of plaster immediately following the death of the organism concerned (Norris, 1989). The key factor, essentially, is how soft sediment was capable moulding an organism, preserving fine details (at sub-mm scale), and holding this mould whilst the organism decayed, and while adjacent sediment subsequently filled and cast the mould.

Such experiments and observations, along with observations of fossils collected from other localities, led several previous researchers (e.g. 1991; Briggs, 1995; Narbonne, 1998; Gehling, 1999) to note that early diagenic decay-related mineralisation (and therefore cementation), of the mould was required for such fossils to be preserved.

Taphonomic evidence for the paropsonemids is clearest at the Tafilalt localities, due to the abundance of specimens and the widespread geographic area over which this preservation occurs. Investigation of the taphonomy of the paropsonemids is therefore herein concentrated on the Tafilalt specimens and sites. The abundance of material available also permitted a range of destructive analyses to be undertaken, in addition to primary observation of the fossils and sediments, to further elucidate the geochemical processes involved in taphonomy and diagenesis.

Details of the specimens analysed are provided in Table 5.03.

5.2.1 Taphonomic observations

As noted in Chapter Four, a slight majority of the collected Tafilalt specimens are preserved in endorelief (within beds). Most of the specimens observed at the localities are preserved on bedding plane surfaces, but both modes of preservation are common. The vast majority of the specimens from bedding plane surfaces are preserved as positive hyporelief casts and/or negative epirelief moulds (terms explained in Fig. 1.04), but a small number of specimens are known preserved in the opposite orientation, as positive epirelief casts or negative hyporelief moulds (e.g. M005-0035, Fig. 4.87e; M005-0183, Fig. 4.87f). Many of the specimens were
collected in float, or by local field assistants who did not record the original sample orientation, and so the sense of relief of these specimens is unknown. On one sample, however, positive relief casts occur on both top and bottom surfaces, providing additional evidence of preservation in positive epirelief (Fig. 5.03). It is important to reiterate, in this context, that only one surface of the organism is ever preserved. Specimens preserved on bed soles, whether in positive or negative hyporelief, occasionally have a corresponding depression on the top surface of the bed.

Folding or deformation of the shape of the fossils from a circular outline or a flat aspect is common in both endorelief and bedding plane specimens, but is more common in specimens preserved in endorelief, where some specimens are rolled up into a cigar-like shape (Fig. 4.111). Some folded specimens preserved in positive hyporelief are folded up into the burying sediment (e.g. Fig. 4.110a,b). Several specimens are also preserved overlapping each other (Figs. 4.110a, 4.113, 4.114). In specimens preserved in positive hyporelief but overlapping, both specimens are preserved in the area of overlap, with the overlying specimen preserved in endorelief in this area.

Potential evidence for post-mortem shrinkage is observed in 11 specimens. This is mostly evident as a broad ridge surrounding the specimen in positive hyporelief, or a corresponding groove in negative epirelief. One of these specimens shows particularly clear evidence of significant shrinkage (Fig. 4.112).

The nature of the preservation of the coiled sac shows significant variation (Fig. 4.87). Specimens preserved in endorelief generally preserve the coiled sac in significant negative relief from casts, and significant positive relief from moulds. Specimens preserved on bedding plane surfaces, however, preserve the coiled sac with very little relief from the surface. In these specimens, this structure is commonly preserved with apparent mineralogical differences, being slightly lighter in colour and slightly more reflective or lustrous. One sample, M008-0042, preserves the coiled sacs of three paropsonemids with increased reflectivity, with no other parts of the anatomy visible (Fig. 5.04). Specimens from M001 and M003 commonly preserve the coiled sac blackened. This is caused by an extremely thin surficial
coating, which is not discernible in thin section. A limited number of specimens also preserve the coiled sac in the opposite sense of relief to the majority, i.e. in positive relief from casts and negative relief from moulds (e.g. Figs. 4.78, 4.87).

The sediment containing the paropsonemids is always sand-grade; no specimens have been found preserved entirely within in the poorly-sorted finer grained sediments at any locality (although for some specimens, the counterpart cast was fine-grained siltstone). However, the fossiliferous sandstones vary considerably, from massive (internally structureless) medium- to coarse-grained beds to thin parallel laminated beds with primary current lineation evident on the surface (e.g. see log in Fig. 3.16). The grain size of fossil moulds and casts varies from very fine sand (around 100μm) to fine gravel (around 5mm) in some rare cases (e.g. Fig. 5.05a). The quality of preservation appears to depend (at least in part) on the grain size of the enclosing sediment, with fossils preserved in coarser sediment generally failing to preserve finer details. For example, dissepiments in the outer area of the disc are rarely preserved at M001 and M003, where the fossiliferous beds are coarser than those at M005 (see logs in Figs. 3.04, 3.08, 3.12, 3.16). Interestingly, the resolution of preservation is often much higher in the region of the coiled sac than in the outer part of the disc, which is again most noticeable at M001 and M003 (e.g. Figs. 4.70-4.74). The quality of preservation also appears to vary with the size of the specimens, with larger specimens preserving more fine details - compare, for example, M001-0021 (Fig. 4.70) with M001-0001 (Fig. 4.87a). However, the quality of preservation is nonetheless highly variable within localities, even amongst specimens of the same size preserved in sediment of similar grain size.

The thickness of the bedding overlying some of the fossils is as low as 10mm in some of the parallel-laminated units, such as Bed 6 in M005 (Fig. 3.12e; see also Fig. 3.16), and most of the beds in M008 (Fig. 3.18e).

Bed surfaces at M001, M005, M008, and M009 are commonly stained red, as are the surfaces of the fossils themselves. The surfaces of specimens preserved as endorelief at M005, M008 and M020 are often stained dark red, whereas the host sandstone is a conspicuously lighter colour (e.g. Fig. 4.100d), indicating a preferential reddening of the fossil surfaces and the bedding surfaces. This is not the
case at M001 and M003, where the fossil surfaces are often the same colour as, or only slightly darker than, the sandstone matrix. Specimens at M010 exhibit blackened surfaces (e.g. Fig. 4.60a), similar to the blackening of the coiled sac at M001 and M003 (e.g. Fig. 4.87a-d), and stand out noticeably from the containing sediment.

Skeletal fossils and trace fossils are occasionally associated with the discoidal fossils; for example, presumed scavenging burrows are observed on M001-0021 (Fig. 4.70), M003-0025 (Fig. 4.73), and M005-0042 (Fig. 4.78). Skeletal remains – including echinoderms and trilobites – are often observed in close proximity to paropsonemid specimens (e.g. M005-0043, Fig. 4.112), and even overlapping them (e.g. Fig. 5.05b).

5.2.2 Analytical taphonomic evidence

Analytical evidence presented here comprises thin section petrography, powder X-ray diffraction, Laser Raman microspectroscopy, SEM BSE imaging and EDS analysis, and ICP-MS bulk geochemical analysis of fossil specimen and matrix samples, as detailed in Table 5.03. Analysed specimens not previously figured are shown in Figs. 5.06-5.09.

5.2.2.1 Thin section petrography

Thin section petrography reveals subtle and minor sedimentological differences between sediments at the various Moroccan sites.

Sediments at M001 (Fig. 5.10a) and M003 (Fig. 5.10b-c) are generally similar; both are dominated by quartz (estimated at around 80% at M001, and only slightly lower at 75% in M003), with authigenic syntaxial overgrowths commonly delineated by thin dust rims around detrital grains (Fig. 5.10b). There is no evidence for pressure dissolution of detrital quartz. Muscovite occurs as both detrital sheets and authigenic fan-shaped crystals (estimated at around 5% at both sites); plagioclase feldspar is a minor detrital component (<5%), and is often very heavily weathered and degraded, replaced by clays. Chlorite is also observed as a thin coating around
authigenic quartz, mixed with red-brownish iron oxides and clay minerals (due to this distribution, the content is difficult to estimate, but is in any case below 1%). Larger aggregates of clay minerals occasionally occur (e.g. Fig. 5.10a), which may represent either clay-grade detrital lithic fragments or authigenic replacement of feldspars. The level of chlorite and particularly iron oxides (estimated at 1% at M001, and 5% at M003) appears to be greater in M003 than M001; larger grains of chlorite are also observed in M003 (e.g. Figs. 5.10b–c). The surfaces of fossils from these localities show no observable differences from the host sediment; nor are any differences observed between moulding and casting sediment, or for sediment in the vicinity of the coiled sac.

Thin sections were made for M005 through Beds 1-5 in the log shown in Fig. 3.12e (Figs. 5.11), as well as through fossils from Bed 6 of Fig. 3.12e (Fig. 5.12), and coarser grained beds from near the base of the succession shown in Fig. 3.16 (Fig. 5.13). Like M001 and M003, the sandstone beds are dominated by detrital quartz with syntaxial overgrowths indicated by dust rims (around 80%) (Fig. 5.11a,d,e), and lesser amounts of both detrital and authigenic white mica (around 5%) (Fig. 5.11). Again, there is no evidence for pressure dissolution of detrital quartz. Feldspars are represented by highly degraded orthoclase (also approximately 5%) (Fig. 5.11a). Iron oxides are more common than at M001, though lower than at M003 (at around 2%), while larger grains of chlorite (<1%) are apparently almost absent. Laminations, which in hand sample appear as red lines within greenish-tinged white sandstones, are seen in thin section to have a greater concentration of clay minerals and iron oxides coating and filling the pore spaces around quartz crystals (e.g. Fig. 5.12b). In Bed 1, rhombohedral carbonate grains with euhedral faces are observed (approximately 1% or less), cross-cutting authigenic and detrital quartz as well as other grains. These are almost universally associated with amorphous iron oxide aggregates (Fig. 5.11a). Carbonate grains with similar iron oxide aggregates are also occasionally observed in Bed 2 (Fig. 5.11c). Fine-grained sediments interbedded with the sandstones have a much higher clay content (approximately 60%), but also contain evidence for detrital and authigenic quartz (around 20%) and mica (around 10-15%) (Fig. 5.11c,f). Coarser grained sediment from the fossiliferous beds near the base of the succession (see log in Fig. 3.16) have
an even higher quartz content (around 90%), with lower mica (2-3%) and clay components (Fig. 5.13).

The surfaces of fossils from Bed 6 are covered by a discontinuous veneer, approximately 100μm thick, consisting of a mixture of iron oxides and clay minerals (Figs. 5.12a,b). This differs considerably in form from the laminations within the beds, and contains a much higher proportion of iron oxides (best seen in a combination of plane polarised and incident light: see Fig. 5.12b). Within this veneer, cubic iron oxides are occasionally observed (discussed further on p. 176 below).

Fossils from the base of the succession (see log in Fig. 3.16), however, lack this veneer; the reddening of the surfaces of fossils from these beds is instead due to a difference in the pore-fillings (Fig. 5.13). In these specimens, iron oxides constitute a majority of the pore-filling and grain-coating minerals in the vicinity of the fossil surface (Fig. 5.13a), but are elsewhere absent, with chlorite constituting the majority of the pore-filling in the remainder of the samples. The boundary between the iron oxide-dominated vicinity of the fossil and the chlorite-dominated remainder is quite sharp (e.g. Fig. 5.13c).

Sediments from M010 are also dominated by quartz (though with a lower content than M005, at approximately 70%), with only rare plagioclase feldspar (around 1%), and again both detrital and authigenic white mica (again around 5%). However, the pore-filling iron oxide, clay, and chlorite content is considerably higher (up to around 10-15%). Carbonate (up to 10% content) is also occasionally observed to fill pore spaces; no detrital carbonate is observed. The fossil surface is best seen in M010-0002, where the endorelief preservation allowed a thin section to be made through the fossil, showing the moulding sediment, casting sediment, and the fossil surface (Fig. 5.14a,b). No discernible differences are evident between the moulding and casting sediment; the fossil surface is seen in thin section as a thin dark line consisting of a concentration of iron oxides and other opaque minerals, clay minerals, and carbonate.
5.2.2.2 X-ray diffraction

XRD analyses of cavity-mounted samples from M001, M003, and M010 (Figs. 5.03-5.05) confirmed the presence of quartz and white mica (as muscovite). Chlorite was detected as clinochlore (Mg-chlorite), while feldspars were detected as albite (sodium-rich plagioclase). Carbonate was also detected in all samples as calcite, but only the M010 sample contained significant peaks (Fig. 5.17). No other minerals were detected; unfortunately, clay minerals were below detection limits for cavity mounted samples and no sample was water mounted.

5.2.2.3 Laser Raman microspectroscopy

Part of the area shown in Fig. 5.12 of specimen M005-0041, including the fossil surface veneer, was mapped by Laser Raman microscopy, with the results presented in Figs. 5.18-5.20. This clearly demonstrates the veneer to be composed of a mixture of:

- clay minerals,
- iron oxides as haematite (Fe₂O₃),
- iron oxyhydroxides as lepidocrocite (γ-FeO·OH), and
- titanium oxides as both anatase and rutile (TiO₂).

Dust rims around authigenic quartz grains are identified as predominantly clay minerals, with limited haematite, lepidocrocite and anatase in places. Clay minerals were unfortunately not identifiable, due to a grain size below the resolution of the laser and also fluorescence obscuring the Raman spectra. Calcite was identified solely as inclusions within quartz. A second map on a different area of the same specimen (Fig. 5.21) confirmed this mineralogy and distribution. Point analyses of cubic red-brown grains in the fossil surface veneer (Fig. 5.22) confirmed these as haematite.

Laser Raman analysis of M005-0062, from the fossiliferous beds near the base of the succession (see Fig. 3.16), showed a similar mineralogy. The area mapped in this specimen (Fig. 5.23) was close to the fossil surface, in an area showing significant reddening, with quartz grains outlined by a red-brown coating. Anatase
was identified in much of the grain coatings, as well as iron oxides. It should be noted that the iron oxide signal in the map is significantly reduced by swamping of the Raman spectra by fluorescent clay minerals.

Laser Raman analysis was also conducted on part of the fossil surface in M010-0002 (Figs. 5.24). A view of this area in reflected light (Fig. 5.24a) demonstrated the presence of cubic crystals, which were identified by point analysis as haematite and goethite (α-FeO·OH), with an additional signal which cannot be specifically identified, but corresponds to mixed manganese oxides and oxyhydroxides (Fig. 5.24c). Subsequent maps (Fig. 5.24b) showed that the fossil surface itself, with a thickness of 20-60μm, is composed of a mixture of iron and manganese oxides and oxyhydroxides, unidentifiable clay minerals, and anatase, with calcite filling pore spaces in and around this surface.

5.2.2.4 SEM and EDS

The elemental distribution in several fossil samples was determined by SEM-EDS mapping.

Six areas were mapped on a thin section of M001-0004, a counterpart cast of Discophyllum peltatum preserved in endorelief, which included the coiled sac and the disc margin. Two of these are shown in Figs. 5.25-5.26 (with the remaining four in the Appendix). No differences were evident between sediment near the surface of the fossil, either near the coiled sac or near the outer margin, and the containing sediment. O is almost evenly distributed throughout, with variations in the concentration of Si clearly outlining quartz grains. Weaker Si signals correspond strongly to concentrations of Al, with lesser amounts of Fe; these occur in the same general area, but do not overlap. A high resolution map near the outer margin of the disc demonstrated the concentrations of Fe to correspond with concentrations of Mn and Ca (Fig. 5.26); however, these do not significantly overlap within these areas. Al and O were significantly reduced in these areas, with Si almost absent, but corresponding precisely to the Al. These areas must therefore be interpreted as containing limited aluminosilicate clay minerals, with larger concentrations of iron and manganese hydroxides and oxyhydroxides and calcite. Outside of these areas,
quartz grains are outlined by Al and reduced Si, representing aluminosilicate clays, with limited Fe.

Five areas were mapped on a thin section through M001-0014, a part mould of *Discophyllum peltatum* preserved in endorelief, which included the coiled sac (Figs. 5.27-5.28 and the Appendix). These produced almost identical results to M001-0004, with Si concentrations defining quartz coated by aluminosilicate clays with limited Fe. Larger pore spaces filled by Fe and Ca, which do not precisely correspond (best seen on Fig. 5.28), indicating the presence of both Fe oxides and likely calcite. A limited amount of Ca was also detected in the absence of Fe. Again, no distinction was evident in sediment close to the fossil surface.

Six areas were mapped on the fossil surface of M001-0029, a counterpart cast of *Discophyllum peltatum* preserved in endorelief, including the coiled sac (Figs. 5.29-5.32 and the Appendix). These maps show considerable differences to those on thin sections orthogonally through fossil specimens, primarily with respect to the concentration of Si, Fe, and Al. While Si is still present almost throughout the mapped areas, the signal is considerably weaker over most of these, with the Al signal both considerably more widespread and stronger. The Fe signal is also considerably stronger. Moreover, both Fe and Al signals are stronger on mapped areas of the coiled sac, as compared to mapped areas on the outer area of the fossil surface (e.g. compare Fig. 5.29 with Fig. 5.30). High resolution maps of areas on the outer disc surface also produced precisely corresponding signals for Ba and S (Figs. 5.31 and 5.32), indicating the presence of barite (barium sulphate).

Five areas were mapped on the fossil surface of M003-0007, a part mould of *Discophyllum peltatum* preserved in endorelief, including the coiled sac (Figs. 5.33-5.35 and the Appendix). As in M001-0029, these show high concentrations of Al and Fe with more limited Si on the fossil surface (Fig. 5.33), and with Al particularly concentrated, and Si particularly reduced, over the coiled sac (Fig. 5.34). Fe also appears to be reduced over the coiled sac (Fig. 5.34). Limited Ca was also detected, with no discernible correspondence to any other element. A very high resolution map (Fig. 5.35) demonstrates the presence of Mn, Ba, and S over the coiled sac. While the Mn shows little correspondence with other elements, S shows a strong,
but not universal correspondence with Ba, but also a more limited correspondence with Fe (particularly towards the bottom right of the map, where Ba is absent), indicating perhaps the remnant presence of iron sulphides.

Eleven areas were mapped on M005-0027, a part mould of *Discophyllum peltatum* preserved in endorelief; seven areas on the surface of the mould, including the coiled sac and inner disc surface (Figs. 5.36-5.38) and the outer disc surface (Figs. 5.39-5.40), and four areas on a section through the mould (Fig. 5.41 and the Appendix). The fossil surface maps show a very strong concentration of Al on the coiled sac, in comparison to the remainder of the disc surface, with a similar concentration at lower levels for Fe, and commensurate reduction in concentration of Si (compare Fig. 5.36 to Fig. 5.37). Ca also occurs at low levels. Two maps (Figs. 5.38 and 5.40) also demonstrate the presence of precisely corresponding Ba and S, indicating barite. One map (Fig. 5.39) demonstrates the localised occurrence of corresponding Fe and S, indicating the presence of limited iron sulphides.

Maps on the section through the fossil (Fig. 5.41 and the Appendix) show considerably lower concentrations of Fe and particularly Al, with Si dominating. Al is shown to strongly correlate with K, indicating that these are present as potassium aluminosilicates.

Seven areas were mapped on M005-0041, a counterpart cast of *Discophyllum peltatum* preserved in positive hyporelief; three areas on the surface of the cast (Figs. 5.42-5.44), and four on a section through the cast (Figs. 5.45-5.46 and the Appendix). The maps on the surface of the cast comprised one map on the disc surface (Fig. 5.42), one over the margin of the disc (Fig. 5.43), and one on the surface of the containing sediment, outside the disc (Fig. 5.44). These show a clear distinction between the disc surface and the host sediment, with the disc surface clearly exhibiting higher concentrations of Fe and Al, and lower Si. This is particularly evident in the map over the disc margin, where both disc surface and containing sediment are included. Limited Ca is also present. Fig. 5.44 shows a correspondence between Al, K, and Ti, suggesting the occurrence of illite, which commonly includes Ti.
In maps of the section taken orthogonally through the cast, the concentration of Fe, and particularly Al, is considerably reduced compared to the maps of the disc surface. Indeed, levels of Al were too low to register in the map in Fig. 5.46, with levels of Fe too low to register in the map in Fig. 5.45.

High resolution BSE images and EDS point spectra of particular minerals were also obtained for a thin section through M005-0041, particularly in the fossil surface veneer (Fig. 5.47-5.48). Outside of the sole veneer, which is clearly visible (Fig. 5.48c), quartz dominates, but (at very high resolution) the pore spaces are seen to be infilled primarily by potassium aluminosilicates, represented by illite, while discrete anatase crystals are also evident (Fig. 5.48d). Fig. 5.48e shows the transition from the quartz-dominated sediment to the fossil surface veneer, with clay minerals mixed with micron to sub-micron scale blocky crystals. EDS point analysis indicates an illitic composition for the clay minerals, with a limited amount of Mg, which may suggest a limited amount of mixed layer illite-smectite. The more blocky crystals are iron oxides and/or oxyhydroxides, which are too small for definitive identification. Fig. 5.48f shows close views of the transition and surface veneer, with mixed iron oxides and/or oxyhydroxides and clay minerals. Curiously, the EDS point analyses of clay minerals in these areas did not register a numeric value for the Al component, although an Al peak is clearly visible in the spectra (immediately left of the Si peak). The spectra again suggest an illitic composition. Fig. 5.48g shows a close view of the clays in the surface veneer, the EDS spectrum of which is typical for illite. No kaolinite was seen in any area.

Four areas were mapped on an orthogonal section through M005-0062, a counterpart cast of *Discophyllum peltatum* preserved in endorelief from the lowermost (Fig. 3.16) fossiliferous beds at this locality (Figs. 5.49-5.52). This specimen clearly shows the discrete reddened area near the surface of the fossil cast, adjacent to a significantly ‘cleaner’ area, although a lesser degree of reddening is again observed further from the fossil surface. The Al and Fe content is clearly greatest in the map closest to the fossil surface (Fig. 5.49), with the lowest amount in the ‘cleaner’ area just below the surface (Fig. 5.50), though both are still present. A higher resolution map in this area (Fig. 5.51) demonstrates the Al to correlate strongly with K, with
Fe in the same general areas. These, however, do not correlate precisely, indicating perhaps separate potassium aluminosilicates and Fe-oxides.

Four areas were mapped on the surface of M005-0083, a counterpart cast of *Discophyllum peltatum* preserved in endorelief again from the lowermost (see log in Fig. 3.16) fossiliferous beds (Fig. 5.53 and the Appendix). This specimen preserves the radial ornamentation as darkened lines on the surface (see p. 130). The maps demonstrate these lines to reflect a higher Fe content, without a corresponding increase in Al content.

Four areas were mapped on a thin section through M010-0002, a specimen of *Praeclarus vanrooi* preserved in endorelief: one on the moulding sediment (Fig. 5.54), two (including one high resolution map) on an area including the fossil surface (Figs. 5.56-5.57), and one on the casting sediment (Fig. 5.57). No discernible differences are evident between the moulding and casting sediment (Figs. 5.54 and 5.57), with both showing Al, Fe, and Ca filling the pore spaces between quartz crystals defined by the Si map. Fe correlates somewhat better with Ca than with Al, but neither correlation is precise, indicating their probable presence in three different phases, likely calcite, clay minerals, and iron oxides. The immediate vicinity of the fossil surface shows a greater concentration of Fe, Al and Ca, with the fossil surface itself defined primarily by a line consisting of Fe and Ca (Fig. 5.55). The high resolution map of the fossil surface (Fig. 5.56) demonstrates a high correlation of Al with K, indicating the presence of potassium aluminosilicates (likely illite), and a lesser correlation between Mg and Al, in areas of low K, perhaps indicating the presence of smectites.

Four areas were mapped on a thin section orthogonally through M010-0017, a counterpart cast of *Praeclarus vanrooi* preserved in endorelief (Figs. 5.58-5.59 and the Appendix). The concentration of Al and Fe appears to decrease marginally away from the fossil surface; the Ca concentration appears to be uniform, except around a fracture (Fig. 5.59), which is infilled solely by Ca. This strongly indicates that at least some Ca is present as part of a late cement.

Three areas were mapped on M010-0018, a part mould of *Praeclarus vanrooi* preserved in endorelief, on a fragment of the disc surface which includes the disc
margin and host sediment. One area was mapped on this host sediment (Fig. 5.60), with a second on the disc surface (Fig. 5.61), and the third covering the actual outer margin of the disc (Fig. 5.62). Clear differences are evident. The host sediment, as for the thin sections of M010-0002 and M010-0017, shows Fe, Al, and Ca filling pore space around quartz grains. The fossil surface shows enriched Fe, reduced Al, considerably reduced Ca and Si, and a considerable amount of Mn. The distinction is clearest on the third map, which straddles the disc margin, with Fe and Mn considerably enriched on the fossil surface, with Ca and Si barely present, while Mn is almost absent and Fe reduced in the containing sediment.

In summary, SEM high-resolution imaging and EDS elemental mapping and point sampling demonstrates:

1. That there is no discernible difference between the moulding sediment and the casting sediment (compare Figs. 5.25 to Fig. 5.27; Fig. 5.41 to Fig. 5.45; and Fig. 5.54 to Fig. 5.57).

2. That fossiliferous bedding surfaces (for specimens preserved in hyporelief/epirelief) are enriched in Fe and Al relative to the internal sediment (see Figs. 5.42-5.45).

3. That the fossil surfaces themselves are enriched in Fe and Al (and Mn, at M010) relative to both the surrounding bedding surfaces and internal sediment (compare Figs. 5.25 and 5.27 to Fig. 5.30; Figs. 5.37 and 5.39 to Fig. 5.41; Fig. 5.42-5.43 to Fig. 5.44-5.46; Fig. 5.60 to Figs. 5.61-5.62).

4. That the coiled sac is preserved enriched in Al, and to a lesser extent Fe (and Mn, at M001 and M003) relative to the surrounding fossil surfaces (compare Fig. 5.29 to Fig. 5.30; Fig. 5.34 to Fig. 5.33; and Fig. 5.36 to Fig. 5.37).

5. That the fossil sole veneer at M005 consists primarily of illite, illite/smectite mixed layer, and iron oxides or oxyhydroxides (Figs. 5.47-5.48). At M010, Mn and Ca are also present (Figs. 5.55-5.56, 5.61-5.62), with Ca representing a probable late cement (Fig. 5.59).
6. That barium sulphates (Figs. 5.31, 5.32, 5.35, 5.38, 5.40) and iron sulphides (Fig. 5.39) are present in small amounts.

5.2.2.5 Bulk geochemical analysis

ICP-MS analysis of both fossil specimens and unfossiliferous sediments confirmed the geochemical differences between the various Moroccan sites (Tables 5.05, 5.06). Samples from M020 and M005, especially coarse-grained samples from the lowermost fossiliferous levels (see Fig. 3.16), possess the highest SiO\(_2\) content, with M010 the lowest. This is mostly due to variation in grain size, but is in part due to the calcite content at M010, with CaO reaching 10 wt% in M010-0016, compared to values of around 1 wt% for M010, 2 wt% for M003, and 0.1 wt% for M005.

The variation in Al\(_2\)O\(_3\) and K\(_2\)O content appears to be linked, which should be expected for samples containing either potassium aluminosilicate clays (e.g. illite), or potassium feldspars, as the principal Al and K minerals. Al\(_2\)O\(_3\) and K\(_2\)O are highest at M001, M003, and fine-grained samples from M005, and lowest in samples from M010 and coarse-grained samples from M005 and M020. This variation coincident with grain size supports potassium aluminosilicate clays as the primary source of Al and K, as these clays are a smaller component of coarser-grained samples. TiO\(_2\) concentration also appears to vary with grain size at M005, though even the coarse-grained samples at M005 have a higher TiO\(_2\) content than samples from M001, M003, and M010, which has the lowest concentration. As Ti is immobile, this likely reflects the original presence of potassium feldspars in M005 sediments, and their absence elsewhere, with detrital illite and smectite the likely source of Ti at other sites. Na content at M001 and M003 is generally around 0.5 wt%, likely representing plagioclase feldspar. At other sites, though, Na content is negligible, registering below 0.01 wt% in 5 samples from M005 and all samples from M008, M009, and M020, likely representing the much lower detrital plagioclase content. Mg content is low in all the samples, but is highest in M003, which likely represents the higher chlorite content, with larger chlorite crystals (as noted above); detrital smectite is likely to have been the original source of the Mg.
Samples from M001, M003, and especially M010 are enriched in MnO compared to those from M005. Ba appears to vary with grain size, with the samples from the upper levels at M005 and M020 containing the lowest concentration at around 100ppm, but the variation in content between samples (between 150 and 300ppm) is quite high.

La/Sc and Th/Sc ratios (Tables 5.05, 5.06) both indicate a predominantly silicic recycled sedimentary provenance (McLennan et al., 1993; Cullers, 2000, and references therein). A recycled sedimentary provenance is also supported by high Zr content, particularly in samples from M005.

Shale samples from M001, M003, M008, M009 (2), and M010 (no shales are present at M005) were analysed to determine the degree of chemical alteration of the fossiliferous sediments by weathering (Tables 5.06, 5.07). Quantitative measures of chemical weathering were calculated from the ICP-MS analysis, including the:

- Chemical Index of Alteration (CIA – Nesbitt and Young, 1982);
- Weathering Index of Parker (WIP – Parker, 1970);
- Chemical Index of Weathering (CIW, sometimes referred to as the CIA-K – Harnois, 1988);
- Silica Titania Index (STI – de Jayawardena and Izawa, 1994).

These indices use ratios of immobile elements (e.g. Al, Ti) to mobile elements (e.g. Ca, Na, Mg, K, Si) to quantitatively estimate the degree of chemical alteration of shale samples (see also Fedo et al., 1995; Price and Velbel, 2003). For all the samples analysed, the CIA, STI, and WIP all indicate a moderate degree of chemical alteration. The CIW values, however, stand out in indicating significant weathering. The CIW represents mobile elements by $Ca_{silicate}$ (Ca in silicate phases) and Na alone, omitting K, thus the anomalously high values represent the original low $Ca_{silicate}$ and Na content of the samples. However, as the CIA, which includes K, indicates a much lower degree of weathering, it is likely that the original $Ca_{silicate}$ and Na content of the samples was low. The CIW results, therefore, likely represent a false positive for significant weathering. Minor loss of $Ca_{silicate}$, Na, K, and Mg is thus
likely to have occurred; this should be considered for all geochemical and petrological interpretations, but is unlikely to have been a significant factor.

While the values for single analyses are useful by comparison to typical values for shales, the variation in chemistry depending on provenance reduces their utility in this respect. The primary utility of weathering indices is comparative, for samples within the same profile or area. Importantly, for each of the indices, the values are all similar, but different indices are not consistent in the relative degree of alteration between sites. This suggests that all of the shales (and thus all the sections) have suffered approximately the same degree of chemical alteration.

5.2.3 Early taphonomy – transport and burial

Most of the Tafilalt paropsonemids appear not to be preserved in situ, but to have been transported from their original life positions. This is indicated by the preservation of specimens in endorelief (within beds), as is the case for multiple specimens of both *D. peltatum* and *Praeclarus vanroii*. Specimens of *D. peltatum* which are preserved overlapping on bedding plane surfaces (Figs. 4.113b, 4.114) are also strongly indicative of transport, as such an original life position would likely have been untenable. Such specimens also indicate that preservation on bedding plane surfaces is not necessarily indicative of burial in situ. The degree of transport in most of these specimens is likely, though, to have been somewhat limited, given that specimens preserved in endorelief indicate the possibility of entrainment within sediment-carrying flows, and given the lack of appreciable distortion of either the circular body outline or the flattened shape. The co-occurrence of specimens in endorelief and on bedding plane surfaces thus suggests a mixture of both short (or no transport) and more significant transport, indicating that the paropsonemids lived over a more widespread area than that in which they are presently preserved (which is already geographically significant).

Specimens preserved in endorelief were buried with the loss of energy of the transporting flow. For specimens preserved on bedding plane surfaces, the thickness of the (overlying) burying sediment varies considerably, with some specimens preserved by as little as 10mm of parallel laminated sandstone. However, there is no
indication that burial was not rapid, and compaction and diagenesis have almost certainly reduced the thickness of certain beds.

A key observation is that several specimens of *D. peltatum* are preserved with a depression on the top surface of the bed, corresponding to the position of the fossil on the bed sole, or within the bed, directly beneath. Such specimens indicate that decay progressed after burial. This is supported by the differential relief of the coiled sac from the disc surface. As noted in Chapter Four (p. 138), the preservation of the coiled sac in strong relief from the disc surface indicates that this was an inflated structure. Four modes of preservation of the coiled sac are common (Fig. 5.63):

1. Specimens with the sac preserved in positive relief on the counterpart cast may indicate that the sac became filled with sediment on or during transport or burial (Fig. 5.63a).

2. Specimens showing little or no relief of the coiled sac from the disc surface may indicate that the coiled sac collapsed rapidly upon burial and compaction (Fig. 5.63b).

3. Specimens buried with the (presumed) dorsal side facing down with the sac preserved in negative relief from casts or positive relief from moulds indicate that the sac remained inflated on burial, but collapsed prior to lithification, as gravity and compaction would force sediment to fill the resultant gap from below. Sediment from above would be blocked from filling the gap by the continued presence of the organic matter of the sac and the organism (Fig. 5.63c).

4. Specimens with the sac preserved in negative relief on both mould and cast indicate that the sac remained inflated until after lithification, as the space was never filled with sediment (Fig. 5.63d). It is possible that a similar result could be produced in specimens in which the coiled sac was filled with sediment prior to burial. If the sediment-filled coiled sac remained discrete, rather than adhering to either the mould (as illustrated in Fig. 5.63a) or cast, and became detached from the specimen prior to examination, it would be observed only as a negative relief structure on both mould and cast. However,
at least one personally collected specimen was clearly observed not to contain a discrete sediment-filled coiled sac.

All of these variations indicate that the organism was still present, thus specimens preserved on bedding plane surfaces are unequivocally body fossils, and cannot be interpreted as Domichnia or Cubichnia trace fossils. The differential relief of the sac also emphasises the requirement of early diagenic mineralisation in the preservation of the fossils, as the surface ornamentation is not preserved where the sac has collapsed.

One particularly interesting factor is the presence of trace fossils not just in the enclosing sediments, but also on the surfaces of the fossils themselves (e.g. Figs. 4.73, 4.78). The absence of bioturbation has long been cited as a key factor in exceptional preservation (Butterfield, 1990; Gehling, 1991; Allison and Briggs, 1993; Butterfield, 1995; Gehling, 1999; Orr, 2001; Orr et al., 2003; Gehling et al., 2005), but more recently, evidence has begun to emerge to suggest that the complete absence of infaunal activity is not as crucial as had been previously thought. In particular, trace fossils have been described in direct association with Pararotadiscus guizhouensis from the Kaili Lagerstätte in the Cambrian of China (Wang et al., 2009); trace fossils are also common in the Fezouata Lagerstätte in the Lower Ordovician of Morocco (Van Roy et al., 2010, personal observations). Most recently, the significance of the absence of bioturbation in Burgess Shale-type preservation has also been called into question (Gaines et al., 2012). The occurrence of trace fossils at Tafilalt further confirms that, to a certain extent, bioturbation does not negate the possibility of exceptional preservation, either by homogenisation or oxygenation of the sediment. The occurrence of trace fossils and minimally transported skeletal fossils (such as eocrinoids) further confirms that the Tafilalt sediments were not deposited under conditions of bottom water euxinia, or generally anoxic pore waters: anaerobic decay must have been confined to the vicinity of the fossils.

5.2.4 Decay and diagenesis

Diagenesis encompasses all geochemical and mineralogical changes in a rock from deposition to metamorphism, and including changes associated with uplift and
weathering. These changes can be categorised into three or four distinct stages (e.g. Barnes et al., 1990; Morad et al., 2000; Worden and Burley, 2003).

- **Eogenesis** refers to processes and changes at or near the original site of deposition, where the pore-water chemistry is principally controlled by the depositional environment. In marine environments in the absence of carbonates or evaporates, these processes are mostly related to the bacterially-mediated decay of organic matter.

- **Mesodiagenesis** (or late diagenesis: Milliken, 2003) broadly refers to burial diagenesis, and can be further divided into shallow mesodiagenesis (2-3km burial, 70-100°C), and deep mesodiagenesis (3+km, >100°C), with the boundary between deep mesodiagenesis and shallow metamorphism somewhat vague.

- **Telodiagenesis** refers to uplift-related processes and changes, mediated by near-surface (usually meteoric) water.

Diagenic processes include compaction, cementation and loss of porosity, mineral dissolution and precipitation, and later weathering. Unlike metamorphism, however, solid state diffusion of ions (within crystal lattices) does not occur, being ineffective at diagenic temperatures and pressures. This is a key distinction between diagenic and metamorphic processes. All diagenic chemical reactions involve either dissolution by, or precipitation from, aqueous pore-water solutions. The rate of diagenic reactions is thus controlled by mineral surface processes. Further, such reactions are kinetically, rather than thermodynamically controlled, and chemical equilibrium is not achieved: diagenic reactions favour the production of phases which have a lower activation energy, rather than those which are more thermodynamically stable (Milliken, 2003). Thus throughout diagenesis, minerals exist which are not in equilibrium with either each other or with pore fluids.

It can often be difficult to distinguish exactly when particular diagenic changes occurred in a rock or fossil. However, based on previous diagenic studies and cross-cutting relationships within rock textures, the sequence of diagenic events in the Tafilalt sediments, including decay processes, can reasonably be established.
5.2.4.1 Eogenesis and taphonomy

Decay processes occur during eogenesis, where the interstitial pore water chemistry is controlled by the surrounding (local) depositional environment. As noted on pp. 154-157, decay of organic matter initially proceeds aerobically, but the limitations on $O_2$ diffusion and the extremely high $O_2$ requirements essentially prevent aerobic decay for large concentrations of organic matter, and macrofossils in particular. The Tafilalt parapsonemids must, therefore, have decayed anaerobically, regardless of the levels of oxygen availability in the enclosing sediments. Other factors noted above (p. 154-159) controlling decay also apply, including the adsorption of organic matter and exoenzymes onto clay minerals.

The key factor is identifying which anaerobic decay process or processes were active. Nitrate reduction is insignificant in the marine environment, and can be essentially ruled out. Manganese reduction must have occurred, and may appear to have been involved in the preservation of the fossils, as suggested by the manganiferous oxide and oxyhydroxide coating on the fossil surfaces at M010 (Figs. 5.24, 5.61, 5.62), and on the coiled sac in particular at M001 and M003 (Figs. 5.34, 5.35). Reduced $Mn^{2+}$, however, is highly soluble in reducing environments except in the presence of sufficient dissolved carbonate, whereupon rhodochrosite may be precipitated (Maynard, 2003). Carbonate in Tafilalt is apparently limited to late pore-filling calcite cements (see telodiagenesis, p. 200 below), thus the original precipitation of rhodochrosite is unsupported. The extremely low Mn concentrations in the other localities also indicate that Mn reduction caused the mobilisation of $Mn^{2+}$ into the pore water, and subsequent upwards diffusion back into the marine environment.

Given that the organisms decayed completely (as indicated by the lack of preserved organic carbon), and that aerobic and manganese reduction could not have operated for sufficient time to allow the complete decay of the carcasses, iron reduction must also, therefore, have occurred. This is supported by the scarcity of iron oxide dust rims around detrital quartz grains (normally seen in marine environments) (e.g. Figs. 5.10a, 5.10b, 5.11a, 5.11d, 5.12b, 5.13a, 5.14a, 5.14b), and the presence of iron oxide both coating authigenic quartz overgrowths and filling late
pore spaces (e.g. Figs. 5.10c, 5.11a, 5.11c, 5.11d, 5.12, 5.13, 5.14). These indicate the likely mobilisation of iron subsequent to mesodiagenesis; oxidised ferric iron (Fe$^{3+}$) is highly immobile, thus the late mobility of iron requires the eogenetic production of reduced ferrous iron (Fe$^{2+}$), which is considerably more mobile. The lack of dispersed iron-rich clay minerals (e.g. berthierine, nontronite), which commonly form in eogenetic environments (Morad et al., 2000; Worden and Burley, 2003), or the subsequent diagenic products thereof (e.g. chamosite: Fe-chlorite) also suggest the eogenetic mobilisation of iron.

As noted for Eldonia ludwigi (p. 162), Fe$^{2+}$ commonly adsorbs onto the functional sites of organic structural biopolymers, preventing enzymatic degradation. As stated above, this process should be expected to occur, and there is no clear evidence to the contrary at the Tafilalt sites. Clay minerals may nucleate around adsorbed ferrous iron, leading to the formation of authigenic iron-rich smectites on the surface of the organic matter. The timing of this clay mineral authigenesis is uncertain, and the extent of this process at Tafilalt is unknown; however, the limited occurrence of Mg-bearing clay minerals in the surface veneer of M005-0041 (particularly at the edge of the surface veneer: Fig. 5.47-5.48e), as well as the high clay mineral content of this veneer, may possibly support the formation of authigenic smectites.

More convincingly, however, the concentration of Al observed in EDS maps on the surfaces of fossils compared to the host sediment at M001 (compare Figs. 5.29-5.35 with Figs. 5.25-5.28) and M005 (compare Figs. 5.36-5.40 with Fig. 5.41 and Figs. 5.42-5.44 with Figs. 5.45-5.46), and, even more importantly, the increased Al content of the coiled sac as compared to the rest of the fossil surface (M001-0029, compare Fig. 5.29 with Fig. 5.32; M003-0007, compare Fig. 5.34 with Fig. 5.33; M005-0027, compare Fig. 5.36 with Fig. 5.37), strongly support the nucleation of authigenic clays around adsorbed Fe$^{2+}$ ions. This is further supported by specimens preserving the coiled sac with increased reflectivity from the fossil surface (e.g. Fig. 5.04), indicating a concentration of sheet silicate minerals. Such a clearly defined distribution of Al (and thus clay minerals) could not simply be produced by detrital clay minerals. The Al concentration on the coiled sac compared to the dorsal surface in particular indicates a strong degree of biological tissue
compositional control over the present-day distribution of clay minerals. That such a
distribution of clay minerals occurs on the surfaces of fossils preserved in endorelief
(e.g. M001-0029, M003-0007) further confirms their authigenic origin. Nor could
late diagenic clay minerals have produced such a distribution (as suggested for the
Burgess Shale specimens by Page et al., 2008); while late diagenic clay minerals may
be present, there is no explanation for why such minerals should be concentrated on
the fossil surfaces, and most particularly on specific organs, long after the organic tissues
had completely decayed.

The high clay mineral content of the fossil surface veneer (e.g. Figs. 5.12,
5.18-5.21, 5.47-5.48) may possibly also partially reflect the adsorption of detrital clay
minerals onto the organic matter of the organisms, but due to hydraulic sorting, the
detrital clay content of the Tafilalt beds was obviously low, and thus this is not likely
to have been a significant factor.

Adsorption of ferrous iron onto organic matter inhibits enzymatic
degradation, and thus decay, of complex structural biopolymers, and leads to the
primary preservation of organic matter. However, as noted by Petrovich (2001), the
Fe$^{2+}$ ions become desorbed as a result of sulphate reduction. The distinct lack of
primary preservation of organic matter in any of the Tafilalt specimens is thus
consistent with the occurrence of sulphate reduction as part of the decay process.

The concentration of iron (in the form of oxides and oxyhydroxides):

1. in the fossil surface veneer observed in finer-grained sediments from
M005 (Figs. 5.12, 5.18-5.22, 5.47-5.48),

2. around the fossil surfaces in the coarser-grained beds from near the
base of the succession at M005 (Figs. 5.13, 5.23, 5.49-5.50),

3. on the fossil surfaces at M010 (Figs. 5.14, 5.24, 5.55-5.56, 5.61-
5.62), and

4. on the coiled sac at M001 (Fig. 5.29) and M005 (Fig. 5.36),

all indicate the mobilisation of reduced iron and a strong degree of diffusion to the
fossil surfaces. The direct observation of cubes of haematite (at M005; Fig. 5.22) and
haematite and goethite (at M010; Fig. 5.24) unequivocally confirm that this concentration of iron minerals was not simply a result of the precipitation of smectites around adsorbed Fe$^{2+}$ ions on structural biopolymers. Neither haematite nor goethite naturally occur as cubic crystals: haematite generally has a tabular habit, while goethite usually takes a prismatic form. However, cubes of haematite or goethite may occur as pseudomorphs after pyrite, which is commonly cubic. While only a small number of such cubes have been observed, these must, therefore, have resulted from the prior presence of iron sulphides, which were subsequently oxidised. The small (<2μm) irregular rounded crystals of haematite in the sole veneer of M005-0041 (Fig. 5.48e,f) may also be pseudomorphs after pyrite, which commonly takes such a form at similar size ranges (Love, 1967; Canfield and Raiswell, 1991; Goldhaber, 2003). The correspondence of Fe and S in certain areas on elemental maps of M003-0007 (Fig. 5.35) and M005-0027 (Fig. 5.39) may also support the presence of iron sulphides, although this correspondence is by no means universal.

Sulphate reduction produces H$_2$S as a byproduct. This reacts readily with sedimentary iron oxides and oxyhydroxides to form iron monosulphides (e.g. mackinawite, FeS$_{1-x}$), which react with elemental sulphur to produce pyrite via intermediate iron sulphides (e.g. greigite, Fe$_3$S$_4$), or with further H$_2$S to produce pyrite directly (e.g. Berner, 1970; D.T. Rickard, 1975; Berner, 1984; Morse et al., 1987; Allison, 1988b; Canfield and Raiswell, 1991; Rickard, 1997; Rickard and Luther III, 1997; Raiswell and Canfield, 1998; Goldhaber, 2003; Mapstone and McIlroy, 2006); for example:

$$2\text{Fe(III)O\cdot OH} + 3\text{H}_2\text{S} \rightarrow 2\text{Fe(II)S} + \text{S} + 4\text{H}_2\text{O}$$

then

$$3\text{Fe(II)S} + \text{S} \rightarrow \text{Fe}_3\text{S}_4$$

$$\text{Fe}_3\text{S}_4 + 2\text{S} \rightarrow 3\text{FeS}_2$$

or

$$\text{FeS} + \text{H}_2\text{S} \rightarrow \text{FeS}_2 + \text{H}_2$$
Fe$^{2+}$ in pore fluids or adsorbed onto organic matter, produced by the reduction of Fe$^{3+}$ as discussed above, also provides a ready source of reactive iron for the production of iron sulphides (e.g. Allison, 1988b; Canfield and Raiswell, 1991).

It may seem contradictory to invoke the reaction of hydrogen sulphide with iron oxides and oxyhydroxides as a mechanism of pyrite formation, given the previous statements that Fe(III) reduction occurred. However, previous studies have demonstrated that the reactivity of iron minerals for the purposes of iron reduction is highly variable (e.g. Lovley, 1991; Petrovich, 2001). Amorphous iron oxide and oxyhydroxide detrital grain coatings, such are common in marine sediments, provide a readily available source of reactive iron for dissimilatory Fe(III) reduction, but crystalline iron oxides, oxyhydroxides, and silicates are much less reactive. This is not the case for reaction with hydrogen sulphide, at least for oxides and oxyhydroxides; the half-lives for the reaction with H$_2$S for haematite, goethite, and lepidocrocite are 31 days, 11.5 days, and <3 days, respectively. Iron silicates have half-lives for this reaction of up to 84,000 years for sheet silicates, and even greater for framework silicates (e.g. garnet, ilmenite) (Canfield et al., 1992; Raiswell and Canfield, 1998). Thus, the factors outlined above in support of the occurrence of Fe(III) reduction (lack of iron oxide rims on detrital grains, lack of iron rich clay minerals, evidence of late stage iron mobility indicating the eogenetic formation of reduced iron) also strongly support the occurrence of sulphate reduction and reduction of less reactive sedimentary Fe(III) by H$_2$S.

In terms of the preservation of the fossils, the most important factor is precisely where the iron sulphides form. In general, this is dependent on the rate of sulphate reduction and the concentration of iron. Where rates of sulphate reduction are very slow, with high iron concentrations, iron sulphides can precipitate in pore spaces or cavities within organic matter, effectively permineralising the original organic structure. Very high rates of sulphate reduction in situations where there is a low concentration of iron will cause diffuse iron sulphide precipitation throughout the fossiliferous sediment, as the decay products will have sufficient time to diffuse through the pore water away from the decaying organic matter. Moderate rates of sulphate reduction and iron concentration will cause the precipitation of iron sulphides in the immediate vicinity of the decaying organism (Allison, 1988b;
Canfield and Raiswell, 1991). An additional key factor is the total organic carbon of the containing sediment; where there is a high proportion of buried organic carbon, iron reduction and subsequent sulphate reduction will occur throughout the sediment, leading to the formation of disseminated iron sulphides. Where the total organic carbon is low, reduction will be focused, producing localised iron sulphides around decaying carcasses. Crucially, the adsorption of Fe$^{2+}$ onto structural biopolymers would provide an \textit{in situ} source of reactive iron on the recalcitrant tissues of the decaying carcass. This would lead to the precipitation of iron monosulphides not simply in the vicinity of, but actually on the surface of the recalcitrant tissues concerned. This theoretical conclusion is strongly supported by experimental taphonomy; in decay experiments with the arthropod \textit{Nephrops}, fine layers of iron monosulphides were progressively added to the surface of the chitinous cuticle (but not, importantly, softer parts) as decay progressed (Allison, 1988a).

For the Tafilalt parapsonemids, it is clear that such a coating of iron monosulphides, which later became pyrite, formed \textit{on the presumed dorsal integument}. This is shown by:

1. the surface veneer in fossils from the finer sediments at M005 (Figs. 5.12, 5.18-5.22, 5.47-5.48),

2. the concentration of iron around the fossil surface in coarser fossiliferous sediments at M005 (Figs. 5.13, 5.23, 5.49-5.50), and

3. the iron-rich layers on the fossil surface at M010 (Figs. 5.14, 5.24, 5.55-5.56, 5.61-5.62).

The concentration of Mn on the fossil surface at M010 (Figs. 5.24, 5.61, 5.62) further supports this; these Mn oxides and oxyhydroxides are late diagenetic products (see Telodiagenesis, section 5.2.4.3, p. 200 below), and Mn oxides and oxyhydroxides preferentially form on pre-existing iron oxides, which are of course oxidation products of pyrite. The surface veneer at M005 and M010 provides particularly strong evidence, with the occurrence of cubic haematite and goethite pseudomorphs after pyrite (Figs. 5.22 and 5.24); and, as noted above (p. 192), the
form of the small (<2μm) irregular-shaped haematite crystals in this veneer (Figs. 5.47 and 5.48) is also consistent with pseudomorphs after pyrite.

As a result of iron (III) and sulphate reduction at Tafilalt, therefore, the dorsal surface of the paropsonemids likely became coated with a mixture of authigenic clay minerals (see p. 190) and iron sulphides (and perhaps adsorbed detrital clay minerals), with additional iron sulphides in the pore spaces of the sediment in the immediate vicinity. This veneer would have formed a cemented mould around the dorsal surface, which could maintain its shape during subsequent decay of the remainder of the organism, with adjacent sediment eventually casting the resultant mould. This is supported by the stronger concentrations of Fe and Al on the fossil surface, as compared to the containing sediment (e.g. compare Figs. 5.29, 5.30, 5.33, 5.34 with Figs. 5.25, 5.27, and Fig. 5.36, 5.37, 5.39 with Fig. 5.40), even on the same surface (e.g. compare Figs. 5.42-5.45, and compare Figs. 5.60-5.62), in the EDS elemental maps.

This model is firmly supported by the occurrence of specimens preserved in negative hyporelief and/or positive epirelief, and specimens preserved in endorelief but with the presumed dorsal surface oriented upwards. In such specimens, the mould formed effectively above the organism, requiring that the casting of this mould involve sediment moving upwards, against the force of gravity, to fill the space left by the decay of the body. Gehling (1991) noted that this orientation of preservation in non-mineralised fossils required early diagenic mineralisation. He later expanded on this statement, noting:

“A preservational model must explain the retention of an external mold in the sand that buried a broad flat organism…while, at the same time, sediment from the substrate replaced the decaying body and cast the external mold from below. Such a process would appear to require two unlikely conditions: (1) a body able to support the overlying sole veneer until the external mold had set; and (2) substrate sediment (sand or silt) that remained unconsolidated until after cementation of the overlying sole veneer of sand. The fact that external molds were filled by sediment from the substrate, and did not simply collapse, demonstrates that the sole veneer was rigid or supported in some way before the organism had entirely decayed.” (Gehling, 1999, p. 47).
Examples of specimens preserved in negative hyporelief and/or positive epirelief, or in endorelief with the presumed dorsal surface oriented upwards, further indicate that the sediment below the organisms remained unconsolidated by the time the decay of the organism was complete. The occurrence of such preservation therefore also confirms that the moulds of specimens preserved in positive hyporelief, or in endorelief with the presumed dorsal surface oriented downwards, were formed while the host sediment was unconsolidated and fluid. This is, of course, quite contradictory, and demonstrates that authigenic mineralisation must have been required in the preservation of all paropsonemid specimens (Fig. 5.64).

The occurrence of specimens preserved in multiple positions with respect to the bedding surfaces – for example, specimens preserved on a bedding plane in positive hyporelief but overlapping, with the area of overlap preserved in endorelief (e.g. Fig. 4.100b,c); or specimens preserved in positive hyporelief, but partially folded up into the overlying bed, with the folded portion preserved in epirelief (Fig. 4.103) also confirm the identical nature of the taphonomic processes involved in preservation in positive hyporelief and endorelief.

Dissolution of detrital feldspars results in the precipitation of authigenic replacement kaolinite, and the release to the pore waters of Ca, Na, and K, depending on the original composition, as well as minor Ti. While much of this Ti is later incorporated into authigenic illite, some of the Ti at Tafilalt occurs in the form of discrete crystals of authigenic anatase and rarer rutile (Figs. 5.18-5.21, 5.23-5.24, 5.47-5.48). Authigenic anatase only forms in low-temperature aqueous environments, in which fine particles precipitate, and their coarsening is generally hindered by surface hydration (Smith et al., 2009). As Ti is only locally mobile, the occurrence of anatase within syntaxial authigenic quartz (e.g. Figs. 5.78, 5.23, 5.24).

5.2.4.2 Mesodiagenesis

Due to burial, sediments are compacted and undergo increases in both temperature and pressure. Brittle deformation of larger grains may occur, as well as plastic
deformation of ductile grains, such as detrital mica laths. These effects are more significant in fine-grained sediments due to greater compaction; plastic deformation of mica laths in particular can be seen in the thin section images of fine-grained sediments from M005 (Figs. 5.11b).

Major geochemical and mineralogical changes can also occur in mesodiagenesis, mediated by pore fluids. It is uncertain whether transport of ions in mesodiagenesis is purely by diffusion through stationary pore fluids, or by active advective fluid flow. Hydrothermal convective flow commonly transports dissolved ions, particularly along fault planes and fractures or gaps, forming veins, but no evidence currently exists to quantify the control over the distribution of non-hydrothermal mesodiagenic reactions by advective flow (Morad et al., 2000).

Common shallow mesodiagenic processes include:

- the precipitation of carbonate cements;
- the dickitisation or illitisation of detrital kaolinite;
- the progressive alteration of smectite to mixed-layer smectite-illite; and
- the albitisation of plagioclase (e.g. Barnes et al., 1990; Morad et al., 2000; Milliken, 2003; Worden and Burley, 2003; Worden and Morad, 2003).

Not all of these processes occurred in the Tafilalt sediments.

Carbonate cements are generally sourced from the dissolution of biogenic carbonate, and from excess CO₂ generated by the thermal decay of organic matter. As the total organic carbon at Tafilalt was low, with a relatively low concentration of skeletal organisms, such carbonate cementation would have been limited. Further, the cross-cutting and pore-filling distribution of the carbonate at Tafilalt (Figs. 5.11, 5.14, 5.24, 5.27, 5.55, 5.56, 5.59) suggests a later diagenic origin.

Dickitisation of detrital kaolinite requires a low K⁺ content; higher K⁺ concentrations promote the alteration of kaolinite to illite (e.g. Ehrenberg et al.,
1983; Morad et al., 2000). The occurrence of illite (Figs. 5.47-5.48) and the presence of degraded K-feldspars at M005 (e.g. Fig. 5.12b), suggest that pore water K+ concentrations were sufficiently high to promote the illitisation of kaolinite. Albitisation of plagioclase is indicated by the detection of albite by XRD (Figs. 5.15-5.17). Several crystals of albite at M001 and M003 are, however, mildly altered in places, but do not show typical authigenic replacement features (e.g. Milliken, 1989), and thus appear to be detrital (Fig. 5.10a,c). However, both Ca and Na are elevated at M001 and M003, as compared to M005 (Tables 5.05, 5.06), perhaps indicating that the plagioclase was not originally albite sensu stricto.

The progressive alteration of smectite to mixed-layer smectite-illite is indicated by the Mg content of clay minerals analysed by EDS point spectra (Figs. 5.47-5.48).

**Deep mesodiagenic** processes include:

- quartz cementation;
- further feldspar dissolution;
- continued progressive alteration of smectite to mixed-layer smectite-illite and illite;
- the formation of Mg-chlorites, usually as grain coatings; and
- precipitation of minor carbonate.

These processes are, for the most part, linked. For example, the dissolution of feldspars commonly results in the precipitation of authigenic kaolinite, and consumes H+ (Morad et al., 2000; Worden and Morad, 2000; Milliken, 2003). If the source of the H+ is dissolved CO2 in the form of carbonic acid, carbonate precipitation results. In the case of plagioclase, this commonly reacts with liberated Ca, as well as possibly pore water Fe and Mg to produce calcite or ferroan dolomite or ankerite (Morad et al., 2000; Milliken, 2003). Similarly, Worden and Morad (2003) and Milliken (2003) noted the possibility of ankerite or ferroan dolomite authigenesis during the smectite-illite transformation. Dissolution of smectite and replacement by illite requires additional Al and K, and produces excess Si as well as lesser amounts of Fe,
and Mg which may be incorporated into ferroan dolomite or ankerite. Such authigenic carbonates are often aggressive replacements, growing with euhedral faces, and causing the dissolution by pressure solution of adjacent phases (Morad et al., 2000; Milliken, 2003; Worden and Morad, 2003). This is likely the origin of the carbonate with euhedral crystal faces in Bed 1 at M005 (Fig. 5.11a).

Continued dissolution of feldspars, and the replacement of smectite by illite, both also produce excess Si, which commonly results in the precipitation of syntaxial overgrowths of detrital quartz. In extreme cases, this can lead to the production of ‘diagenic quartz arenites’ (Harris, 1989; Worden and Burley, 2003). The high authigenic quartz content and lack of unaltered detrital feldspar in the Tafilalt sediments supports the operation of such processes.

The presence of clinochlore (Figs. 5.10-5.13, 5.15-5.17) in the Tafilalt sediments may possibly indicate, however, that not all of the detrital and eogenic smectite was replaced by illite. Deep mesodiagenic chlorites are commonly produced as coatings on grain surfaces, and usually form by precipitation and/or replacement of detrital or authigenic smectites (Humphreys et al., 1994; Morad et al., 2000). The clinochlore at Tafilalt must have formed quite late in mesodiagenesis, as chlorite effectively blocks the formation of quartz overgrowths (e.g. Ehrenberg, 1993).

Deep mesodiagenesis also included the limited alteration of illite to mica, or the formation of primary authigenic mica (Figs. 5.10-5.12).

The occurrence of authigenic anatase and rutile at Tafilalt (Figs. 5.18-5.21, 5.23-5.24, 5.47-5.48) provides broad constraints on the thermodynamic history of the sediments. Anatase has a much lower surface energy than rutile (Levchenko et al., 2006), and is thus the stable form of TiO$_2$ at small crystal sizes (where the surface to volume ratio is high). At higher temperatures, however, the surface-bonded water in anatase is removed, leading to destabilisation and transformation to rutile (Li et al., 2005). Similarly, as anatase has a higher molar volume than rutile, increases in pressure will also promote the same transformation (Smith et al., 2009). In a single component TiO$_2$ system, anatase has no P/T stability field at sizes greater than 14nm. In multi-phase systems such as rocks, evidence indicates that the anatase to rutile transformation occurs at approximately 400-600°C (Smith et al., 2009). As
anatase is still present, this figure represents an upper limit for the maximum burial temperature for the Tafilalt sediments. The true maximum value is likely to have been significantly lower, as this estimate does not account for overburden pressure. Such temperatures would also have resulted in partial metamorphic recrystallisation, which is clearly not evident.

5.2.4.3 Telodiagenesis

Telodiagenesis refers to changes associated with uplift, the release of overburden pressure, cooling, and interaction with meteoric water. Common telodiagenetic reactions include:

- oxidation of reduced iron;
- the dissolution or precipitation of carbonate cements (depending on the particular conditions); and
- the dissolution of aluminosilicates such as mica and feldspars, accompanied by the precipitation of replacement kaolinite (Morad et al., 2000).

No kaolinite was observed in the Tafilalt sediments, thus it is unlikely that extensive telodiagenetic dissolution of aluminosilicates occurred.

The presence of both barite (Figs. 5.31, 5.32, 5.35, 5.36, 5.40) and manganese minerals (Figs. 5.24, 5.26, 5.34, 5.35, 5.61, 5.62; see also Tables 5.05 and 5.06) in the Tafilalt sediments further indicate a degree of hydrothermal mineralisation by convective metal-bearing flows, post-dating the quartz cementation. The precipitation of manganese oxides is favoured by a pre-existing surface of iron oxide (Maynard, 2003). The presence of Mn oxides and oxyhydroxides on the fossil surfaces at M010 (e.g. Figs. 5.24, 5.61-5.62), and on the coiled sac at M001 and M003 (e.g. Fig. 5.34), therefore implies that these surfaces were oxidised from pyrite to iron oxide either before or by the manganese oxides, which have previously been shown to oxidise pyrite (Schippers and Jørgensen, 2001). That the manganese oxides preferentially precipitated on pre-existing iron oxide surfaces is shown clearly by the presence of manganese oxides on the coiled sac, but
not the remainder of the disc, at M001 and M003 (e.g. Figs. 5.33-5.35; see also Figs. 4.87a-d, 4.103a, 5.05a, 5.06, 5.07). As the thickest and apparently the most recalcitrant structure, the coiled sac would have resisted decay and thus would have been present for longer than the other organic tissues, and thus should be expected to have had the thickest coating of iron sulphides, and therefore of iron oxides after subsequent oxidation. Mesodiagenic pore fluids are almost generally reducing, thus it is likely that the hydrothermal mineralisation occurred during uplift-related telodiagenesis.

Pyrite is initially oxidised to sulphate and reduced Fe$^{2+}$ (Raiswell and Canfield, 1998):

$$2\text{FeS}_2 + 2\text{H}_2\text{O} + 7\text{O}_2 \rightarrow 2\text{Fe}^{2+} + 4\text{H}^+ + 4\text{SO}_4^{2-}$$

The Fe$^{2+}$ is then subsequently reduced by O$_2$ and H$_2$O, to produce haematite and goethite and/or lepidocrocite (Mapstone and McIlroy, 2006):

$$4\text{Fe}^{2+} + \text{O}_2 + 4\text{H}_2\text{O} \rightarrow 4\text{Fe(III)}_2\text{O}_3 + 4\text{H}^+$$

$$4\text{Fe}^{2+} + \text{O}_2 + 6\text{H}_2\text{O} \rightarrow 4\text{Fe(III)}\text{O} \cdot \text{OH} + 8\text{H}^+$$

These iron oxides may pseudomorph the original pyrite crystals (as previously discussed briefly in section 5.2.4.1, p. 192).

The released H$^+$ also acidifies the pore water. As a result, the calcite observed at M001, M003, and M010 must post-date the pyrite oxidation, as it would otherwise have been dissolved by the acidic pore waters produced. It is also likely that the calcite post-dates the manganese mineralisation, as indicated by the texture and distribution of the calcite, particularly the calcite-filled fracture in M010-0017 (Fig. 5.59).

The barite mineralisation appears to post-date both the manganese mineralisation and the late calcite cement, as it is primarily a surficial feature, indicating an inability to penetrate the cemented rock.
A summary of the taphonomy of the fossils is shown in Fig. 5.65, with a broader summary of the diagenic sequence and history presented in Fig. 5.66.

5.3 Taphonomy of other eldonides preserved as moulds and casts

Only a limited amount of taphonomic data was collected for other eldonides. A thin section was made through a specimen of *Seputzus pomeroii*, and subjected to petrographic examination; EDS elemental maps were also made of five areas on this thin section. Aside from this, only observations of the positions and relief of the fossils, and the sedimentology and palaeontology of the host sediments, were considered. Nonetheless, some inferences may be drawn.

5.3.1 *Seputzus pomeroii*

The specimens from Pomeroy (Ordovician, Ireland) are preserved in a medium-grained micaceous quartz arenite, with minor chlorite and abundant iron oxides (Fig. 5.67). Secondary porosity is common. The bed is densely packed with skeletal remains, and several delicate fossils (e.g. asteroids, carpoids) in the bed are preserved largely intact, although the original calcite or aragonite is often significantly or completely degraded, leaving excellent mouldic preservation (Fig. 4.36). Articulation of shells is common; however, orientation is random and no sorting is evident. No trace fossils or evidence of bioturbation have been observed in the material, nor have any sedimentary structures. The surfaces of the fossils are darkened with respect to the sediment; micaceous minerals also appear to be concentrated on the fossil surfaces.

The EDS elemental maps are on a thin section cut orthogonally through the fossil, and do not show the fossil surface itself (shown in Figs. 5.68–70, and the Appendix). The Al content is high, and correlates strongly with K (Fig. 5.68), especially at high resolution (Fig. 5.69), indicating a high degree of potassium aluminosilicates. Mg is more limited, but is also well dispersed, perhaps indicating
remnant smectites (Fig. 5.70). Fe co-occurs with Al, but not precisely, indicating separate Fe and aluminosilicate minerals in the same vicinity (most evident in Fig. 5.69).

As noted above, experimental studies of cnidarian taphonomy (Norris, 1989) have demonstrated that once decay has started, fine details of truly soft-bodied organisms cannot be preserved. The sediment which moulded S. pomeroii must therefore have been coherent enough to retain these subtle features prior to the onset of decay of this part of the organism. However, given that most of the organism appears not to have been preserved at all, decay of the more labile tissues must have been underway prior to lithification. Whilst it may be possible that some labile tissues are simply too insubstantial to be preserved as moulds and casts by siliciclastic sediments (irrespective of how rapidly lithification occurred), in this instance the entire internal anatomy (including any potential feeding structures, a mouth, oesophagus, stomach, intestine, anus, musculature, or internal body structure etc.) of the animal is clearly not evident. It is unlikely that all of these features were sufficiently insubstantial as to leave absolutely no trace, indicating that these must have been in an advanced state of decay upon lithification. This produces a definitive timescale for the lithification of the sediment, which thus appears to have been extremely rapid.

Close examination of the shelly fossils also supports rapid lithification: Scrutton et al. (1998) noted that while calcitic fossils were always preserved undistorted, aragonite-shelled organisms, including the kilburchophyllid corals, were often preserved flattened or as composite moulds within the formation, but not in the richly fossiliferous beds at the top (including the horizon hosting S. pomeroii) where

"all material, whether originally of aragonitic or calcitic composition, is preserved undistorted" (Scrutton et al., 1998, p. 122).

This clearly supports the suggestion that the S. pomeroii bed was more rapidly lithified than most other beds within the formation. As noted above, preservation in this style requires:
1. lithification of the moulding sediment prior to the decay of the preserved part of the organisms, and

2. lithification of the casting sediment after decay.

The fact that the same surface of *S. pomeroii* is preserved in all four specimens, irrespective of their orientation (as is the case for *Discophyllum peltatum* and *Praeclarus vanroii* from Tafilalt), seems to suggest that rapid lithification occurred preferentially on one side of the organism only. This may have been controlled by the original morphology of the animal, with softer and more labile tissues interfering with the lithification process on the opposite side of the disc. Decay of the softer parts must therefore have been underway during the rapid lithification of the casting sediment.

The darkening of the fossil surfaces, and the preferential concentration of aluminosilicates on these strongly suggest a similar mode of preservation to that of the Tafilalt fossils, albeit with a slightly different diagenic history. This is supported by the correlation of Al with K and more limited Mg, and near Fe in the elemental maps, indicating a relatively high content of iron oxides and oxyhydroxides, illite, and smectite-illite mixed layer or smectite. In this model, the surfaces of the fossils would have been preserved by iron reduction releasing reduced iron, which adsorbed to the surface, providing a substrate for the nucleation of authigenic clay minerals, and for the precipitation of iron sulphides once decay proceeded to sulphate reduction. The iron sulphides and clay minerals moulded the surface of the fossils, with this mould subsequently cast once the entire organism had decayed. The concentration of micaceous minerals on the surfaces of the fossils may also suggest the adsorption of clay minerals to the organic surfaces.

The lack of preserved biogenic carbonate, despite the high fossil content, and the high porosity, may suggest an originally calcitic cement. This is consistent with the postulated taphonomic model as the oxidation of pyrite, as noted above, produces excess H⁺, which would dissolve any calcite present.
5.3.2 *Paropsonema cryptophya*

The specimens of *Paropsonema cryptophya* are preserved within and on the soles of light grey massive, laminated, or cross-laminated siltstones, separated by blue-grey shales. Preservation of specimens within siltstone beds indicates that for these specimens, at least some degree of transport occurred (although, given the fine grain size, questions remain with regards to the flow velocity and the strength of the flow). One specimen, the lectotype NYSM 447, exhibits a corresponding depression on the top surface of the host bed, indicating that the organism was present on burial, with sediment moving downwards under the force of gravity to cast the mould following the decay of the organism. This indicates that the specimens were present on burial.

This also indicates that decay of the organism was complete while the host sediment was still unconsolidated. It is therefore likely that early diagenic mineralisation was required to stabilise the moulds, a hypothesis supported by the preservation of extremely fine details on the surfaces of several specimens. It is plausible that the specimens were preserved in the same manner as the Tafilalt paropsonemids; however, in the absence of further petrographic and geochemical evidence, such a conclusion remains speculative for the present.

5.3.3 *Paropsonema mirabile* and *Praeclarus* sp.

The specimens of *Paropsonema mirabile* and *Praeclarus* sp. were examined from latex moulds and plaster casts, with only photographs of the original specimens. No primary taphonomic evidence could thus be collected. However, the preservation of one specimen of each species overlapping on MV P26661 (Figs. 4.54, 4.66) indicates that for these specimens, at least some degree of transport preceded burial. Additionally, the red colouration of the disc surface in *Praeclarus* sp. MV P30713 is similar to that noted for certain Tafilalt specimens of *D. peltatum*. As in *Paropsonema cryptophya*, the preservation of fine details would seem to indicate that early diagenic mineralisation was required, but this too remains theoretical, pending further research.
5.3.4 *Discophyllum peltatum* from New York and England

The specimens of *D. peltatum* from New York and England are preserved in shales, rather than sandstones. Only three specimens in this style of preservation are available, and so destructive analysis was not possible. However, the contrast between these specimens and *Eldonia ludwigi*, both preserved in shales, is interesting. *E. ludwigi* is preserved as aluminosilicate and carbonaceous compressions, while *D. peltatum* preserves no observed organic carbon or aluminosilicates, but retains relief on the ornamentation of the dorsal integument. While it is purely speculative, it may be interesting to consider the possibility that while the supply of sulphate ions was curtailed early in the case of the Burgess Shale, leaving iron ions and authigenic minerals nucleated on these as well as adsorbed detrital clays to protect the organic matter from enzymatic decay, and replicate the specimens in aluminosilicates, the supply of sulphate may not have been limited for the specimens of *D. peltatum*, leading to iron sulphide mineralisation. While the Burgess Shale specimens would thus have been subject to the full effects of compression, with no stabilisation of the original morphology, the specimens of *D. peltatum* would thus have retained their relief due to the authigenic iron sulphide mould.

Further research is necessary to clarify the taphonomic processes involved in the preservation of *D. peltatum* in shales. The answer to this question could potentially shed further light on the reasons for the disappearance of Burgess Shale-type preservation from the fossil record in the Cambrian.

5.4 Taphonomic summary

*Eldonia ludwigi*, from the Cambrian Burgess Shale of Canada, and *Discophyllum peltatum* and *Praeclarus vanrooi*, from the Ordovician of Tafilalt in Morocco, are preserved in contrasting taphonomic modes. Specimens of *Eldonia* are preserved as compressions in shales, while specimens of *Discophyllum* and *Praeclarus* are found as moulds and casts in shallow marine sandstones. However, their taphonomic history is, in many respects, quite similar.
Burgess Shale specimens of *Eldonia ludwigi* preserve the coiled sac as original organic carbon, with compositional differences previously analytically identified between the outer membrane and inner sac. The circumoral tentacles also appear to be carbonaceous, but most of the rest of the anatomy is replicated by aluminosilicate clay minerals.

The adsorption of detrital clay minerals onto both microbial extracellular digestive exoenzymes and the organic tissues of the organisms themselves during transport and deposition may have retarded enzymatic degradation of complex organic biopolymers. However, this did not prevent the decay of the most labile tissues.

In aqueous settings, the decay of almost every organism is controlled by anaerobic processes, due to constraints on the rate of supply of oxygen. Due to the lack of nitrate and manganese, in marine environments, anaerobic decay proceeds primarily by iron and sulphate reduction. In Burgess Shale specimens of *Eldonia ludwigi*, the decay of the most labile tissues by Fe$^{3+}$ reduction produced excess aqueous Fe$^{2+}$ ions. These ions would have adsorbed to the active sites on complex organic biopolymers, due to a natural affinity between such tissues and metal ions. This would not only have prevented enzymatic degradation of these tissues (a necessary prerequisite for decay, as such molecules are too large to be primarily utilised as a food source by microbiological organisms), but would also have provided ready sites for the nucleation and growth of authigenic aluminosilicate clay minerals, replicating the organic tissues.

The presence of some pyrite associated with a limited number of Burgess Shale specimens indicates the decay of organic matter by sulphate reduction. However, sulphate reduction produces hydrogen sulphide and free sulphur, which react readily with iron. If such a process occurred in a carcass in which Fe$^{2+}$ ions had been adsorbed to organic biopolymers, the hydrogen sulphide and free sulphur would react with the adsorbed iron, producing iron monosulphides (which later transform to pyrite). This would remove the iron ions from the biopolymers, allowing enzymatic degradation and decay. As original organic carbon is undoubtedly present.
in Burgess Shale specimens, including *Eldonia ludwigi*, sulphate reduction must have been restricted, likely due to an originally low sulphate concentration.

While these processes were capable of preserving some labile tissues, the decay of the preserved organisms must have consumed the available O\(_2\), Mn\(^{4+}\), and Fe\(^{3+}\). Even in the best preserved specimens, therefore, the most labile tissues must have decayed, and thus are not represented.

Specimens of *Discophyllum peltatum* and *Praeclarus vanrooi* at Tafilalt were preserved by authigenic mineralisation cementing sediment moulds around the organisms. The eogenic processes described for *Eldonia ludwigi*, including the adsorption of Fe\(^{2+}\) ions on to the active sites of structural biopolymers and the growth of authigenic clay minerals around the adsorbed ions, also occurred at Tafilalt. This is confirmed by the concentration of Al and clay minerals on the surfaces of the fossils, as compared to the host sediment, and in particular their concentration on the coiled sac, as compared to the remainder of the fossil surfaces. This distribution indicates a biogenic control, in the form of compositional variation, over the distribution of Al and clay minerals. As there is no reason for late diagenic minerals to form on specific biological components after the organism had decayed, this distribution also confirms the early diagenic syn-decay nature of these clay minerals.

The lack of organic carbon at Tafilalt is likely due to the occurrence of sulphate reduction during the decay of the Tafilalt specimens, which would have caused the removal of adsorbed iron ions from the organic tissues, exposing them to enzymatic degradation. The concentration of iron oxides on Tafilalt fossil surfaces, and the occurrence of cubic iron oxide and oxyhydroxide pseudomorphs after pyrite confirm that sulphate reduction did occur. The distribution of the iron oxides (along with manganese oxides and oxyhydroxides on some specimens, which preferentially form on iron oxide-rich surfaces) confirms that the initial iron sulphides were formed directly on the surfaces of the organisms, and not distributed within the surrounding sediments.

This early diagenic iron sulphide mineralisation stabilised the surrounding sediment, cementing a mould, which essentially formed a ‘death mask’ over the organism. The reduction in volume of the organic tissues due to decay allowed the
mould to be progressively cast by adjacent sediment, which must therefore have been unconsolidated until decay had been completed. The fossils are thus preserved as moulds and casts, with aluminosilicate-rich surfaces.

Preservation of Tafilalt specimens within sandstone beds, on sandstone bedding surfaces (in both positive and negative hyporelief) and, in rare cases, on both the surface and within the bed (where part of the specimen was folded up into the overlying sediment), confirm that such early diagenic mineralisation was required in all instances of this preservation at Tafilalt.

Subsequent deeper burial and mesodiagenesis led to the dissolution of feldspars and degradation to kaolinite, with limited authigenic anatase also precipitating. Detrital smectites and authigenic kaolinite so produced were progressively transformed with burial into smectite-illite mixed layer, and eventually illite. Limited authigenic muscovite was also produced. Complete dissolution of most feldspars, as well as the smectite-illite replacement reaction, produced excess pore water silicate, leading to authigenic syntactical quartz overgrowths, cementing the beds. Limited authigenic carbonate was produced by aggressive replacement of feldspars.

Telodiagenesis involved the oxidation of iron sulphides to iron oxides and oxyhydroxides, haematite, lepidocrocite and goethite. At some sites, hydrothermal activity led to an excess of Mn, which precipitated on the pre-existing iron oxide fossil surface veneer as manganese oxides and hydroxides. Limited calcite cementation also occurred at M010. Late hydrothermal activity saw the precipitation of barite on bed surfaces and fractures.

Evidence from specimens of *Seputus pomeroii* from the Ordovician of Ireland, also preserved as moulds and casts in sandstones, suggest that a similar taphonomic process was involved in their preservation. Similarly preserved specimens of *Paropsonema cryptophya* from the Devonian of New York, *Paropsonema mirabile* and *Praeclarus sp.* from the Silurian of Australia also probably required similar early diagenic mineralisation, likely through the same taphonomic processes, although there are insufficient numbers of specimens and thus insufficient taphonomic evidence to confirm this at present. Insufficient taphonomic evidence also prevents
the understanding of the taphonomy of specimens of *Discophyllum peltatum* preserved in shales. A full exploration of the taphonomy of these specimens would be particularly interesting, as it could help clarify the reasons for the effective disappearance of Burgess Shale-type preservation from the fossil record.
6

Discussion and Conclusions

6.1 What were the eldonides?

The eldonides are perhaps the most poorly known significant group of Palaeozoic fossils. Thousands of specimens are known from sites of exceptional preservation, from the Early Cambrian to the Late Devonian, including some of the most famous Konservat-Lagerstätten in the world. However, it is only in very recent times that the relationship between the various eldonide species has been realised.

At this point in the discussion, it is perhaps logical to explore the phylogeny of this rather enigmatic group. In order for an informed and balanced opinion to be developed, it is first necessary to review the history of interpretation of these organisms.

6.1.1 History of Research

The first eldonide to be described was *Discophyllum peltatum* Hall, 1847, from the Ordovician of Troy, New York. Two specimens were included, though only one (UC 12517) was illustrated. Hall (1847) included the description of *D. peltatum* in a section on corals from New York, but did not discuss the interpretation or the reason for this placement. Both specimens were subsequently illustrated by Walcott (1898), who included *D. peltatum* in his monograph on fossil medusae, but expressed reservations about such an interpretation.

*Paropsonema cryptophya* Clarke, 1900 was originally described as an echinoderm, with Clarke (1900) comparing the radial structures to echinoid
ambulacra. Clarke (1900) also noted the similarity of *P. cryptophya* to *D. peltatum*, but did not, however,

*‘look on the two as identical in all structural features’* (Clarke, 1900, p.178).

Shortly thereafter, *P. cryptophya* was suggested to be a porpitid hydrozoan by Fuchs (1905), an interpretation that was followed by Ruedemann (1916, 1933b), in a note describing several subsequently recovered specimens. Ruedemann (1916) went further than Clarke (1900), and asserted a close relationship between *P. cryptophya* and *D. peltatum*, considering both to represent fossil porpitids.

The porpitid interpretation was not followed by Chapman (1926b), who described *Paropsonema mirabile* as a jellyfish from a single specimen, the holotype, under the name *Discophyllum mirabile*. However, the porpitid interpretation otherwise persisted for decades, with Harrington and Moore (1956b) including both *D. peltatum* and *P. cryptophya* within this group in the Siphonophorida section of the coelenterate Treatise volume, calling Ruedemann’s interpretation “very plausible” (p. F150), and reassigning *D. mirabile* to *Paropsonema mirabile*. Scrutton (1979) followed Harrington and Moore in interpreting *Discophyllum* as a porpitid, as did Stanley (1986), who referred to *Discophyllum* as an elliptic but otherwise very modern porpitid, thereby misunderstanding both its taxonomy and taphonomy, and referred to *Paropsonema* as:

*‘very modern appearing porpitids’* (p. 81).

Conway Morris and Robinson (1982) also referred to *Paropsonema* as a porpitid, and noted that there was

*‘more than a superficial similarity’* (p. 116)

between *Paropsonema* and *Eomedusa datsenkoi* (Fig. 4.100a), which had been described as a scyphozoan based on two specimens from the Upper Cambrian of Siberia under the name *Camptostroma datsenkoi* by Popov (1967). However, *Camptostroma roddyi*, the type species of the genus (Ruedemann, 1933a), was even then known to be an echinoderm (Durham, 1966), and the specimens were reassigned to the new genus *Eomedusa* by Datsenko et al. (1968). Scrutton (1979) and Stanley (1986) also both suggested that *Eomedusa datsenkoi* was a porpitid.
Up to this stage, a relationship between these parapsonemids and *Eldonia ludwigi* had not yet been considered, which in some respects is surprising as *Eldonia* had been described by Walcott as far back as 1911, and with a curiously similar variation in interpretations. Walcott (1911) noted that he initially believed *Eldonia ludwigi* to be a cnidarian medusa, with the coiled sac being a commensal annelid, but the volume of specimens convinced him that this was actually part of the animal. He compared the coiled shape of the sac to the spiral alimentary canal of the holothurians (commonly known as ‘sea cucumbers’: Class Holothuroidea, Phylum Echinodermata), and although noting significant differences with extant pelagic examples, thus interpreted *Eldonia* as a holothurian in a new Family Eldoniidae.

A.H. Clark (1912) supported this interpretation, and provided the first reconstruction of *E. ludwigi* (reproduced in Fig. 4.23a). H. L. Clark (1912), however, argued strenuously against this interpretation, but also noted that the coiled sac precluded an interpretation as a cnidarian, stating that:

"the general appearance of the animal is that of a free-swimming coelenterate, except for the apparently distinct and extraordinary alimentary canal" (p. 278).

A. H. Clark (1913) wholeheartedly agreed with the latter statement, noting that:

"the highly specialised digestive tube at once negatives the supposition that Eldonia may be a coelenterate" (p. 494),

but reiterated his support for Walcott's (1911) holothurian interpretation. This was also supported by Ryan and Hallissy (1912) who described a purported second species, *Eldonia antonii*, from Cambrian strata of Bray, Ireland (although Ryan (1912) later noted that there was considerable scepticism on the validity of this new species from other Irish scientists). Eastman (1913) included *E. ludwigi* without reservations in the holothurian section of the second edition of the *Text-Book on Palaeontology†††*. Others, however, remained sceptical: Steinmann (1912) described the interpretation of *E. ludwigi* as doubtful, but refrained from outright scepticism.

††† A footnote to this section notes that H.L. Clark was responsible for the discussion of the holothurians, with the exception of the Cambrian specimens. The authorship of the section is thus unclear: both A.H. Clark and Walcott also contributed to the book.
disagreement, pending the publication of further descriptions, while Osborn (1916) described *Eldonia* as:

“problematic” (p. 324),

and Fedotov (1928) agreed with H.L. Clark’s criticisms, as did Cuénot (1948). Croneis & McCormack (1932) quoted H.L. Clark, but concluded only that:

“further information is needed before...Eldonia can be classified to the satisfaction of all” (p. 127),

although they did dismiss the earlier description of *E. antonii* by Ryan & Hallissy (1912), saying that there was:

“little or nothing in Ryan and Hallissy’s figures...to warrant such a comparison” (p. 127).

*Eldonia* was not discussed in either the coelenterate (Harrington and Moore, 1956a) or holothurian (Frizzell et al., 1966) sections of the *Treatise on Invertebrate Paleontology*.

Madsen (1956, 1957) was the first to firmly propose an alternative to the holothurian interpretation for *Eldonia*. Until this point, the discussion had centred on whether or not Walcott’s interpretation as a holothurian had been correct, with H.L. Clarke (1912)’s statement:

“It is far less of a strain on my credulity to believe that Eldonia, whose extraordinary nature I have no inclination to deny, is some sort of a Coelenterate with a commensal worm inside or under the subumbrella, or even that it represents a hitherto unknown phylum, than to believe that it is a holothurian or is connected, save in the remotest way, with the Echinoderms” (p. 278)

coming closest to an alternative classification. Madsen (1956, 1957) agreed with H.L. Clarke, and reinterpreted *E. ludwigi* as a siphonophorid (colonial hydrozoan cnidarians in the Order Siphonophorae, then incorrectly thought to include the ‘chondrophorines’), considering the coiled sac to represent a gastrozooid, providing a reconstruction to support his hypothesis (Fig. 4.23b). Seilacher (1961) also suggested a siphonophorid interpretation. Lemche (1960) proposed that *Eldonia* represented a coelenterate medusa.
“as it shows similarities to the Coronata in the bell margin and to trachyline medusae in what appears to be the manubrium” (p. 95),

though he later partially reconsidered, maintaining a coelenterate interpretation, but believing it to be sessile (Lemche in Madsen, 1962). Madsen (1962) rejected this suggestion of a sessile mode of life, reiterating his siphonophorid interpretation.

Durham (1969, 1974), however, convincingly dismissed this interpretation, showing that the coiled sac was suspended within a coelomic cavity. He stressed that this ruled out any interpretation of Eldonia as a diploblast, stating

“If the gut of Eldonia is an internal structure, it cannot be referred to the Coelenterata” (p. 754).

He supported Walcott’s original holothurian interpretation, and provided a third reconstruction of the animal (Fig. 4.23c). Conway Morris (1979b) accepted Durham (1974)’s reaffirmation of the holothurian interpretation, and also noted that Dhonau and Holland (1974) had confirmed the inorganic nature of the specimens attributed to ‘Eldonia antonii’, as suggested by Croneis and McCormack (1932). Scrutton (1979) followed Durham in accepting an echinoderm interpretation, as did Conway Morris and Robinson (1982), but Paul and Smith (1984) and Smith (1988) expressed renewed doubt, causing Conway Morris and Robinson (1988) to note that

“the higher taxonomic affinities of this genus are best regarded as uncertain” (p. 38).

Conway Morris (1990b) subsequently regarded Eldonia as problematic.

Around this time, Sun and Hou (1987) established four genera of supposed “medusoids” from the Chengjiang Lagerstätte, including Stellostomites eumorphus, Yunannomedusa eleganta, and Rotadiscus grandis, the latter of which was described as a ‘chondrophorine’. Conway Morris and Robinson (1988) noted the similarity of Yunannomedusa eleganta and Stellostomites eumorphus to Eldonia ludwigi, and proposed that these were synonymous.

Dzik (1991) agreed that Yunannomedusa eleganta and Stellostomites eumorphus were related to Eldonia (though he did not consider them to be synonymous), and further suggested that Rotadiscus grandis, as well as Eomedusa datsenkoi and three
other previously described species — *Velumbrella czarnockii* Stasińska 1960, *Dinomischus isolatus* Conway Morris 1977 and *Dinomischus venustum* Chen *et al.* 1989 — also formed part of this group. These latter two species (both within the genus *Dinomischus*) are unusual in that they were both clearly sessile and pedunculate. In particular, Dzik (1991) suggested that *Velumbrella* was closely related to *Yunnanomedusa*, and he also described specimens co-occurring with *Velumbrella* as *Rotadiscus* sp. He interpreted the entire group as a distinct class of lophophorates (the ‘Class Eldonioidea’), based on a revised interpretation of the circumoral tentacles at the proximal end of the coiled sac. However, he regarded *Paropsonema* as a coelenterate, and made no mention of *Discophyllum*.

In the same volume, Chen and Erdtmann (1991) also affirmed that *Yunnanomedusa* and *Stellostomites* were related to *Eldonia*, interpreting them only as problematic, but noting that they could not be coelenterates. They did not extend this relationship to include *Rotadiscus* or any of the other forms mentioned by Dzik (1991). However, Runnegar and Fedonkin (1992) also noted the similarities between *Eldonia*, *Yunnanomedusa* and *Stellostomites*, and proposed, like Dzik (1991), that *Velumbrella czarnockii* and *Eomedusa datsenkoi*, too, could be related to *Eldonia*.

*Velumbrella czarnockii* (Fig. 4.33) had originally been described by Polish geologist Jan Czarnocki in a manuscript from 1941 under the name ‘Brzechowia brzechowiensis’. However, this was not published, and the manuscript contained neither descriptions nor illustrations. As a result, this name was declared *nomen nudum* by Anna Stasińska (1960), who redescribed the forms under their current name, believing them to be Trachymedusae or Limnomedusae. Scrutton (1979) also compared them to Trachymedusae, but additionally suggested that they could represent ‘chondrophorines’, a suggestion followed by Stanley (1986), who stated that they strongly resembled porpitids. A single specimen was assigned to a highly questionable second species as *?Velumbrella bayeri* by Yochelson and Mason (1986). Pickerill (1982) also compared specimens from the Cambrian of New Brunswick, Canada to *Velumbrella* in a preliminary note (these specimens have subsequently been reinterpreted as sedimentary structures by Hagadorn and Miller, 2011). Rozanov and Zhuravlev (1992) (who regarded *Paropsonema* as a coelenterate) also
considered *Velumbrella* to be a porpitid, and suggested that it was closely related to *Eomedusa datsenkoi*.

Conway Morris (1993b) suggested that *Velumbrella* was closely related to the rotadiscids, citing the co-occurrence of *Rotadiscus* sp., as described by Dzik (1991), proposing that these formed part of the same organism (Masiak and Żylińska (1994), in their redescription of *Velumbrella*, later demonstrated that these are, in fact, separate). He agreed that both were related to *Eldonia*. Conway Morris (1993b) also proposed that *Paropsonema cryptophya*, *Paropsonema mirabile*, and *Eomedusa datsenkoi* all belonged to the eldonide group. However, he remained unconvinced on *Discophyllum peltatum*, noting that Harrington and Moore (1956a) had reaffirmed Ruedemann (1916)’s redescriptions of this form as a porpitid ‘chondrophorine’, and stating that evidence

“for a close relationship between Discophyllum and Paropsonema remains wanting”

*(p. 598)*

(which, at that point, was quite true). He also broadly accepted Clarke (1900)’s echinoderm interpretation of *Paropsonema* (and hence the eldonide group). He subsequently reiterated this interpretation (Conway Morris, 1993a), suggesting that the group could represent pre-echinoderm deuterostomes.

A comprehensive re-examination of the eldonide group, concentrating on *Eldonia* and *Rotadiscus* in particular, was undertaken by Duncan Friend (1995), in work which was unfortunately never published. He convincingly dismissed the lophophorate and coelenterate interpretations for the eldonides, supporting the pre-echinoderm deuterostome interpretation of Conway Morris (1993a, b), and provided the most accurate reconstruction of *E. ludwigi* to date (Fig. 4.24). Friend (1995) agreed with previous authors that the Chinese genera *Stellostomites* and *Yunnanomedusa* were synonymous with *Eldonia* at the generic level, but believed the Chinese specimens to represent a second species, *Eldonia eumorphus*. He also firmly established the relationship between *Eldonia*, *Rotadiscus*, *Paropsonema*, *Discophyllum*, and *Velumbrella*, tentatively comparing *Eomedusa* to *Velumbrella*, and suggesting that *Paropsonema* was synonymous with *Discophyllum* at the generic level. His work, however, did not become widely known.
Chen et al. (1995) later formalised the relationship of *Stellostomites eumorphus* and *Yunnanomedusa eleganta* to *Eldonia*, synonymising these at the generic level, and assigning the Chinese specimens to *Eldonia eumorpha* (correcting the specific name for the gender of the generic name). In redescribing the specimens, they supported Dzik (1991)’s lophophorate interpretation. Dzik et al. (1997) continued to maintain this interpretation in their discussion of a second species of *Rotadiscus*, *R. guizhouensis*, which had been described by Zhao and Zhu (1994), from the early Middle Cambrian Kaili Lagerstätte in Guizhou Province, South China. Zhu et al. (2002) likewise endorsed the lophophorate interpretation. These authors restored the genus *Stellostomites* for the specimens previously assigned to *Eldonia eumorpha*, and reassigned the Kaili specimens initially described as *Rotadiscus guizhouensis* to a separate genus as *Pararotadiscus guizhouensis*. Zhu et al. (2002) also stated that further work was required to conclusively demonstrate any relationship between *Discophyllum* and the eldonides, despite being aware of Friend (1995)’s work.

Friend et al. (2002) noted both echinoderm and lophophorate interpretations in a short paper describing a single specimen of *E. ludwigi* from Siberia, but did not advocate either (these authors also considered *Eomedusa* to represent *Eldonia*). The holothurian interpretation of *Eldonia* was again dismissed by Haude (2002), in a review of holothurian origins, who stated that *Eldonia* had been misidentified.

Fryer and Stanley (2004), clearly unaware of much of the previous work on the eldonides, described a single eldonide specimen from the Silurian of England as a new species of porpitid, under the name *Pseudodiscophyllum windermerensis*. They also regarded *Paropsonema cryptophya* as a porpitid, incorrectly describing it as exhibiting concentric rings.

Van Roy (2006a) correctly demonstrated that *Pseudodiscophyllum* was clearly an eldonide, and not a porpitid. He also provided a brief redescription of Moroccan eldonide specimens described under the name *Eldonia berbera* by Alessandrello and Bracchi (2003), illuminating several significant errors in their account. He suggested that these specimens should be reassigned to *Discophyllum* (which, following Friend (1995), he correctly placed with the eldonides) as *D. berberum*. 
Caron and Jackson (2006) subsequently referred to *Eldonia* as a putative holothurian, though in a following paper, however, they related *Eldonia* only more broadly to the Echinodermata, while interpreting it as a nekto-benthic hunter-scavenger (Caron and Jackson, 2008). New material of *Eldonia* was noted to occur in the Sinsk Formation biota in Siberia by Ivantsov *et al.* (2005), and stratigraphically above the Burgess Shale in British Columbia by Johnston *et al.* (2009), both without expressing a preferred phylogenetic interpretation. Romero *et al.* (2011), in a description of Cretaceous discoidal specimens from Spain, also referred only to *Eldonia* as enigmatic.

Most recently, Caron *et al.* (2010) described a new species from the Burgess Shale, *Herpetogaster collinsi* Caron, Conway Morris, and Shu, 2010 (Fig. 6.01), which they believed to be related to the eldonides, despite having a distinctly non-discoidal pedunculate morphology and sessile habit (though significantly different in detailed morphology to the likewise pedunculate and sessile *Dinomischus*, which Dzik (1991) had linked to the eldonides). This interpretation was based partly on the presence of circumoral tentacles and a curved structure interpreted as the gut, which strongly resembles the coiled sac of Burgess Shale *Eldonia ludwigi* specimens in terms of structure and reflectivity. Caron *et al.* (2010) placed this form with the Chinese Cambrian fossil *Phlogites longus* Luo and Hu, 1999, and the eldonides (specifically mentioning *Rotadiscus*, *Pararotadiscus*, *Stellossomites*, and *Poropsonema*, but not *Discophyllum* or any other genera discussed above) in the unranked primitive deuterostome stem-group Cambroernids.

### 6.1.2 Revised classification

The higher-level taxonomy of the eldonides has also been significantly revised herein. The **Class Eldoniata** class nov. is placed within the unranked early deuterostome clade Cambroernids. Three families, all placed here in the **Order Eldonida** ord. nov., are represented within the class. All of the fossils of this order are characterised by a discoidal shape, bifurcating internal radially-arranged lobes, and a coiled structure (the coiled sac) towards the centre of the disc, suspended within a coelomic cavity. This contains the digestive tract of the animal, with
branched circumoral tentacles at the inner end of the coil interpreted as probable feeding structures. The three families are distinguished on the form and nature of their dorsal surface.

The Family Eldoniidae Walcott, 1911 is characterised by a flexible dorsal surface, simply ornamented with grooves defining bifurcated radial strips, which correspond in number to the internal lobes. The family, which is believed to be the most primitive in the Order, contains two species in a single genus: *Eldonia eumorpha* (Sun and Hou, 1987) from the early Cambrian Maotianshan Shales of the Chengjiang Lagerstätte, China, and *Eldonia ludwigi* Walcott, 1911, known from the Burgess Shale Lagerstätte of British Columbia, Canada, the Chancellor Group of British Columbia, Canada, the Spence Shale and Marjum formations of Utah, USA, and the Siligir Formation of Siberia, Russia. All known specimens of *E. ludwigi* are middle Cambrian in age. These species are distinguished on the basis of the number of radial structures and the form of the circumoral tentacles.

The Family Maoyanidiscidae fam. nov. is characterised by a sclerotised (stiffened) dorsal surface, ornamented with both concentric and radial structures. Two monospecific genera are included within the family: *Maoyanidiscus grandis* (Sun and Hou, 1987) (renamed herein due to the preoccupation of the original name *Rotadiscus*) is known from the Lower Cambrian Maotianshan Shales of the Chengjiang Lagerstätte, China, and *Pararotadiscus guizhouensis* Zhao and Zhu 1994 is known from the Middle Cambrian Kaili Formation Lagerstätte in Guizhou, China. These are distinguished on the basis of the number of radial structures, the form of the circumoral tentacles, and the degree of sclerotisation of the disc surface. Additional specimens of *Maoyanidiscus* sp. are known from the Middle Cambrian of Poland. Two additional monospecific genera are more questionably assigned to this particular family: *Velumbrella czarnockii* Stasińska 1960, from the Middle Cambrian of Poland, and *Seputus pomeroii* MacGabhann and Murray 2010 from the upper Ordovician Bardahessiagh Formation of Ireland. These are distinguished on the form of the presumed dorsal surface, the only part of these organisms preserved.

The Family Paropsonemidae fam. nov. is characterised by a flexible dorsal integument, covered in a complex ornamentation consisting of radial ridges and
perpendicular dissepiments. Three genera are known, containing a possible five species:

- *Paropsonema cryptophya* Clarke, 1900 from the Upper Devonian Grimes Formation of New York, USA,
- *Paropsonema mirabile* (Chapman 1926) from the Silurian Melbourne and Dargile formations of Victoria, Australia,
- *Praeclarus vanroii* gen. et sp. nov. from the upper Ordovician Lower Ktaoua Formation of the Tafilalt Lagerstätte in Morocco,
- *Praeclarus* sp. from the Silurian Dargile and McIvor formations of Victoria, Australia, and
- *Discophyllum peltatum* Hall, 1847 from the Ordovician Troy Frontal Zone of New York, USA, the upper Ordovician First Bani Group and Ktaoua Group of the Tafilalt Lagerstätte in Morocco, and the Silurian Bannisdale Formation of England.

These genera and species are distinguished based on the form of the dorsal ornamentation.

Other forms likely referable to the eldonides, are *Eomedusa datsenkoi* (Popov 1967) from the Cambrian of Siberia, and un-named supposed trace fossils described by Le Heron (2010) from the upper Ordovician of Algeria. A re-examination of these specimens is required to confirm or negate such a relationship. *Sinoflabrum antiquum* Zhang and Babcock, 2005, from the Cambrian of China may also be related to the eldonides, but additional material would be required before such a hypothesis could be considered.

### 6.1.3 Mode of life

The mode of life and feeding strategy of the eldonides (or members thereof) has been discussed by a number of previous authors, with interpretations ranging from benthic deposit feeders to filter feeders permanently attached to the substrate or even free-swimming predators (Chen *et al.*, 1995; Friend, 1995; Dzik *et al.*, 1997; Zhu *et
al., 2002; Fryer and Stanley, 2004). Their overall discoidal shape, reminiscent of cnidarian medusae and certain pelagic holothurians, certainly suggests a (potentially convergent) functional morphological adaptation to pelagic or nektic behaviour. Their wide palaeoenvironmental distribution would also seem to support a lifestyle that was at least in part pelagic or nektic. Eldonide specimens have been found in a wide range of environments, from deep marine shales (e.g. *Eldonia ludwigi* from the Burgess Shale, *Discophyllum peltatum* from the Ordovician of New York and the Silurian of England) to shallow marine sandstones in the vicinity of fair-weather wave base (e.g. *Discophyllum peltatum* from the Ordovician of Morocco). It is difficult to reconcile such a cosmopolitan distribution with a wholly benthic lifestyle.

A key factor in assessing the mode of life of the eldonides is the degree to which their fossil remains can be interpreted as either autochthonous or allochthonous, with the vast majority of the known eldonides specimens apparently transported prior to burial. While a substantial degree of relocation would reduce the palaeoecological significance of the observed wide environmental distribution, the degree of transport in both the Burgess Shale (Caron and Jackson, 2006) and Tafilalt (herein, p. 185) Lagerstätten appears to be limited, with both representing largely para-autochthonous biotas. However, it is difficult to reconcile a fully nektic or pelagic mode of life for the eldonides with the preservation (often in large numbers) of specimens in obrution deposits, due to the practical difficulties of entraining pelagic or nektic organisms within density (or other sediment-carrying) currents. Indeed, to have become incorporated within such flows, the organisms must have been on, or in close proximity to, the seafloor.

It is particularly difficult to reconcile a pelagic or nektic mode of life with the preservation of specimens in positive hyporelief on the soles of obrution deposits, due to the disparity in density between the (non-biomineralised) organisms themselves and such sediment-containing currents (see, for example, comments by Palmer (1996) and MacGabhann et al. (2007) on ‘*Ediacaria* booleyi’ from the Cambrian of Ireland). It may be possible that low density contour or turbidity currents could have had insufficient energy to lift such relatively large organisms completely from the seafloor as suspended load, while having enough energy to transport them as bed load. It is difficult to relate this interpretation with a purely
pelagic mode of life, and an at least partially benthic habit is thus considered more likely. Such a conclusion is strongly supported by the extremely low occurrence of fully pelagic or nektic specimens in the Burgess Shale (Caron and Jackson, 2008) and Tafilalt (personal observations) Lagerstätten.

The evidence therefore indicates that the eldonides were probably generally demersal (benthopelagic or nektobenthic). This was recognised by Caron and Jackson (2008), who classified *Eldonia* as nektobenthic.

Both the morphology and position of the interpreted feeding structures (the circumoral tentacles) and anus, with both opening on the presumed ‘ventral’ surface, has significant implications for the mode of life of the eldonides. Friend (1995) believed that *Eldonia* was a suspension feeder, based on the dendritic form of the circumoral tentacles, noting that in extant holothurians dendritic tentacles were most commonly associated with suspension feeding behaviour (e.g. Roberts and Bryce, 1982). It is plausible that this form represents a convergent functional morphological adaptation to a similar feeding strategy.

An important consideration in such an interpretation would be whether or not the circumoral tentacles permanently protrude through the ventral aperture, as an internal position may be less conducive to filter feeding (although the filter feeding apparatus in brachiopods, for example, is internal). In some specimens of *E. ludwigi*, the tentacles do appear to protrude (e.g. Figs. 4.07, 4.11), but this is quite unclear in other examples (e.g. Figs. 4.02, 4.04, 4.05). It may be the case, however, that the apparent lack of protrusion is due to the 2D compression of originally 3D organisms.

Citing the preferential preservation of *Eldonia* specimens with the presumed ventral side facing down (in both the Burgess Shale and Chengjiang), Friend (1995) further proposed that *Eldonia* was either wholly pelagic or nektonic, as a benthic ‘ventral-side-down’ life orientation would be inconsistent with a suspension feeding strategy. The validity of this interpretation is doubtful, due to the transported nature of both Burgess Shale and Chengjiang assemblages, as there is no guarantee that the life orientation and preserved orientation are identical. Moreover, although Zhu *et al.* (2002) confirmed that 95% of *E. eumorpha* specimens are preserved with the ventral
surface oriented downwards, there does not appear to be a similar consistent preservation orientation for the Burgess Shale *E. ludwigi* specimens (see p. 76).

However, from a theoretical standpoint, a purely benthic mode of life, with the interpreted ventral side permanently in contact with the seafloor, would be inconsistent with the suggestion that the dendritic structures were adapted for filter feeding. It would further be inconsistent with the implied permanent position of the anus directly beneath the body, regardless of the feeding strategy. A purely benthic mode of life with the interpreted (opposite) 'dorsal' side in contact with the substrate cannot be ruled out, but such an orientation would have left the weakest parts of the organism entirely open to predation: not, perhaps, the most viable position in an environment with anomalocarids and other plentiful predators. The morphology of *Eldonia* would seem, therefore, to be consistent with the interpreted benthopelagic or nektobenthic mode of life.

A nektobenthic lifestyle would also fit with the observed variation in the shape of the lobes of *E. ludwigi* (Fig. 4.26), which may have either hydraulically controlled the expansion and retraction of the entire disc, or simply resulted from muscular expansion and contraction. Both concepts may have provided a means of propulsion (see p. 81). In this context, it should also be noted that an alternative and highly speculative suggestion as to the function of the internal lobes was postulated by Zhu *et al.* (2002). These authors proposed that the lobes could have been filled with air, to pneumatically control the buoyancy of the organisms. This is indeed consistent with the interpretation of the lobes as hollow structures (p. 80), as well as with the evidence for the variation in the lobe morphology, and a nektobenthic lifestyle. However, the internal air pressure required to maintain the shape of such organically-constructed lobes, given the weight of the water column above, would have been enormous. Indeed, while certain cephalopods (e.g. nautiloids) do maintain air-filled chambers for exactly this purpose, they can only do so due to the presence of a mineralised exoskeleton. Such a construction has significant ecological limitations (e.g. Saunders and Wehman, 1977; Kanie *et al.*, 1980). Moreover, in the absence of biomineralisation, the density differential between air and seawater at such depths, rather than controlling buoyancy, would likely have been sufficient to induce significant acceleration with a negative depth vector.
Eldonia is thus interpreted as a nektobenthic filter feeder.

This interpretation may not necessarily apply to all members of the eldoniidae. For example, Dzik et al. (1997) proposed that Pararotadiscus guizhouensis was fully benthic, on the basis of the presence of attached bivalved epibionts of uncertain affinities (thought likely to have been inarticulate brachiopods), which were believed to have adhered to the sclerotised dorsal surface in life. These were primarily located towards the edge of the disc, and Dzik et al. (1997) therefore suggested that Pararotadiscus guizhouensis lived partially within the upper layer of the substrate, with the ‘dorsal’ surface (as termed herein) oriented facing downwards.

However, Zhu et al. (2002) disagreed with Dzik et al. (1997)’s interpretation of the epibionts, noting:

- That these inarticulate brachiopods were the only epibionts observed on specimens of Pararotadiscus guizhouensis,
- That they did not occur as epibionts elsewhere in the Kaili Lagerstätte, and
- That hard skeletons of a variety of other organisms were commonly used as attachment sites by other forms of epibionts at Kaili.

They also observed that if Dzik et al. (1997)’s interpretation is correct, the epibionts should be preferentially oriented with the oral end towards the outer edge of the disc, as the brachiopods are observed only on the ‘dorsal’ side, which Dzik et al. (1997) had postulated to have been oriented downwards and partially buried within the uppermost layers of the substrate. In this scenario, the outer margin of the disc would be the only area where epibionts on the ‘dorsal’ surface could have access to the seawater for the purposes of feeding, and such epibionts should thus be preferentially oriented with the anterior (commissural) end facing outwards. However, Zhu et al. (2002) noted that no such preferred orientation is evident. On this basis, they interpreted that Pararotadiscus guizhouensis (with associated epibionts) must have been pelagic.
The logic of this assertion is questionable. For example, the uniqueness of the epibionts does not necessarily indicate that *P. guizhouensis* must have been pelagic, but instead could merely be a function of the allochthonous nature of the *Pararotadiscus guizhouensis* specimens, or may indicate a unique commensal or symbiotic relationship. Likewise, the lack of a preferred orientation amongst the epibionts does not require that *P. guizhouensis* was pelagic, but may simply indicate an orientation with the dorsal surface upwards. Indeed, Zhu *et al.* (2002) noted that the specimens with epibionts were universally preserved on bedding surfaces oriented with the dorsal surface upwards.

A key factor in Dzik *et al.* (1997)'s interpretation was the preferred position of the epibionts near the margin of the disc, with only small shells noted towards the centre of the specimens. These authors believed this distribution to indicate that the central area of the disc was in some way generally unavailable for epibiontic encrustation, and proposed a benthic lifestyle with the ‘dorsal’ surface oriented downwards to explain this observation. However, there are two problems with this interpretation, which is based on the assumption that the disc of *P. guizhouensis* grew by marginal accretion:

- epibionts on an organism growing in this style should show a preferential distribution with smaller specimens closer to the outer margin of the disc.

- Evidence from the paropsonemids indicates that the eldonides grew by inflation, rather than margin accretion (see pp. 103, 116, 141, 148). If this is the case, then the distribution may simply reflect encrustation early in life, with the smaller number of epibionts towards the centre of the disc due to a lack of new epibionts during the later years of growth. Such an interpretation does not necessarily require any particular lifestyle.

Although the arguments of Zhu *et al.* (2002) in favour of a pelagic lifestyle are by themselves unconvincing, such an interpretation is likely to be correct. As discussed for *Eldonia*, the similar dendritic form of the circumoral tentacles in *P. guizhouensis* likely indicates a filter-feeding mode of life. A purely benthic position
with the ventral side down would not be consistent with such a feeding strategy, while a benthic position with the dorsal side facing downwards would leave the soft parts permanently open to predation. This suggests that *Pararotadiscus guizhouensis* was at least in part pelagic. The occurrence of mineralised epibionts does not rule out this more mobile interpretation: indeed, mineralised epibionts are common on certain pelagic cephalopods (e.g. Seilacher, 1960; Rakús and Zitt, 1993; Rakociński, 2011).

Similarly to *Eldonia*, therefore, *Pararotadiscus guizhouensis* was likely nektobenthic.

The presumed dorsal surface of *Maoyanidiscus grandis* was apparently fully stiffened, and perhaps sclerotised, which may indicate slightly different lifestyle requirements than that of other eldonides. Previous authors have noted the possibility that a sclerotised disc may have reduced the buoyancy of *Maoyanidiscus* or *Pararotadiscus* (e.g. Dzik *et al.*, 1997; Zhu *et al.*, 2002; Van Roy, 2006a). However, given the small density differential between sclerotised and non-sclerotised unmineralised tissues, there is no particular reason why any form of non-mineralised surface should have precluded such a pelagic lifestyle, a point which was also supported by Zhu *et al.* (2002).

Friend (1995) noted that the digitate circumoral tentacles of *Maoyanidiscus grandis* may indicate a deposit-feeding lifestyle. This was based on a functional morphological comparison to holothurian circumoral tentacles, and is certainly plausible.

Specimens of *M. grandis* are almost universally found with the dorsal surface oriented upwards (Friend, 1995). Unlike *Pararotadiscus* and *Eldonia*, a benthic position with the ventral surface oriented downwards might make sense in view of the interpretation of *M. grandis* as a possible deposit feeder. However, such an orientation would still leave the anal opening underneath the body, in close proximity to the mouth. It is thus thought more likely that *M. grandis* was also nektobenthic.
Friend (1995) suggested that the paropsonemids, likewise, may have been deposit feeders. There is no evidence to support this hypothesis, with only one Tafilalt specimen containing sediment within the coiled sac, and no evidence for the original form of the circumoral tentacles in any paropsonemid specimen. Indeed, thin sections through Tafilalt paropsonemid specimens examined by either petrological microscope or SEM EDS elemental mapping show no difference in sediment composition or chemistry in the region of the coiled sac, as compared to the remainder of the specimen or host sediment, save for surficial coatings of eodiagenic origin (see sections 5.2.2.1, p. 173, and 5.2.2.4, p. 177). A deposit-feeding strategy may thus be unlikely.

Unlike Eldonia, Pararotadiscus, and Maoyanidiscus, paropsonemid specimens (from Tafilalt and elsewhere) for which the orientation is known are almost universally preserved with the dorsal surface oriented downwards. This is likely an artefact of transport rather than due to the actual original life orientation, as all of these specimens appear to have been relocated to at least some degree. This interpretation is supported by the observation that there is no difference in orientation between specimens preserved on bedding plane surfaces, and those preserved in endorelief, at any locality. As such, the life orientation of the paropsonemids is not clearly indicated by any of the presently available evidence.

This preferred orientation may reflect a greater density of the dorsal surface of the animal, given the presence of a complex ornamentation interpreted as consisting of a relatively tougher material, and the location of the coiled sac (containing the alimentary canal) just beneath this surface. However, such an interpretation is not without problems. The density differential between various kinds of non-mineralised tissues is almost invariably diminutive, and would have been eclipsed by the overall difference in density between the organisms and the transporting (sediment-carrying) current. It may thus be difficult to envisage quite how the minor density differential between the dorsal and ventral sides was able to invert the orientation of the organism within such transporting currents. It may, alternatively, be possible that additional hydrodynamic factors influenced this preferred orientation, but this suggestion is merely speculative.
Due again to the opening of both the feeding structures and the anus on the ventral surface, and the overall discoidal morphology, the paropsonemids are also interpreted to have been nektobenthic. Their feeding strategy remains unclear, but the evidence does suggest that they may not have been deposit feeders.

In summary, therefore, all of the eldonides for which sufficient evidence is available appear to have been nektobenthic. Eldonia ludwigi, Eldonia eumorpha, and Pararotadiscus guizhouensis are interpreted as filter feeders based on the morphology of the circumoral tentacles, while Maoyanidiscus grandis is interpreted as a possible deposit feeder, for the same reasons. The feeding mode of the paropsonemids, and other eldonide species, remains a mystery.

### 6.1.4 Phylogenetic affinities

The eldonides, or various members thereof, have (as discussed in section 6.1.1, p. 211 above) been interpreted as cnidarian medusae, porpitid hydrozoans (“chondrophorines”), siphonophores, holothurians, lophophorates, stem-group echinoderms, and Cambroernids (basal deuterostomes). There is, as yet, no agreement on their precise phylogenetic placement, and their affinities remain controversial. This is compounded by the lack of popular knowledge of the group, and the lack of realisation that the paropsonemids are eldonides, as evidenced by the recent description of a specimen of Discophyllum peltatum as a porpitid hydrozoan under the name Pseudodiscophyllum windemerensis (Fryer and Stanley, 2004), without any mention of Eldonia or the eldonide group.

In fact, not only this particular specimen, but all four previously described species assigned herein to the Family Paropsonemidae have previously been regarded as porpitid hydrozoans (Fuchs, 1905; Ruedemann, 1916, 1933b; Harrington and Moore, 1956b; Scrutton, 1979; Stanley, 1986; Fryer and Stanley, 2004), often referred to in the palaeontological literature as “chondrophorines”. Originally regarded as colonial siphonophores (Harrington and Moore, 1956b), and often still mistakenly cited as colonial organisms in the Suborder Chondrophorina (e.g. Stanley and Kanie, 1985; Stanley, 1986; Stanley and Yancey, 1986; Bogler and Hanger, 1989; Bell et al., 2001), the porpitids are now classified in the athecate hydrozoan
Order Capitata, and are known to be solitary individuals (e.g. Garstang, 1946; Mackie, 1959; Fields and Mackie, 1971; Fryer and Stanley, 2004), as originally recognized by Haeckel (1869). An air-filled concentrically-chambered chitinous float, with chambers connected to each other and to the exterior by means of small pores, allows the organisms to vary their buoyancy and thereby to float or submerge as necessary; new chambers are added to this float at the periphery as the organism grows. Tentacles, blastostyles, and a tube ending in the mouth hang downwards below the disc.

It is abundantly clear that no specimens in any of the species described herein display any of these features. While tentacles and blastostyles would be difficult to preserve faithfully, there is in particular no evidence of an internal concentrically-chambered chitinous structure, even where internal structures are preserved. The mode of life of the porpitids, floating at or near the marine surface, is also inconsistent with the postulated mode of life of the paropsonemids and their preservation in large numbers in what are essentially obrution deposits, as discussed in the preceding section. Moreover, the complex surface ornamentation, the coiled sac, and especially the bifurcating internal lobes of the paropsonemids have no analogue in porpitid biology. Instead, the presence of a coiled sac and bifurcating internal lobes undoubtedly confirms that the affinities of the paropsonemids lie with the eldonides.

Indeed, the presence of a coiled sac, suspended by mesenterial elements within an internal cavity, demonstrates beyond all doubt that the eldonide group as a whole comprises unequivocally triploblastic organisms. Therefore any potential affinity of the eldonides with any part of the Cnidaria can be firmly discounted.

As noted above, Dzik (1991) proposed that the eldonides were lophophorates, a view which has gained a certain level of credence (e.g. Chen et al., 1995; Dzik et al., 1997; Zhu et al., 2002). This interpretation was based on several factors:

1. The description of the coiled sac as U-shaped, and proposed homology of this structure with the U-shaped intestine of *Dinomischus*;
2. The presence of ‘two tentacles’ at the mouth of the U-shaped intestine, as observed in *Eldonia ludwigi*, interpreted as a lophophore;

3. The proposed homology of the eldonide disc, which Dzik (1991) described as sclerotised, with the mantle of brachiopods and bryozoaos.

This comparison is fundamentally flawed.

1. The coiled sac is not U-shaped, but an open spiral (although this may admittedly be an artefact of the 2D preservation of a 3D structure, and is unlikely to be a significant issue).

2. The tentacles appear to be four in number, rather than two, and are distinctly different in morphology from all previously described lophophores. It should also be noted that even if the eldonide circumoral tentacles were considered similar to lophophores, such similarity would not necessarily imply homology. Indeed, the tentacles of the Pterobranchia were previously thought to be homologous to the lophophores of brachiopods, bryozoaos, and phoronids due to their extremely similar morphology and function (e.g. Halanych, 1993), but are now known to be an unequivocal example of convergence (e.g. Halanych, 1996).

3. The mantle in brachiopods grows by marginal accretion. The eldonides are demonstrated herein (see pp. 103, 116, 141, 148) to grow by inflation, a fundamentally different mode of growth, implying a distinct phylogenetic separation.

Friend (1995) additionally noted that a deposit-feeding strategy was inconsistent with a lophophorate interpretation, while Caron *et al.* (2010) highlighted molecular phylogenetic evidence indicating the polyphyletic nature of the “Lophophorata”, rendering such comparisons largely redundant. There is thus no firm basis for proposing an affinity between the eldonides and any form of lophotrochozoans, and a lophophorate interpretation for the eldonides can be discounted.
The demonstration that the eldonides cannot be readily placed within the Lophotrochozoa removes any possibility of a placement within the Protostomia. Due to their unequivocally triploblastic nature, this implies a position within, or related to, the Deuterostomia.

Such an interpretation was amongst the first considered for the eldonides, with Clarke (1900) interpreting *Paropsonema cryophya* as a peculiar echinoderm (comparing the radial structures to echinoid ambulacra), and with Walcott (1911) originally interpreting *Eldonia ludwigi* as a holothurian. While the interpretation of *Paropsonema* as an echinoderm was (perhaps unfortunately) rapidly dismissed (Fuchs, 1905; Ruedemann, 1916), and in more recent times has even been mocked (Fryer and Stanley, 2004), the interpretation of *Eldonia ludwigi* as a holothurian echinoderm has been controversial, and has been discussed repeatedly (e.g. A.H. Clark, 1912; H.L. Clark, 1912; Clark, 1913; Madsen, 1957; Caron et al., 2010).

Two factors in particular would seem to favour a holothurian affinity:

1. The shape of the coiled sac, and its striking comparison to the spiral gut of certain holothurians (Fig. 6.02), and

2. The presence of circumoral tentacles.

Some of the morphological similarities are quite striking. The variation in form of the circumoral tentacles in particular – including both digitate and dendritic morphologies – is completely consistent with that seen in holothurians.

However, in detail, the morphology of the holothurians differs quite considerably from that of the eldonides. Taken individually, some of the major differences may not necessarily be conclusive, for example:

1. Friend (1995) cited the absence in the eldonides of a calcareous ring surrounding the oesophagus, a defining feature of the Holothuroidea (e.g. Kerr and Kim, 2001), as a key distinction. However, this ring is often indistinct or absent in elasipod holothurians (Kerr and Kim, 2001), including all known pelagic forms.
2. Friend (1995) also noted the absence of a ring canal surrounding the mouth, another universal feature of holothurian biology. As discussed above, however, all eldonide specimens have suffered at least some degree of decay, and it is quite possible that such a feature may simply not have been preserved. Moreover, if the internal lobes were fluid filled, as suggested by Friend (1995) and herein, these may also have formed part of the internal water vascular system, with the central ring (where the lobes meet: see e.g. Fig. 4.19) perhaps representing the ring canal or even the madreporite (although an external connection to seawater through this feature is not required – the water vascular system of holothurians is closed and filled with coelomic fluid). Indeed, the internal lobes of the eldonides are comparable in size to holothurian papillae, which form part of their water vascular system (e.g. Kerr and Kim, 2001; see also description of *Enypniastes globosa*, which has 12 large papillae up to 7cm in length, in Hansen and Madsen, 1956), and in some species assist in locomotion. While this interpretation would fit with respiratory and/or locomotory functions proposed for the lobes, one potential problem would be the apparent lack of a connection between the internal lobes and the circumoral tentacles, which appear to have been hollow and must have formed part of a water vascular system if this was present. It is possible, however, that such a connection existed, and is simply not clear in the preserved fossil specimens.

3. The complex dorsal ornamentation of the paropsonemids, and the stiffened dorsal surface of the maoyanidiscids, have no analogue in holothurian biology. However, if the eldonides were holothurians, this could merely be a synapomorphic trait of the Eldonida within the Holothuroidea.

Taken together, however, the anatomical differences make clear the problems with proposing a holothurian interpretation for the eldonides. This was expressed by Walcott (1911) in his original description of *Eldonia ludwigi*, who stated:
“To the zoologist acquainted with the Holothuroidea more questions will be raised by
this remarkable fossil than I have answered in text or illustration…Dr. Austin H.
Clark suggested that as the spiral alimentary canal was characteristic of the
Echinodermata, it might be that this form was allied to the free swimming
Pelagothuria. This led to a comparison with Pelagothuria natatrix Ludwig. I finally
concluded that our new form was related to the holothurians, but that it was quite
unlike Pelagothuria, the only described free swimming holothurian, and far more
unlike the typical forms of the class. Except for the presence of the large spiral
alimentary canal I should have returned to the medusa view at this point. There was
no a priori reason why a holothurian should not have a medusa-like form, as noted by
Dr. A. G. Mayer, but I found that the body of Pelagothuria was cylindrical; the disk
an enlargement of the body at the base of the tentacles; and that the mouth opened at
the dorsal surface, and the anus at the end of the proboscis-like lower portion of the
body. In contrast the Middle Cambrian type had a true medusa-like umbrella;
concentric subumbrella muscle band; spiral subhorizontal alimentary canal, with
mouth and anus off to one side of the center; and, judging from what is known of the
umbrella-like body, opening at the ventral surface.” (pp. 50-51; emphasis mine)

This was put into even more stark contrast by H. L. Clark (1912), who, in his
rebuttal of Walcott’s interpretation, stated:

“Eldonia shows absolutely no trace of pentamerous symmetry, no trace of calcareous
structure, no longitudinal muscles and no podia. The radial canal system is utterly
unlike the water-vascular system of any known Echinoderm and it is perfectly
inconceivable how the fundamental, circumoral ring of a holothurian could disengage
itself from the esophagus and migrate to the opposite end of the body.

If Eldonia is a holothurian, it becomes virtually impossible to define the class,
except in terms of the alimentary canal. Indeed if Eldonia is a holothurian, the
Echinoderms themselves can be defined in no other terms, for Eldonia lacks every
single character which justifies the customary view that holothurians are
echinoderms” (p. 277; emphasis mine).

These gross differences leave significant problems with any interpretation of the
eldonides as related to the holothurians. These problems are compounded by more
recent molecular and morphological phylogenies for the Holothuroidea and
Echinodermata. The holothurians are now considered to be amongst the most
derived echinoderms, placed as a sister group to the Echinoidea (Fig. 6.03), based on
both morphological and molecular data (Smith, 1988; Kerr and Kim, 2001; X. Shen et al., 2009; Caron et al., 2010; Reich, 2010; Janies et al., 2011; Pisani et al., 2012; Janies, 2001). If the eldonides are to be considered as crown-group holothurians, they must have been a derived sister clade of the elasipod holothurians (which includes all known pelagic forms, and is itself a derived sister group of the Apodida), having secondarily lost almost all characteristic features of not only the holothurians, but also of the echinoderms in general (any alternative hypothesis placing the eldonides as primitive crown-group holothurians would be untenable, as it would require that those typical echinoderm characters present in extant holothurians but absent in the eldonides were lost and then subsequently regained in other groups). However, while the fossil record of the holothurians is admittedly poor, the oldest known holothurian remains are of Middle Ordovician (Darwillian) age (Reich, 2010), with the elasipod holothurians in particular estimated (based on a morphologically-generated fossil-calibrated tree) to have first appeared during the Devonian (Kerr and Kim, 2001), in agreement with their fossil record (Reich, 2010). Moreover, it should be noted that this estimate is at the taxonomic level of order, with particular pelagic forms within this order perhaps not appearing until much later. This is in stark contrast to the fossil record of the eldonides, which first appear in the Early Cambrian, and disappear in the Devonian. Accepting the eldonides as crown-group holothurians requires that not only the apodid and elasipodid holothurians, but also the crinoids, asteroids, echinoids, and ophiuroids were all present in the early Cambrian without leaving any fossil record, and in direct contradiction of all available molecular clock estimates. Even accounting for fossilisation potential, and the paucity of the holothurian fossil record in particular, such a conclusion would be nothing short of astonishing.

Interpretation of the eldonides as holothurians is thus completely inconsistent with all available molecular palaeontological data and also the entire fossil record of the Echinodermata (Fig. 6.03). The eldonides thus cannot represent ‘true’ holothurians. The similarities between eldonide and holothurian morphology must instead represent convergent homoplasic adaptation to a similar mode of life. However, this, in fact, reinforces the functional morphological comparison of the various components of eldonide morphology to those of the holothurians, and
supports the interpretation of the eldonides as nektobenthic filter and deposit feeders.

The dismissal of a close phylogenetic relationship between the eldonides and holothurians does not rule out interpretation of the eldonides as stem-group echinoderms, as suggested by Conway Morris (1993a, b) and Friend (1995), or as early deuterostomes. Indeed, the homoplasic resemblance of the eldonides to the holothurians may support a position close to the echinoderms, with multiple similar cases of convergent resemblance occurring within the broad Echinodermata (Fig. 6.04). Such an interpretation was recently advocated by Caron et al. (2010), who placed the eldonides, together with Herpogaster collinsi Caron et al. 2010 from the Burgess Shale (Fig. 6.01), and Phlogites longus Luo and Hu, 1999, and Conicula striata Luo and Hu, 1999, from Chengjiang, in the unranked clade Cambroernids. Although none of these additional forms are discoidal in overall morphology, the similarities are striking, with H. collinsi in particular possessing circumoral tentacles and an alimentary canal suspended within a coelomic cavity which is extremely similar in terms of morphology and preservation to the coiled sac of Eldonia ludwigi. The redescriptions herein of the eldonides are consistent with a relationship between the eldonides and Herpogaster (and related taxa), and thus the placement of the eldonides in the Cambroernids. Caron et al. (2010) placed the Cambroernids as early deuterostomes, suggesting that they could represent amongst the earliest ambulacrarians, but were unable to confirm a precise phylogenetic placement.

As noted by Caron et al. (2010), discussion of such a placement is highly problematic. H. L. Clark (1912) (quoted above) observed the eldonides lack virtually every characteristic feature of echinoderms, save perhaps for the alimentary canal. Any discussion of the placement of the eldonides in any particular crown-group clade would thus necessarily involve suggesting the apomorphic loss of certain characters, with the obvious problem that it is impossible to know precisely which characters have been lost. Moreover, it is also difficult to ascertain which of any potential shared characters may be plesiomorphic, and which may instead be homoplasic. A stem-group placement would similarly lead to a discussion of which characters were secondarily absent, and which occurred only in clades closer to the
crown group. A similar set of problems likewise exists for any possible placement within the broader deuterostomes.

Given this debate, it is possible to consider placement in any number of positions. For example, if the internal lobes and/or circumoral tentacles form part of a water vascular system, this implies a position only within the stem- or crown-group Ambulacraria (Echinodermata + Hemichordata). The coiled digestive tract is similar to that seen in certain echinoderms, but also broadly resembles the U-shaped gut of the hemichordate pterobranchs. Circumoral tentacles are also present in the pterobranchs as well as echinoderms. The lack of any elements of the morphology showing radial symmetry (even holothurians exhibit pentaradial symmetry, in the form of the skeletal plates forming the circumoral ring) may indicate a position stemwards of the crown Echinodermata, prior to the development of defined radial symmetry. Likewise, the absence of a calcitic stereom, or any calcitic elements, similarly indicates a basal position within the Ambulacraria. However, while the absence of both symmetry and mineralisation in Herpetogaster as well as the Eldoniata may suggest that these features are plesiomorphic to the entire Cambroernid clade, it may be equally possible that these were apomorphic to the Cambroernids within the broader Deuterostomia, or Echinodermata, or Hemichordata.

One factor which may be particularly interesting in determining the affinity of the eldonides (and broader Cambroernids) is the potential presence of chitin. As discussed in section 5.1.2, Petrovich (2001, p. 689) proposed that the coiled sac of Eldonia ludwigi was composed of an inner chitinous layer (the coiled sac sensu stricto) and an outer collagenous layer. This was based on the high tendency for adsorption of Fe²⁺ ions by chitin (see p. 162-163), and which appears to be indirectly supported by decay experiments (Allison, 1988a) on arthropods (see p. 194). However, the ability to synthesize chitin is rare in deuterostomes, and appears to have been lost at or near the base of the deuterostome lineage (e.g. Merzendorfer, 2009). It is possible that the components here discussed as potentially chitinous may have been composed of an alternative glycopolymeric chitin-like material, or perhaps a different form of protein-based collagenous biopolymer. If chitinous, this would likely place the Cambroernids either at the very base of the deuterostomes, or even
outside the crown-group deuterostomes entirely, while a collagenous composition without any chitin present would support a deuterostome position. It is possible that laboratory experiments on the fossilisation potential of various biopolymers in this style could clarify this issue. However, at present, the available information merely suggests that two different compositions are represented.

Caron et al. (2010) are thus likely correct in advocating a basal ambulacrarian position as the most likely phylogenetic placement of the Cambroernids on the basis of the presently available evidence. However, the evidence is insufficient to either confidently support such a position, or to equally refute a position elsewhere within the Deuterostomia. At present, therefore, the Cambroernids, including the eldonides, are best regarded broadly as incertae sedis early deuterostomes.

6.2 Comparative taphonomy

Due to their morphologically conservative nature and cosmopolitan environmental distribution, the eldonides have little value as either palaeoecological or biostratigraphic indicators (Fig. 4.113). Their greatest significance lies instead in the fact that they are entirely non-mineralised organisms, known in two apparently very different modes of preservation: as organic compressions in shales within the Burgess Shale and Chengjiang Lagerstätten, and as moulds and casts in sandstones in the case of the paropsonemids.

6.2.1 Burgess Shale-type preservation of the eldonides (recap summary)

The Burgess Shale specimens were preserved by replication in clay minerals, and the inhibition of decay. Rapidly buried in fine-grained sediments, the pore-water oxygen supply was quickly exhausted, and decay proceeded anaerobically by the reduction of reactive iron (III) and sulphate. Iron (III) reduction released Fe\(^{2+}\) ions to the pore waters; these adsorbed onto the complex organic biopolymers comprising the integument and digestive tract, preventing the enzymatic degradation required for their anaerobic decay. Decay was also likely inhibited by the surficial adsorption of
detrital clay minerals onto free extracellular exoenzymes, and the organic matter of the fossils. Authigenic clay minerals nucleated around the adsorbed Fe\(^{2+}\) ions, replicating the tissues in aluminosilicates. Once the supply of reactive iron (III) had been exhausted, decay proceeded by sulphate reduction. Hydrogen sulphide produced by this process reacted with less reactive sedimentary iron (III) oxides, and the Fe\(^{2+}\) ions adsorbed to the fossil surfaces, producing iron monosulphides (which subsequently transform to pyrite). Where it occurred, this reaction removed the decay protection. However, the curtailment of the sulphate supply prior to the complete decay of the organisms led to the cessation of sulphate reduction, leaving the protection in place, and preserving the organic carbon, which was later kerogenised by diagenic and metamorphic processes.

### 6.2.2 Tafilalt-type preservation of the eldonides (recap summary)

In the case of the paropsonemids, the most useful data comes from the Tafilalt Lagerstätte in the upper Ordovician of Morocco. This is one of the most widespread Lagerstätte known of any age, comprising thousands of specimens in several different species occurring over a lateral extent of at least 200km. The majority of the Tafilalt fossils are eldonides, represented by the two paropsonemid species *Discophyllum peltatum* and *Praeclarus vanroii*. These are preserved as moulds and casts in shallow marine shelf sandstones, both on bedding plane surfaces (as either negative epirelief moulds and positive hyporelief counterpart casts or negative hyporelief moulds and positive hyporelief counterpart casts), and within sandstone beds in endorelief. The large number of available specimens permitted destructive analyses, in the form of ICP-MS (section 5.2.2.5, p. 183) and XRD (section 5.2.2.2, p. 176) whole rock analysis, SEM EDS elemental mapping (section 5.2.2.4, p. 177), and laser Raman microscopy (section 5.2.2.3, p. 176), as well as thin section petrography (section 5.2.2.1, p. 173). This allowed the establishment of a complete diagenic history of the fossiliferous strata (Fig. 5.66).

The paropsonemids were preserved by a taphonomic process similar to that of the Burgess Shale fossils, differing mainly in the larger grain size of the enclosing sediment, and a greater supply of sulphate. Anaerobic decay by iron (III) reduction
released Fe\(^{2+}\) ions into the pore waters; these adsorbed to the surfaces of the organisms. Subsequent sulphate reduction produced hydrogen sulphide, which reacted with these ions, forming iron sulphides (which later transformed to pyrite) \textit{in situ} on the surfaces of the organisms, removing the decay protection. Clay minerals also nucleated around the adsorbed ions. These clay minerals and iron sulphides formed a cemented mould (or death mask) over the surface of the organism, which was later cast by adjacent sediment once decay was complete.

6.2.3 \textit{Comparative taphonomy of the eldonides}

Over the past three decades, comparative taphonomy – the comparison of sites preserving fossils in contrasting taphonomic modes – has been recognised as a useful technique, both for palaeoecological analysis (e.g. Brett and Baird, 1986; Speyer, 1987; Behrensmeyer \textit{et al}., 2000), and as a tool to elicit a greater understanding of certain organisms or types of organism (e.g. Greenstein and Moffat, 1996; Zhu \textit{et al}., 2008). This is particularly useful in the case of extinct non-mineralised creatures with no obvious extant analogues (Zhu \textit{et al}., 2008), and may allow a greater understanding of what parts of the organism are preserved in the fossil record, and, more importantly, what parts are not.

The taphonomic processes involved in the preservation of the eldonides from the Burgess Shale and Tafilalt is compared in Table 6.01. The key differences between the two sites are:

1. The considerably lower detrital clay content at Tafilalt, leading to lower predicted adsorption of detrital clay minerals onto exoenzymes and organic tissue (indeed, no evidence exists to indicate this was a factor in the preservation of the Tafilalt fossils);

2. The rapid curtailment of sulphate reduction in the Burgess Shale. Continued sulphate reduction in the Tafilalt sediments (as evidenced by the iron oxide and oxyhydroxide fossil surface veneer, including haematite and goethite pseudomorphs after
Differential taphonomy of Palaeozoic and Ediacaran non-mineralised fossils

pyrite; see p. 191 and Fig. 5.22) caused the reaction of hydrogen sulphide with the adsorbed reduced iron on organic surfaces; this removed the decay protection from these tissues, and moulded them in iron sulphides.

These key differences in the taphonomic processes caused significant variation in what is preserved in the fossils – both in terms of organic content and 3D form, and more importantly, in terms of which anatomical features are, and are not, evident (Table 6.02). It is abundantly clear that the preservation as moulds and casts at Tafilalt is incapable of preserving most of the eldonide anatomy: all that is unequivocally preserved in the Tafilalt specimens, effectively, is:

1. the dorsal surface,
2. the coiled sac (where it is preserved by aluminosilicification), and
3. internal structures which were inflated in life and either became filled with sediment prior to burial (e.g. the internal lobes) or collapsed subsequent to burial (e.g. the coiled sac, where it is preserved with relief), modifying the shape of the surface.

More labile parts of the anatomy, including the radial strands and fibres, the central ring, the oval sacs, the circumoral tentacles, and even the bifurcating lobes, where they are not filled with sediment, are not preserved.

Importantly, the preservation of the coiled sac by aluminosilicification in several Tafilalt specimens (Fig. 5.04; see also p. 190) confirms that internal structures can be preserved in this style. The lack of preservation of the other internal structures cannot, therefore, simply be due to the fact that they were internal, but must reflect their lack of preservation potential in this particular taphonomic mode.

As is shown by the Burgess Shale Eldonia, the coiled sac is the most resistant anatomical feature, even more so than the dorsal integument. Petrovich (2001) suggested that the two layers of the coiled sac identified by Butterfield (1996) (p. 162; see also Figs. 4.09a, 4.10, 4.27) could represent an outer collagenous layer (the outer coiled membrane) and an inner chitinous layer (the inner coiled sac). Based on
the high potential of chitin and slightly lesser potential of collagen for the adsorption of Fe$^{2+}$ ions, as discussed above (p. 163), this interpretation is plausible. The outer integument may similarly have been chitinous or collagenous. But regardless of the precise nature of the composition, it is clear that these tissues must have been complex biopolymers, with a strong potential for the adsorption of Fe$^{2+}$ ions, and that tissues without this potential could not be preserved in the taphonomic mode responsible for the preservation of the non-mineralised fossils at Tafilalt.

Perhaps most importantly, taphonomic models for both Tafilalt and the Burgess Shale require that decay was substantially in progress when these tissues were preserved (and more so in the case of the Tafilalt fossils). The most labile tissues (including musculature, cellular structures etc.; see p. 169) thus cannot be preserved in either taphonomic mode; not simply because their composition does not favour preservation, but rather their decay by iron and/or sulphate reduction is required to facilitate the preservation of the more recalcitrant tissues. Therefore, only organisms with recalcitrant tissues composed of organic biopolymers with a tendency to adsorb Fe$^{2+}$ ions can be preserved in either style, with a higher tendency for adsorption required in Tafilalt-type preservation, as compared to Burgess Shale-type preservation.

6.3 Differential taphonomy

Unfortunately, most problematic non-mineralised fossils are known in only one taphonomic mode, leaving this potentially useful comparative source of information out of reach. An extension of comparative taphonomy to differential taphonomy, however, may circumvent this problem. Differential taphonomy (defined here), involves applying the results of a comparative taphonomic analysis of one type of fossil preserved in two different taphonomic modes, to the taphonomy of a second type of fossil, preserved in only one of those two taphonomic modes (Fig. 6.05).

Such a differential taphonomic analysis could be particularly useful in the case of certain fossils of Ediacaran age. As noted in Chapter One (see p. 6), the
interpretation of these has proved difficult and has often been controversial. This is due both to the occurrence of many forms which do not appear to resemble Phanerozoic fossils, and also to the preservation of many non-mineralised specimens as moulds and casts, principally in siliciclastic sediments, a mode of preservation which has repeatedly been cited as unique to the Ediacaran (e.g. Wade, 1968; Gehling et al., 1998; Jensen et al., 1998; Gehling, 1999; Dzik, 2001; Gehling et al., 2005; Narbonne, 2005). The preservation of the eldonides, however, as moulds and casts in Palaeozoic shallow marine sandstones, appears to be strikingly similar to that of certain Ediacaran-aged fossils, and thus may allow a differential taphonomic analysis of these forms (Fig. 6.06).

The key question lies in the similarity of the modes of preservation exhibited in both the Ordovician (Tafilalt) and Ediacaran-aged specimens. The first part of the null hypothesis of this thesis is:

1. That the processes involved in the preservation of the non-mineralised fossils at Tafilalt are effectively identical to those involved in the preservation of many fossils of Ediacaran age.

If this null hypothesis cannot be falsified, then such a differential taphonomic analysis would therefore be plausible.

6.3.1 The taphonomy of Ediacaran-aged fossils

The preservation of non-mineralised fossils in the Ediacaran varies considerably, and cannot be universally ascribed to one single taphonomic model. However, some generalisations are possible. Four considerably different modes of preservation have been identified in the literature:

1. Preservation in shales, for example the Miaohe Biota (e.g. Xiao et al., 2002; Zhu et al., 2008) and Lantian Biota (e.g. Yuan et al., 2011) of South China (Fig. 6.07);
2. Preservation in **carbonates**, such as in the Khatyspyt Formation in Siberia and Dengying Formation of South China (e.g. Grazhdankin et al., 2008; B. Shen et al., 2009) (Fig. 6.08);

3. Preservation **under volcanic ash** deposits, as in the Ediacaran of the Avalon Zone of Newfoundland and England (e.g. Ford, 1958; Misra, 1969; Ford, 1999; Narbonne and Gehling, 2003; Narbonne, 2005; Hofmann et al., 2008) (Fig. 6.09);

4. Preservation in **siliciclastic sediments**. This is the most common mode of preservation, as seen in the “type” locality in South Australia (Figs. 6.06c, 6.10), and many other localities (e.g. Sprigg, 1947, 1948; Sprigg, 1949; Glaessner and Dailly, 1959; Fedonkin, 1978; Glaessner, 1984; Fedonkin, 1990; Gehling, 1991; Narbonne et al., 1997; Dzik, 1999, 2003; Gehling et al., 2005).

Within these broad taphonomic modes, fossils are generally preserved as carbonaceous compressions, or as moulds and casts, either on bed surfaces in positive hyporelief and/or negative epirelief (termed ‘gravity casts’ by MacGabhann, 2007a), on bed surfaces in negative hyporelief and/or positive epirelief (termed ‘death masks’ by Gehling, 1999), or within beds in endorelief.

For fossils preserved as moulds and casts in siliciclastic sediments, Narbonne (2005) identified four particular Ediacaran taphonomic assemblages, namely:

A. **Conception-style**: preservation of fossils in positive epirelief beneath ash beds (Mode 2 overleaf);

B. **Flinders-style**: preservation of fossils as both gravity casts and death masks on the soles and tops of siliciclastic beds (Mode 4);

C. **Fermeuse-style**: preservation of discoidal fossils as gravity casts only (Mode 4);

D. **Nama-style**: preservation of fossils in endorelief, within siliciclastic beds (Mode 4).
To this list must be added the carbonate-hosted preservation (Mode 2) exhibited in the Khatyspyt and Dengying formations (Fig. 6.08), and the Burgess Shale-type assemblages (Mode 1) of carbonaceous compression fossils (Fig. 6.07), which were omitted from Narbonne (2005)'s analysis (due in part to the tendency to consider those fossil preserved as moulds and casts as a group, excluding those preserved as compressions in shales; and in part to the limited information available at that time with regard to carbonate-hosted fossils of Ediacaran age).

The Flinders-, Fermeuse-, and Nama-type assemblages appear to be preserved similarly to the Tafilalt parapsonemids, which as discussed above, are preserved as death masks, gravity casts, and in endorelief, in shallow marine siliciclastic sediments (with the type Fermeuse assemblage in Newfoundland, preserved in delta-front deposits around storm wave base, apparently representing the deepest of these localities). It is these assemblages that will be compared to the Tafilalt taphonomy.

The taphonomy of Ediacaran-aged fossils preserved as moulds and casts in sandstones was first considered in depth by Wade (1968), who considered the preservation of fossils in the Ediacara member of the Rawnsley Quartzite, Pound Subgroup, in South Australia (then referred to only as the Pound Quartzite). Wade (1968) noted the consistent preservation of some forms, mostly discoidal fossils (which were then interpreted almost universally as cnidarian medusae), in positive hyporelief (gravity casts), with some specimens preserving a depression on the top surface of the burying bed corresponding to the position of the fossil cast on the bed sole. Other specimens were consistently observed to be preserved in positive epirelief (death masks), with infilling sediment laminae in fossils of Tribrachidium heraldicum and Dickinsonia costata in particular observed arching upwards inside the specimen, forming a cast in positive epirelief. Based on this consistent preservation of fossils as either gravity casts or death masks, Wade (1968) divided the fossils into two categories:

1. **Non-resistant organisms** were proposed to have decayed prior to the onset of diagenesis, and were thought to have been preserved only
where they were moulded by the underlying sediment and/or cast by the burying sediment.

2. **Resistant organisms** were proposed to have decayed only after diagenic processes had cemented a mould in the base of the burying bed.

The occurrence of a limited number of fossils, particularly *Pteridinium simplex*, preserved in sandstone beds was also noted; these were also assigned as resistant forms, but were not discussed in detail.

Left unanswered was the question of how ‘resistant’ organisms were capable of eluding decay until after diagenic processes had cemented the mould, nor were the diagenic processes discussed.

Seilacher (1984) took issue with the interpretation of the discoidal fossils, proposing, based on their taphonomy, that they represented benthic organisms. He agreed with Wade (1968), however, that the fossils preserved as gravity casts must have resisted decay until diagenic processes had cemented the overlying sediment into a mould. He suggested that this resistance was due to the presence of a cuticular, non-mineralised, flexible skeleton. Based on this, as well as observations of the morphology of the fossils, and the affirmation that such preservation was unknown in the Phanerozoic, he radically proposed that they represented a distinct but extinct Kingdom, which he later termed Vendobionta (Seilacher, 1992).

Gehling (1991) briefly discussed the preservation of the fossils, agreeing with Seilacher that such preservation was confined to the Precambrian. On this basis, he noted that

> "either there was something different about Ediacaran organisms, or else the process of preservation was different" (Gehling, 1991, p.215).

However, he disagreed with Seilacher’s biological interpretations, reaffirming the links between fossils of Ediacaran and Cambrian age, and on this basis, proposed that it was **the taphonomic processes in the late Precambrian which were fundamentally different**. Noting the presence of unusual bedding plane textures on
the fossiliferous surfaces in the Ediacara member, Gehling (1991) proposed that these indicated the former presence of seafloor microbial mats, and suggested that these mats caused the rapid cementation of the burying bed soles, moulding the more resistant fossils beneath. He subsequently expanded on this hypothesis (Gehling, 1999), noting that the arching up of sediment laminae inside specimens preserved as positive epirelief casts indicated that:

1. The external mould (in negative hyporelief on the base of the overlying burying bed) was cemented, whilst

2. The underlying sediment remained unconsolidated and fluid.

He considered that the preservation of fossils as gravity casts was less problematic, with moulds of these specimens forming in the underlying bed, and burying sediment moving downwards to occupy the space vacated by the decay of the organisms. He did, however, note that

“Strangely, even after collapse, the undersurface morphology of fossils is often well defined, and lacks evidence of tissue degeneration. The fine morphological detail found in Ediacaran fossils is difficult to duplicate in taphonomic experiments (Norris, 1989; Bruton, 1991). The subtle contours of a modern invertebrate body surface can only be replicated experimentally by rapid application of a plaster mix, before bodies begin to disintegrate.” (Gehling, 1999, p. 48).

Gehling (1999) thus proposed a taphonomic scenario for the fossils of the Ediacara Member (Fig. 6.11). Seafloor surfaces were universally covered in microbial mats, with the fossils representing communities that lived on them. Discoidal forms (which were suggested to represent a mixture of frond holdfasts, anemones, and other benthic organisms) were attached to the microbial mat, partially within the upper parts of the sediment, whilst other organisms lived on top of the mat surfaces. Rapid burial (obrution) killed the organisms, and compacted all of them to some degree. Delicate creatures collapsed completely under compactional pressure, while others of a more resistant nature maintained their form for days or even weeks. A new microbial mat grew on the surface of the entombing bed, effectively preventing oxygen from diffusing from the open seawater above to the pore waters trapped
beneath. Decay of the buried microbial mat proceeded by sulphate reduction, with the hydrogen sulphide produced reacting with sedimentary iron oxides to precipitate iron monosulphides (which later transformed to pyrite) in the sediment immediately above the microbial mat, cementing the bed sole, and forming a death mask for both the microbial mat the associated organisms. Recent (surface) weathering altered this pyrite to iron oxides and oxyhydroxides, principally haematite and limonite.

No pyrite has ever been directly observed in the beds at Ediacara; however, support for this hypothesis was noted to come from the distribution of iron oxides. Haematite was observed to be concentrated along laminae and on the soles of beds, with the part and counterpart of some specimens separated by a thin coating of limonite (hydrated iron oxyhydroxides). Examples of burial deformation and post-mortem shrinkage were cited to support the formation of this mineral encrustation during diagenesis, rather than prior to deposition, as has been observed in the case of some fossil plant material (Spicer, 1977).

The Gehling (1999) interpretation has gained widespread acceptance as a taphonomic model both for the fossils of the Ediacara member, and for similarly preserved fossils in Ediacaran sediments elsewhere (e.g. Narbonne et al., 1997; Dzik, 2003; Peterson et al., 2003; Jensen et al., 2005; Narbonne, 2005; Droser et al., 2006; Grazhdankin and Gerdes, 2007; Laflamme and Narbonne, 2008; Zhu et al., 2008; Narbonne et al., 2009; Laflamme et al., 2010). The disappearance of ubiquitous microbial mats from marine seafloors in the early Cambrian has led to descriptions of the Ediacaran as a time of special taphonomic conditions, referred to as the ‘Ediacaran taphonomic window’ (e.g. Gehling et al., 1998; Jensen et al., 1998).

6.3.2 Taphonomic evidence at Ediacaran localities

It should be apparent that the widely accepted Gehling (1999) taphonomic model (presented above and illustrated in Fig. 6.11) is extremely similar to the taphonomic scenario described in Section 5.2 above (p. 169) for the Ordovician Tafilalt paropsonemids, but is considerably less detailed. No mention is made of:

- Iron (III) reduction,
- Adsorption of reduced iron, or
- Clay mineral authigenesis on organic tissues.

Perhaps the key distinction lies in the presence of microbial mats in Ediacaran sediments, and the proposal that it was the decay by sulphate reduction of these mats, rather than the organisms themselves, which produced the diagenic iron sulphides, with these precipitating not only around the surfaces of the macrofossils, but over the entire sole of the burying bed.

To fully evaluate this taphonomic model, the taphonomic and diagenic evidence at Ediacara and other Ediacaran localities must be considered. In particular, taphonomic data is available for the fossils from five localities:

<table>
<thead>
<tr>
<th>Unit</th>
<th>Location</th>
<th>Data from:</th>
<th>This thesis:</th>
</tr>
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<tbody>
<tr>
<td>I Ediacara Member</td>
<td>South Australia</td>
<td>Wade, 1968; Gehling, 1999; Gehling et al., 2005</td>
<td>Figs. 6.10 § 6.3.2.1</td>
</tr>
<tr>
<td>(Rawnsley Quartzite Formation, Pound Subgroup)</td>
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<tr>
<td>II Erga and Zimnie Gory formations</td>
<td>White Sea, Russia</td>
<td>Steiner and Reitner, 2001; Ivantsov and Malakhovskaya, 2002; Dzik, 2003; Gehling et al., 2005</td>
<td>Fig. 6.14 Fig. 6.15 § 6.3.2.2</td>
</tr>
<tr>
<td>III Kliphoek Member</td>
<td>Namibia</td>
<td>Dzik, 1999; Grazhdankin and Seilacher, 2002; Elliott et al., 2011</td>
<td>Fig. 6.16 § 6.3.2.3</td>
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<tr>
<td>(Dabis Formation, Kuibis Subgroup)</td>
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<tr>
<td>IV Arumbera Formation</td>
<td>Central Australia</td>
<td>Mapstone and McIlroy, 2006</td>
<td>Fig. 6.17 § 6.3.2.4</td>
</tr>
<tr>
<td>V Fermeuse Formation</td>
<td>Newfoundland, Canada</td>
<td>Gehling et al., 2000; MacGabhann, 2007a; Laflamme et al., 2010; personal observations</td>
<td>Fig. 6.18 Fig. 6.19 § 6.3.2.5</td>
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<tr>
<td>(St. John’s Group)</td>
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This data is summarised in Table 6.03. Each of these sites will be tested against the null hypothesis given above.
6.3.2.1 Ediacara member, South Australia [Locality I]

The fossils from the Ediacara Member (Fig. 6.10) are preserved as gravity casts, death masks, and rarely in endorelief, in white sandstones with red-stained soles (Wade, 1968; Gehling, 1999; Gehling et al., 2005). Unfortunately, little petrographic or geochemical data has been published. Wade (1968) regarded the beds as quartzites, with minor feldspar. Most of the beds were noted to be indurated, with weathering of feldspars considered to have increased the friability of certain beds. Smale and Trueman (in Wade, 1968) noted the presence of authigenic quartz, and that clays (which were dominantly illitic) had impeded the growth of this authigenic quartz (where present). If this were to be confirmed, it may suggest the previous presence of chlorite, as while chlorite tends to impede the growth of authigenic quartz, illite, in fact, has the opposite effect (Morad et al., 2000; Worden and Morad, 2000). This, however, appears to be inconsistent with the observed indurated nature of the sandstones. Wade (1968) also noted the red-stained soles to be the result of haematite coatings on quartz grains. More recently, Retallack (2012) has presented (limited) geochemical evidence indicating the feldspars to be predominantly orthoclase, and the clays to comprise smectite as well as illite.

Gehling (1999) also noted the presence of

- haematitic laminae within beds, and
- a haematite sole veneer on the fossiliferous beds,

both formed by the concentration of haematite in the pore spaces between grains, and haematitic grain coatings. Additionally, it was recognised that fossil part and counterpart pairs were often separated by a thin coating of limonite, and that the surfaces of specimens preserved in endorelief were coated in haematite.

While the fossils at Ediacara had previously been regarded as largely allochthonous (e.g. Wade, 1968), Gehling (1999) convincingly showed that they were instead, for the most part, preserved in situ, with only rare torn or folded bedding-plane specimens, and specimens preserved in endorelief, indicating a limited degree of transport. Gehling (1999) also presented compelling
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sedimentological evidence for the presence of microbial mats, recently confirmed by the identification of microbial filamentous structures by Retallack (2012).

This available geochemical and petrographic data is considerably more limited than that presented above for Tafilalt, preventing a full comparative analysis of whether the Ediacara fossils were preserved in the Tafilalt-style. In particular, the lack of information as to the distribution of clay minerals does not allow an assessment of whether the growth of authigenic clays on fossil surfaces aided their preservation. Nonetheless, the available data suggests a diagenic history only slightly different to the Tafilalt sediments, particularly those at M005.

Most significantly, there is no evidence to contradict the null hypothesis. The restriction of iron oxides to sedimentary laminae, fossil surfaces, and bed surfaces at Ediacara is exactly the same as at Tafilalt site M005, and implies a phase of iron reduction, due to the immobility of oxidised Fe$^{3+}$. The limonite fossil surface veneer between part and counterpart (distinct from the haematite sole veneer), and the haematitic fossil surface veneer on specimens preserved in endorelief, are consistent with a concentration of iron sulphides on the surfaces of the fossils, similar to the fossil surface veneer at M005. Further, such a veneer suggests that an earlier stage of iron reduction caused the adsorption of Fe$^{2+}$ ions to the surfaces of the organisms, providing a source of in situ Fe$^{2+}$ to react with the H$_2$S produced by sulphate reduction.

The preservation of filamentous microbial structures at Ediacara is also consistent with this taphonomic mechanism; as noted above (p. 162), taphonomic experiments have demonstrated that adsorption of Fe$^{2+}$ significantly enhances the preservation potential of certain bacteria. The haematite sole veneer likely reflects the preservation of these microbial mat filaments by iron sulphides, with redistribution of iron oxides into the overlying bed sole following oxidation. This interpretation differs from that of Gehling (1999) and Gehling et al. (2005), who proposed that it instead reflected the primary cementation of the bed sole by disseminated iron sulphides, rather than those formed directly on organic surfaces where Fe$^{2+}$ had been adsorbed. This interpretation is falsified by the observation that haematite occurs concentrated around (present-day) authigenic grains, rather than the original detrital
grains. Disseminated iron sulphides would have precipitated in the pore spaces between detrital grains, and should, therefore, have been overgrown by subsequent syntaxial authigenic quartz, to be preserved as dust rims.

The condition of a low total organic carbon content (TOC), believed to be a requirement of this taphonomic mechanism, may appear to have been contravened by the presence of widespread microbial mats. This is not the case. A high TOC would tend to decrease fossilisation potential via this mechanism, due to the large available surface area for the adsorption of Fe$^{2+}$ ions. The surface area of a microbial mat, however, as compared to dispersed particulate organic matter throughout a sediment bed, is actually relatively low, due to the gelatinous nature of the mat restricting the pore water, and, thus, ionic diffusion. The surface area of the TOC, therefore, would have been comparatively low.

Previous discussions of the microbial mat preservation hypothesis (Gehling, 1999; Gehling et al., 2005) have emphasised the growth of a new microbial mat on the surface of the burying bed as a key step in the taphonomic process, by restricting the diffusion of oxygen from the open marine environment above into the pore water below. This step is, however, unnecessary. As noted above, previous studies have shown that any organic matter particles greater than 2mm in diameter will decay anaerobically, even in well oxygenated conditions (Jørgenson, 1977; Allison and Briggs, 1991). Due to their size, and the fact that oxygen diffusion through pore waters is always limited, the decay of the organisms at Ediacara must have been largely anaerobic, regardless of whether or not a new microbial mat had developed across the surface of the burying bed.

It is important to concede, however, that evidence in the case of one fossil does not necessarily extrapolate to all fossils. The key question, therefore, is whether the presence of the microbial mats at Ediacara allowed the preservation of fossils which would not have been preserved at Tafilalt (assuming the absence of microbial mats there).

In the case of the fossils preserved in positive epirelief with an iron oxide surface veneer, the evidence is completely consistent with Tafilalt taphonomic mechanism, including the adsorption of Fe$^{3+}$ to organic tissues. There is no evidence,
and thus no reason, to suggest that these organisms could not have been preserved at Tafilalt.

In the case of specimens **without this fossil surface veneer**, the evidence is equivocal. In particular, specimens preserved in positive hyporelief and/or negative epirelief (gravity casts) may indeed have had their lower surfaces moulded by the microbial mat. These specimens may be divided into two categories:

1. Those showing significant relief, such as discoidal holdfasts, and

2. Those with little relief, for example *Phyllozoon*.

Consideration of the taphonomy of these specimens in association with microbial mats helps to illuminate the preservation of both these forms.

It is generally recognised that Ediacaran microbial mats protected the surface of the sediment. Gehling *et al.* (2005) noted that the lack of trace fossils in the Ediacara Member was

> “not evidence of immobility but rather a function of the inability of the substrate to record any locomotion that did not disrupt the biomat”.

Given this degree of protection, how could a soft-bodied organism leave a significant impression in the substrate below? Gehling (1999) suggested that specimens preserved in low relief represented the compaction of non-resistant forms into the substrate, but it is difficult to envisage how such an easily compacted body would leave an impression through a gelatinous microbial mat. This was tacitly admitted by Gehling *et al.* (2005), who stated:

> “Given that the density of the Dickinsonia body must have been little more than seawater, the weight of the organism on a sandy substrate would not have left a significant impression.”

This difficulty in making an impression also applies to specimens other than *Dickinsonia* (Fig. 6.12), and applies equally both pre- and post-depositionally. This interpretation is therefore untenable; these fossil specimens cannot represent organisms simply lying on top of the substrate, but must instead represent a modification of the microbially-bound substrate prior to burial (Fig. 6.12). Ivantsov
and Malakhovskaya (2002) and Ivanstov (2011) suggested that such forms represented the traces of organisms feeding on the microbial mat, which is certainly plausible, and was supported by Gehling et al. (2005). McIlroy et al. (2009) have also recently suggested that an organism simply resting on a microbial mat for an extended period would degrade the mat, leaving an impression; this may also be a factor in the preservation of such low relief fossils.

Forms with greater relief likewise cannot represent compaction into the substrate, but must have been in some way partially infaunal (Fig. 6.12), as noted by Gehling (1999) and Gehling et al. (2005), with their lower surfaces moulded by the microbial mat. Therefore, specimens preserved in positive hyporelief at Ediacara are not body fossils sensu stricto, but represent a combination of infaunal living traces and epifaunal feeding traces (Fig. 6.12). As the preservation of both of these forms is dependent on the presence of a microbial mat, such specimens are not consistent with the Tafili t taphonomic style.

For specimens preserved in positive epirelief/negative hyporelief (death masks) without a fossil surface veneer (although it is not clear from the published evidence that any such examples exist), the crucial factor is the observation that the haematite sole veneer must represent the telodiagenetic oxidation and mobilisation of iron sulphides which previously had replicated bacterial structures within the microbial mat, and not the early diagenic lithification of the bed sole by disseminated iron sulphides (see discussion on p. 251). As the microbial mat would, of course, have been underneath these macroscopic organisms, the pyritisation of the mat itself would have been inconsequential to the preservation of the upper surface of these fossils above (Fig. 6.13). Indeed, as it is the microbial mat which is pyritised, and not the overlying sediment, the preservation of fossils in positive epirelief requires that the microbial mat was mineralised only after mineralisation and moulding of the fossil lying above it (Fig. 6.13). This must be the case, as the microbial mat covered the top surface of the bed underlying the fossils and sediment from there moved upwards to fill the mould following the complete decay of the organism. Had the microbial mat been mineralised prior to the completion of decay of the organism, it would have prevented sediment from moving upwards to fill the mould, and a void.
would have resulted in the sediment. Thus part moulds would not be accompanied by counterpart casts (Fig. 6.13).

In such cases, therefore, while evidence of a macrofossil surface veneer may presently be absent, their relief requires that such a veneer was originally present. It should also be noted that the preservation of fine details requires the direct authigenesis of iron sulphides on the surfaces of the fossils. Moulding by iron sulphides precipitating directly onto the surface of the decaying organisms facilitates the preservation of morphological details in high resolution, while moulding by coarse sediment lithified by disseminated iron sulphides dramatically lowers the resolution of preservation (Fig. 6.13). Where fine details are preserved on death mask specimens, therefore, direct precipitation of iron sulphides on the upper surface of the organism must have occurred.

The direct precipitation of iron sulphides on the organic surfaces of the organisms requires that they themselves were actually the source of the reduced iron and H₂S. In other words, the organisms were actually in an advanced stage of decay when the fossil surface was replicated through moulding. The decay of the microbial mat may have assisted this by providing additional organic matter, and therefore leading to the availability of more Fe²⁺ ions and hydrogen sulphide than could be produced by the decay of the organism alone, but the observation that the mat must have been lithified only after the organisms had fully decayed appears to indicate that this was not the case. Additionally, the preservation of small fossils at Tafilalt (e.g. Fig. 3.06b,c) suggests that this was not required.

Based on the presently published evidence, therefore, the preservation of specimens in the Ediacara Member in positive hyporelief (gravity casts) is dependent on the presence of a microbial mat; in these cases, therefore, the null hypothesis is falsified, due to the lack of microbial mats at Tafilalt. For specimens preserved with in positive epirelief (death masks), however, no evidence currently exists to falsify the null hypothesis.
6.3.2.2 Erga and Zimnie Gory formations, White Sea, Russia [Locality II]

The Erga and Zimnie Gory formations (included within the Mezen and Ust'Pinega formations in older publications) of the White Sea region, Russia, are interpreted as representing a pro-delta and delta-plain environment, with a coarsening upwards complex of interbedded sandstones, siltstones, and mudstones (Grazhdankin, 2003). At Zimnie Gory itself, fossils occur particularly densely in two horizons:

- An upper uniform 10cm thick fine-grained quartzose sandstone bed overlying a mudstone, and
- A lower lenticular but otherwise similar sandstone bed overlying mudstone (Steiner and Reitner, 2001; Dzik, 2003; Grazhdankin, 2003).

Both beds are barely lithified.

Fossils are preserved as negative hyporelief external moulds (death masks) or positive hyporelief counterpart casts on the soles of the sandstone beds (Fig. 6.14); a limited number of fossils are also preserved in endorelief within the sandstone beds (Dzik, 2003). Specimens in positive hyporelief exhibit the same variation in relief noted for the fossils of the Ediacara Member. Significantly, organic preservation sometimes accompanies the mould/cast preservation: Steiner and Reitner (2001) described a frondose specimen with a basal attachment disc preserved in negative hyporelief, with the stalk and petalodium preserved in endorelief within the bed (Fig. 6.15a). SEM EDX analysis determined that while certain parts of the organism were replaced by pyrite and potassium aluminosilicates, organic material remained in the unreplaced parts (Fig. 6.15c).

Clear palaeoenvironmental evidence exists for the presence of microbial mats, with the mats visible in cross-section, now wholly composed of (unidentified) clay minerals (Dzik, 2003). Microbial textures are also visible on the bed surfaces, and some filamentous microbial structures are preserved pyritised (Steiner and Reitner, 2001; Dzik, 2003; Gehling et al., 2005). Steiner and Reitner (2001) also identified organic preservation of microbial filaments (Fig. 6.15b), along with pyrite with $\delta^{34}S$ values indicating a sulphate reduction origin.
Perhaps the most important observation was made by Dzik (2003, p. 117), who noted that:

> "Although potentially the microbial mat offered source of organic matter for the whole surface of the fossiliferous bed, the pyrite formation seems to be restricted to external molds and their proximities. The decaying body was thus more important."

As Dzik correctly pointed out, this restriction (or concentration) of the pyrite to the surface of the fossils and immediate vicinity implies that the decay of the organisms themselves was substantially in progress when they were moulded. Further, the localisation of pyrite on the specimens is again consistent with the hypothesis that earlier iron (III) reduction led to the adsorption of reduced Fe$^{2+}$ on to the surfaces of the organisms, providing an *in situ* source of iron to react with hydrogen sulphide produced by sulphate reduction. As discussed for the Ediacara Member (see p. 251), the pyritisation of microbial filaments is also entirely consistent with this process.

The most significant difference between the fossils of the Erga and Ust'Pinega formations and those of the Ediacara Member lies in the organic preservation of some tissues in the Russian sediments. While such preservation is completely unknown at Tafilalt, and may thus appear to be inconsistent with the Tafilalt taphonomic model, this is not necessarily the case. As discussed above (see p. 240), the Tafilalt specimens are preserved via similar taphonomic processes to those in operation in the Burgess Shale, save that in the Burgess Shale, the curtailment of the sulphate supply restricted iron sulphide formation, and left Fe$^{2+}$ ions adsorbed to the organic matter. This prevented ectoenzymatic breakdown, a necessary prerequisite for decay. Authigenic clay minerals then nucleated around the adsorbed ions. In the White Sea localities, the observation that the organic matter is *only preserved in parts of the specimens not pyritised* is entirely consistent with this observation. Reaction of adsorbed iron with hydrogen sulphide would produce pyrite in certain parts of the specimens, removing the decay protection. Where iron was left adsorbed, the protection remained and facilitated the primary preservation of the organic carbon. Importantly, the EDS analysis of this organic carbon reported by Steiner and Reitner (2001) (Fig. 6.15c) demonstrates that this organic matter is
preserved together with K, Al, Si, Fe, Mg, and Ti, in proportions that suggest smectite and/or illite/smectite mixed layer clay minerals – just as hypothesised for the authigenic clays nucleating around the adsorbed iron (see pp. 162, 190, 197 herein and Fig. 5.65).

As for the Ediacara Member fossils, the specimens preserved in positive hyporelief are regarded as either partially infaunal, or as feeding traces (Ivantsov and Malakhovskaya, 2002; Dzik, 2003; Ivantsov, 2011), and their preservation was dependant on the presence of a microbial mat. The null hypothesis is therefore falsified for these specimens.

However, there is no published evidence that contradicts the Tafilalt taphonomic model for the specimens preserved either in negative hyporelief, or in endorelief. Indeed, the occurrence of organic preservation, in regions of specimens where pyrite is absent, strongly supports this model for the Erga and Ust'Pinega Formation fossils. For these specimens, therefore, the null hypothesis cannot be falsified.

6.3.2.3 Kliphoek Member, Namibia [Locality III]

Fossils of the Kliphoek Member of the Dabis Formation, Kuibis Subgroup, in Namibia, are preserved in endorelief within sandstone and siltstone beds (Fig. 6.16) (Dzik, 1999; Gehling, 1999; Grazhdankin and Seilacher, 2002; Elliott et al., 2011). Assemblages commonly comprise one or more of four particular organisms: Rangea schneiderbohni, Pteridinium simplex, Ernietta plateauensis, and Namalia villiersiensis. There is strong evidence to indicate transport prior to the preservation within beds, although Grazhdankin and Seilacher (2002) proposed that at least some specimens of Pteridinium were preserved in situ, and thus proposed an infaunal lifestyle. No position is taken on this interpretation here.

Little taphonomic data has been published for the Namibian fossils; however, Gehling (1999) and Dzik (1999) both noted that fossil surfaces are coated in iron oxides, and that pyrite occurs within certain fossils, particularly Ernietta, which is 3D. Both Gehling (1999) and Dzik (1999) suggested that these were a product of
sulphate reduction produced by the decay of the organisms themselves. Dzik (1999) further proposed for Ernietta that this indicated that the preserved part of the organism represented only a decay resistant integument. He believed that this integument must have been more flexible and elastic than the eldonide integument (although this was based on an underestimation of eldonide flexibility), and suggested a collagenous composition.

This is entirely consistent with the Tafilalt taphonomic model. Indeed, the preservation of iron oxide remnants of pyrite on the surfaces of the fossils strongly suggests the reaction of hydrogen sulphide with reduced iron ions adsorbed onto the outer integument. In the absence of such adsorbed ions, the pyrite would have precipitated disseminated throughout the fossil bed in the vicinity of the organisms.

For the fossils of the Kliphoek Member, therefore, the available evidence is consistent with Tafilalt taphonomy, and no evidence presently exists to falsify the null hypothesis.

6.3.2.4 Arumbera Sandstone, central Australia [Locality IV]

Discoidal fossils in the Arumbera Formation, central Australia, occur in positive hyporelief and/or negative epirelief on the soles and tops of fine to very fine sandstone interbedded with siltstone and shales (Glaessner and Walter, 1975; McIlroy et al., 1997; McIlroy and Walter, 1997; Mapstone and McIlroy, 2006). The taphonomy and diagenic history of the Arumbera fossiliferous sediments was traced in detail by Mapstone and McIlroy (2006), and the taphonomic information available for this site is unparalleled in the Ediacaran (Fig. 6.17).

The taphonomy and diagenic sequence, as described by Mapstone and McIlroy (2006), is extremely similar to that proposed herein for Tafilalt. The fossil surfaces are coated with a veneer of mixed haematite and clay minerals; the nature of the clay minerals in the veneer in particular is not specified, but smectite, illite and glauconite were identified in the sediments. The veneer was noted to occur not only on the fossil hyporelief surfaces, but also on the top of the burying bed above the
fossils, and thinner and more intermittently on other parts of the sole of the burying bed (Fig. 6.17b,c).

Thin sections through several of the fossils reveal the existence of disturbed laminations in the form of both parallel lamination and cross lamination, picked out by the alternation of sand-rich pale layers with thin haematite and clay rich layers (Fig. 6.17b). These laminations show disturbance due to post-depositional downward movement. As noted by Mapstone and McIlroy (2006), this indicates that the organism was present on burial, and subsequently decayed, with sediment moving downwards under gravity to fill the space vacated by the tissues; the very definition of a gravity cast fossil.

The organism must therefore have decayed prior to the onset of early diagenic mineralisation. The haematite and clay mineral veneer observed must instead, therefore, represent authigenic mineralisation of the microbial mat, as suggested by Mapstone and McIlroy (2006). The discrete nature of the mat, with haematite concentrated within a distinct layer at the surface, strongly supports this, and provides further support to the hypothesis that authigenic iron sulphides, resulting from the decay of the microbial mat, precipitated directly on mat bacteria, as suggested for the Ediacara Member and Erga Formation, and not disseminated within the lower layers of the burying sediment. This hypothesis is further reinforced by the fact that this veneer occurs on the top surfaces of the fossiliferous beds. Such a veneer clearly could not have formed due to the decay of an organism, as these were not in contact with this surface. Thus to precipitate iron sulphides here, the hydrogen sulphide and reduced iron would both have had to migrate through the sediment of the burying bed, and react in the basal layer of the overlying water column. This is not tenable. Instead, it is likely that this veneer represents the mineralisation of a new microbial mat formed on the top surface of the burying bed, after it itself had subsequently been buried.

The geochemical and diagenetic processes which occurred in the Arumbera Formation were therefore identical to those at Tafilalt. However, as the fossils exhibit positive hyporelief, they must have been at least partially infaunal, modifying the upper layers of the substrate, and with the microbial mat passing both above and
below the holdfast and enclosing it, as suggested by Mapstone and McIlroy (2006). The lower surfaces of the organisms were preserved not by the mineralisation of the fossil surfaces, but of the underlying microbial mat. As microbial mats were apparently not a part of the taphonomic process at Tafilalt, these fossils could not, therefore, have been preserved there. The null hypothesis is therefore falsified.

6.3.2.5 Fermeuse Formation, Newfoundland [Locality V]

Discoidal fossils preserved in positive hyporelief on the soles of thin fine sandstone to siltstone beds interbedded with mudstones in the Fermeuse Formation, St. John’s Group, Newfoundland (Fig. 6.18), were first described by Billings (1872), but were not widely recognised as fossils prior to their redescription by Gehling et al. (2000). Despite the wide variation in form of the discoidal remains, Gehling et al. (2000) considered that it was not possible to assign these to individual genera and species, due principally to the occurrence of several morphologically intermediate forms. Consequently, they assigned all of the discoidal fossils to the single species *Aspidella terranovica*, interpreting *Aspidella* as a holdfast. Narbonne (2005) considered that the Fermeuse Formation assemblages represented a slightly different taphonomic window on the Mistaken Point biota, preserved in Conception-style under volcanic ash beds. MacGabhann (2007a), however, disagreed, principally citing taphonomic, biological, and palaeoecological grounds, proposing that two distinct communities were represented at Mistaken Point and in the Fermeuse Formation, and suggesting that the Fermeuse fossils may have lived, an been preserved, in an area lacking the development of typical Ediacaran microbial mats. The discoidal fossils were interpreted as a heterogeneous mixture of holdfasts, bacterial colonies, infaunal actinians, and poriferans, all preserved due to a partially infaunal position on the substrate. This was in part based on the earlier interpretation of some Ediacaran-aged discoidal fossils as bacterial colonies by Grazhdankin and Gerdes (2007).

A thorough investigation of the taphonomy of certain specimens from the Fermeuse Formation was undertaken by Laflamme et al. (2010). Supporting MacGabhann (2007a) and Grazhdankin and Gerdes (2007)’s interpretations of heterogeneity, they particularly selected specimens which they were confident
represented holdfasts, based on morphological and palaeoecological criteria. Examination of sections through four specimens by SEM EDS demonstrated that these were preserved as a volume, rather than as surficial impressions (Fig. 6.19). The fossils were observed to be bounded both above and below by a thin distinct sediment layer (which merged to either side of the fossils and continued beyond them) principally comprising Fe, S, K, Al, Mg, and Ti, with a lower Si content than the enclosing sediment. This is consistent with iron sulphides and clay minerals of smectite/illite mixed layer or glauconitic origin. The sediment contained within the volume representing the organism was noted to be different from the host sediment, and Laflamme et al. (2010) suggested that this may indicate the incorporation of sediment into the holdfast during life. Such a hypothesis is interesting, and reminiscent of the psamocorralids (Seilacher, 1992, 1996; Savazzi, 2007).

While the clay mineral and iron sulphide veneer indicates that geochemically, the preservation of these fossils was identical to Tafilalt, the form of the veneer indicates that it represents the mineralisation of the microbial mat, rather than of the organic macrofossil surfaces themselves. The preservation as a volume is also quite distinct from the Tafilalt specimens. Consequently, the taphonomic processes differed from those at Tafilalt, and the null hypothesis is falsified.

### 6.3.3 Differential taphonomy

The taphonomy of specimens from the sites [I-V] considered in subsections 6.3.2.1-6.3.2.5 is summarised in Fig. 6.20. The null hypothesis is falsified above for all fossils preserved in negative epirelief and/or positive hyporelief (gravity casts), but on the basis of currently published evidence, cannot be falsified for specimens preserved in either positive epirelief/negative hyporelief (death masks) or in endorelief at these five sites. Thus, for these specimens, the differential taphonomic analysis is valid. The conclusions of the comparative taphonomic analysis of the Tafilalt eldonides against the Burgess Shale eldonides can, therefore, be applied to these Ediacaran-aged fossils.
The first such conclusion to be drawn is that Wade (1968) was indeed correct in the characterisation of the Ediacara Member fossils as including both resistant and non-resistant forms, and that Seilacher (1984) was also correct when he asserted that it was the composition of the integument that facilitated preservation in positive epirelief. Those fossils preserved as death masks must have had an outer integument with a composition similar to that of the eldonides, consisting of complex organic biopolymers which required enzymatic breakdown prior to anaerobic decay, and to which Fe$^{2+}$ ions would readily adsorb. Dzik (1999) has argued that the integument of *Ernietta* was more flexible and elastic than that of the eldonides, but it should be noted that this statement was made prior to the discovery of the Tafilalt fossils, which show considerable evidence of deformation and elasticity, with specimens stretched, folded, and even rolled up into a cigar-like shape (e.g. Figs. 4.100-4.101). The specimens of *Paropsonema*, which Dzik had not previously recognised as an eldonide (e.g. Dzik, 1991), also show similar evidence for elasticity (Figs. 4.42, 4.44, 4.45). The differences between the integuments of the Ediacaran-aged fossils preserved in positive epirelief, and those of the eldonides, are therefore likely much smaller than Dzik (1999) suggested. This does not imply that they were identical, but does indicate a close similarity in physical properties and composition. Dzik (1999) suggested a collagenous composition for *Ernietta*, consistent with the taphonomic models presented herein, as discussed above (e.g. pp. 163, 169).

As a corollary to this point, it should be noted that the similarity of eldonide and certain Ediacaran integuments removes one key part of Seilacher (1984, 1989, 1992)'s justification for the establishment of the Vendobionta, namely that the integument of the Ediacaran-aged forms was quite unlike metazoan integuments. The eldonides are clearly metazoan, negating any need to invoke a non-metazoan
construction to explain the nature of the integument of comparable Ediacaran forms.

Secondly, in the Tafilalt fossils, the softer parts of the anatomy visible in the Burgess Shale specimens are evidently not preserved. Further, both the Burgess Shale and Tafilalt fossils were already in an advanced state of decay when the mould was cemented, as the authigenic iron sulphides and clay minerals which formed the mould precipitated only as a result of the decay by iron (III) and sulphate reduction of other parts of the organism. This indicates that for organisms preserved in this style:

1. First the more labile tissues decayed;
2. Then the authigenic iron sulphide minerals formed a mould; and
3. Finally, the outer integument decayed.

This also applies to the Ediacaran-aged fossils for which the null hypothesis cannot be falsified. Thus these organisms were likely already in an advanced state of decay when they were moulded and preserved, and softer tissues would, similarly, not have been capable of preservation in this taphonomic style.

Third, and modifying slightly the second conclusion, internal structures can actually be preserved in this style, provided they are ‘inflated’ in life, and either deflate subsequent to burial, modifying the surface, or become infilled with sediment. Interpretations of internal anatomy based on irregularities in the surface of fossils preserved in this style, such as that of Dzik (2003), may thus be valid. More resistant internal structures may also be preserved by aluminosilicification, like the

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§§§ A second component of Seilacher (1984, 1989, 1992)’s Vendobionta theory was that these organisms were ‘quilted’, and inflated, somewhat akin to an air mattress. The postulated inflated nature of the eldonide coiled sac (see Fig. 5.63) may appear to support this facet of the Vendobionta hypothesis; however, this is clearly falsified by the clear lack of such inflation of the general eldonide integument. In fact, this facet of the interpretation was purely to explain how such organisms could be preserved as fossils in positive epirelief, a characteristic which has since been explained by early diagenic mineralisation, and is thus no longer a crucial aspect of the Vendobionta hypothesis.
coiled sac of the Tafilalt eldonides; an examination of the distribution of clay minerals on the surfaces of such Ediacaran-aged fossils may thus be illuminating.

6.4 Conclusions

The null hypothesis of this thesis, provided in Chapter One (p. 19), included three supplementary parts, in addition to that explored in the preceding section. These were:

2. That these taphonomic processes preserve only recalcitrant, decay-resistant structures, and cannot preserve the more labile tissues preserved in Burgess Shale-type preservation;

3. That the apparent biotic change across the Precambrian-Cambrian boundary is not a taphonomic artefact;

and,

4. That Darwin was likely correct in his assumption of a long pre-Cambrian fossil record, as the fossils of the Ediacaran System cannot represent fossils of the oldest animals, but merely the oldest known animals to be fossilised.

As discussed in the preceding section (p. 264), differential taphonomic analysis indicates that the Ediacaran-aged fossils preserved as death masks or in endorelief cannot preserve labile tissues, but only a decay-resistant integument. The second part of the null hypothesis, therefore, cannot be falsified.

Further, the fossils of Ediacaran age for which the first part of the null hypothesis cannot be falsified could actually have been preserved in Phanerozoic sediments, as the similar taphonomic mode of the Ordovician Tafilalt fossils clearly demonstrates. The apparent absence of these fossils, and this type of taphonomy, in the Cambrian cannot, therefore, be merely a taphonomic artefact caused by the demise of microbial mats, but must instead reflect a real biological change. The third part of the null hypothesis thus cannot be falsified.
Given the recognised dependence of Ediacaran ecology on microbial mats, it is likely that this biological change represents an ecological revolution predicated on the evolution of bioturbation and the disappearance of widespread seafloor microbial mats in the earliest Cambrian (Fig. 1.05). Given the degree of biological change, it would not, perhaps, be inappropriate to refer to this as a palaeoecologically-enduced mass extinction.

Finally, given that the Ediacaran organisms for which the first part of the null hypothesis cannot be disproved can represent only an outer integument composed of complex structural biopolymers which require enzymatic degradation prior to decay, or modifications of this surface by inflated 3D internal structures, it follows that organisms without such an outer integument cannot be preserved in this manner. This hypothesis is proved by the lack of preservation in positive epirelief of organisms which are preserved only in positive hyporelief.

Moreover, given that preservation in positive hyporelief requires a pre-burial modification of the microbial mat (as discussed on p. 253), the Ediacaran organisms preserved as moulds and casts in sandstones must represent only organisms with such an outer integument, or organisms which were capable of modifying the microbial-mat covered surface.

Organisms which did not have such an outer integument, and which were unable to (or simply did not) modify the microbially-bound substrate, thus cannot be preserved as moulds and casts in sandstones, of any age. The lack of such an outer integument would have precluded their preservation in positive epirelief or in endorelief via early diagenic mineralisation, while the presence of microbial mats in the Precambrian would have prevented them leaving any trace of their presence in the underlying substrate (it is possible, however, that such organisms may responsible for trace fossils in Phanerozoic sediments).

The Ediacaran radiation thus reflects two things:

- The evolution of outer integuments composed of complex biopolymers requiring enzymatic degradation prior to decay, and to which Fe$^{3+}$ ions readily adsorbed; and
- The evolution of behaviour which was capable of modifying a microbially-bound substrate.

Such an adaptive radiation not only implies, but fundamentally requires, a prior stage of animal evolution. Pre-Ediacaran metazoans without this either this form of integument, or such a substrate-modifying lifestyle, thus must have existed, and could not have been preserved as fossils. Part four of the null hypothesis thus cannot be falsified.

Darwin (1859) must therefore have been correct in his suggestion of a long Precambrian interval of animal evolution without a fossil record.

6.5 Further work

This thesis should not be considered from the last word on any of the topics discussed, and has probably raised more questions than it hoped to solve. Future research on the eldonides will likely reveal the existence of new genera and species, perhaps even new families and orders, and may clarify their position in metazoan evolution. Examination of the presently available sites and fossils is also incomplete. Further exploration of the Ordovician and Devonian of New York and the Silurian of both Australia and England is likely to reveal further specimens, which may provide further information on the biology and taphonomy of *Paropsonema crytophya*, *Paropsonema mirabile*, *Praeclarus* sp., and in particular the taphonomy of *Discophyllum peltatum* specimens preserved in shales.

The observed deformation of eldonide fossils from true circularity may allow an estimate of the elasticity of their integuments. The Tafilalt fossils are the most likely source of information in this regard. Here, fossils are found on bedding plane surfaces, both circular, and deformed from circular. A mathematical value for the deviation from circularity, combined with estimates of the shear stress from deposition, may produce such an elasticity estimate. A MATLAB/OCTAVE script for the determination of the deviation from circularity has already been written, and it is fully intended to undertake this analysis.
The similarity of the taphonomic processes in the Burgess Shale, Tafilalt, Ediacara, White Sea, Kliphoek, Arumbera, and Fermeuse Lagerstätte is extremely interesting, and certainly requires further investigation. In particular, it would appear that pyritisation at other fossil sites – for example, Beecher’s Trilobite Bed, and the Hunsrück Slate – may be preserved in an extremely similar way. The taphonomic process proposed is amenable to actualistic experimentation, and should be tested. Individual stages in the decay process are also amenable to experimentation; in particular, the susceptibility of various organic tissues to the adsorption of Fe\(^{3+}\) ions may help to clarify the nature of not only eldonide integuments, but the integuments of certain Ediacaran-aged organisms and other problematic fossils.

Additional information on integuments may also be provided from future work on the Burgess Shale fossils. As various tissues are preserved replicated in different clay minerals of different compositions, it would be extremely interesting to compare this not just within, but also between taxa. By examining the clay mineralogy replicating tissues in both more familiar organisms, such as trilobites, anemones, and poriferans, and more problematic organisms, such as the eldonides, it may be possible to identify specific clay mineralogies replicating particular tissues.

Further examination of the taphonomy of specimens these Ediacaran sites is also required, to further attempt to disprove the null hypothesis presented herein. In particular, the fact that a full diagenetic sequence can be established for both the Arumbera and Tafilalt sites indicates that, despite previous assertions, a full analysis of the Ediacara specimens could prove extremely fruitful. The least-altered fossils of the White Sea biota are, however, the best opportunity for evaluating the taphonomic model outlined herein. The taphonomy of other Ediacaran-aged sites must also be explored in more detail, particularly those of the sub-volcanic ash preservation at Mistaken Point and the preservation in limestones in the Khatyspyt and Dengying formations in Russia and China respectively.

Finally, the eldonides are far from the only fossils exceptionally preserved at Tafilalt. Other non-mineralised organisms are also known, including at least two other discoidal morphologies, known arthropods, palaeoscolecid worms, agglutinated tubular organisms, and non-mineralised arthropods. Mineralised forms exceptionally
preserved include trilobites and echinoderms. Without doubt, further examination of the taphonomy of these fossils would greatly increase our understanding of these processes. Description of the specimens themselves would undoubtedly add to our knowledge of Ordovician biodiversity and palaeoecology.

As repeated on page one, in the Origin of Species, Darwin suggested that if his theory was true, there must have been a long stage of prior evolution without a fossil record. Strange as it may seem, it is an Ordovician, and not Precambrian, Konservat-Lagerstätte, which confirms that Darwin was correct. The oldest known animal fossils are not fossils of the oldest animals; but simply the first animals to be preserved as fossils.
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