

MISSISSIPPIAN OSTRACODS AND ISOTOPES OF THE MIDLAND
VALLEY, SCOTLAND: TESTING FOR THE ECOLOGICAL SHIFT INTO
NON-MARINE ENVIRONMENTS

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Abstract

Ostracods are a diverse group of arthropod crustaceans with a geological record from the Ordovician. Their radiation from marine to non-marine environments is a key step in the evolution of the group. The nature and chronology of this transition is examined, and proxies for non-marine environments determined. The Mississippian of the Midland Valley of Scotland contains a wide range of marine to non-marine ostracods, macrofauna and sediments that make it an ideal study area. This study documents the evidence for early Mississippian freshwater ostracods, 20 million years older than previously recorded.

Twentyfive ostracod species from the orders Myodocopida, Palaeocopida and Podocopida are described, four of which are new species. Macrofossils are used to interpret the environmental tolerance of the ostracods. Important brackish to freshwater macrofauna are the bivalves *Carbonicola*, *Curvimula* and *Naiadites*, the vermiform microconchid "*Spirorbis*", conchostracans and fish. Eurytopic ostracods are species of *Cavellina*, palaeocopes and *Shemonaella siveteri* n. sp. Key brackish to freshwater ostracods are species of *Geisina arcuata*, and *Paraparchites circularis* n. sp. Freshwater ostracods are species of *Carbonita*. Non-marine sediments contain three new types of algal palynomorph, *Botryococcus* sp., and arthropod fragments. The algal palynomorphs are interpreted as freshwater. Brackish to freshwater habitats identified include estuaries, lakes, temporary pools and swamps.

A protocol for the examination of diagenetic alteration of ostracods and macrofossils is proposed, which is essential prior to any isotope analysis. Diagenetically altered ostracods may be mistaken as pristine specimens, without a study of the carapace ultrastructure. This is assessed by comparing Carboniferous and Recent specimens. The Carboniferous ostracods have undergone seven diagenetic stages: 1. neomorphic calcite; 2. dissolution and pitting; 3. euhedral pyrite; 4. ferroan calcite; 5. ferroan dolomite; 6. iron oxide; 7. sphalerite and barite. The carbon and oxygen stable isotope data from the ostracods reflect these stages of diagenesis.

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Chapter 1: Introduction

Introduction

Ostracods are a diverse group of small aquatic crustaceans, common from the Ordovician to the present. They are used to investigate climatic changes, ecology, genetics, and regional biostratigraphy throughout their geological record and in modern faunas (for example Boomer *et al.* 2003, Frenzel & Boomer 2005, Newman 2005, Yasuhara & Cronin 2008). Their colonisation of non-marine habitats in the Mississippian is a key step in the ecological radiation of the group. Many questions remain as to how, when and why ostracods colonised non-marine environments.

This study examines the first non-marine colonisation by ostracods and the different proxies that can be used to determine a non-marine environment. Freshwater ostracods are common by the middle Pennsylvanian, and the first putative freshwater ostracods occur in the late Mississippian. This study puts back the timing of colonisation from the late to the early Mississippian. The nature of non-marine colonisation was passive or active radiation from marginal marine to brackish and freshwater environments, for example by estuarine routes. Potential physiological adaptations in the ostracods include changes in osmoregulation, feeding and reproduction. The different proxies used to determine a non-marine environment are sedimentology, macrofauna, ostracods, palynology and ostracod and macrofossil shell geochemistry.

The aims of the study are:

- To examine the nature and chronology of the transition of ostracods from marine to non-marine aquatic environments.
- To examine how non-marine environments can be determined by different proxies.

The objectives of the study employed to realise the aims are:

- To produce an early Carboniferous ostracod biostratigraphy for the Midland Valley of Scotland.
- To identify ostracods from a range of marine to non-marine environments, and record their taxonomy.
- To investigate non-marine proxies such as certain macrofossils and algal palynomorphs.
- To recognise the effects of diagenesis on ostracod and macrofossil shells.
- To analyse pristine specimens of fossil shells for carbon and oxygen isotopes, to assess the palaeoenvironment.

The Midland Valley of Scotland

The Mississippian of the Midland Valley of Scotland represents a range of environments from marine to freshwater, and has an abundance of macrofossils and ostracods. The sediments contain some of the earliest evidence of non-marine ostracods (Williams *et al.* 2005, 2006, Bennett 2008). The sediments of the Strathclyde Group of Fife consist mainly

of marine and non-marine mudstones, siltstones, sandstones, marine and non-marine limestones, coals and evaporites. These deposits usually form in a pattern of upward coarsening deltaic cycles (Browne *et al.* 1999).

The Fife formations can be correlated with other formations across the Midland Valley using distinctive marine horizons (Browne *et al.* 1999, Forsyth & Chrisholm 1977, Wilson 1989). Table 1 links by lithostratigraphy the different formations seen across the Midland Valley of Scotland. Contemporaneous volcanism, present as small dolerite intrusions and tuffs, and abundant palynomorphs also provide robust dating tools (Monaghan & Parrish 2005, Owens *et al.* 2005, Stephenson *et al.* 2004).

A multi-proxy analysis of the Tournaisian Ballagan Formation (from the Midland Valley of Scotland), including isotope, ostracod and palynological studies, provided evidence for hypersaline and brackish water conditions (Stephenson *et al.* 2002, 2004, Williams *et al.* 2005, 2006).

Material

The sections studied from the formations of Fife are correlated by using key marine horizons or non-marine limestone beds (Figure 1). Sandstone lithology is the most common in all the formations, comprising about 70% of the rock volume. Some formations have thick sandstone units, and those with a thickness greater than 20 m are shown on Figure 1. The important marine horizons, and all the limestones present are highlighted, to distinguish at a glance the character of the formations.

System	Subsystem	Series	Age (Ma)	Regional Stages (Western Europe)	Regional Substages (W. Europe)
CARBONIFEROUS	Pennsylvanian	Upper	299	Autunian (lower)	C B A Barruelian Cantabrian
				Stephanian	
		Middle		Westphalian	D Asturian
		Lower			C Bolsovian B Duckmantian A Langsettian
	Mississippian	Upper	318	Namurian (upper)	B
			326	Namurian (lower)	A Arnsbergian Pendleian
		Middle		Viséan	Brigantian
					Asbian
					Holkerian
					Arundian
		Lower	345	Tournaisian	Chadian Ivorian
					Hastarian
DEVONIAN	Upper		359	Famennian	
			385	Frasnian	

Yeadonian
Marsdenian
Kinderscoutian
Alportian
Chokierian

Midland Valley of Scotland Formations & Groups in Fife	
Pathhead Fm	Strathclyde Group
Sandy Craig Fm	
Pittenweem Fm	
Anstruther Fm	
Fife Ness Fm	
Clyde Sandstone Fm	Inverclyde Group
Ballagan Fm	
Kinneswood Fm	

Table 1. Stratigraphic chart of the late Devonian and Carboniferous, the key time periods of interest when ostracods were first colonising non-marine environments. This study focuses on the Mississippian Strathclyde Group Formations and the Inverclyde Group Ballagan Formation. The Carboniferous stratigraphy of western Europe is adapted from Heckel & Clayton (2006), the Midland Valley of Scotland lithostratigraphy is adapted from Browne *et al.* (1999). Dates are taken from the International Commission of Stratigraphy timescale 2004, rounded to the nearest million years.

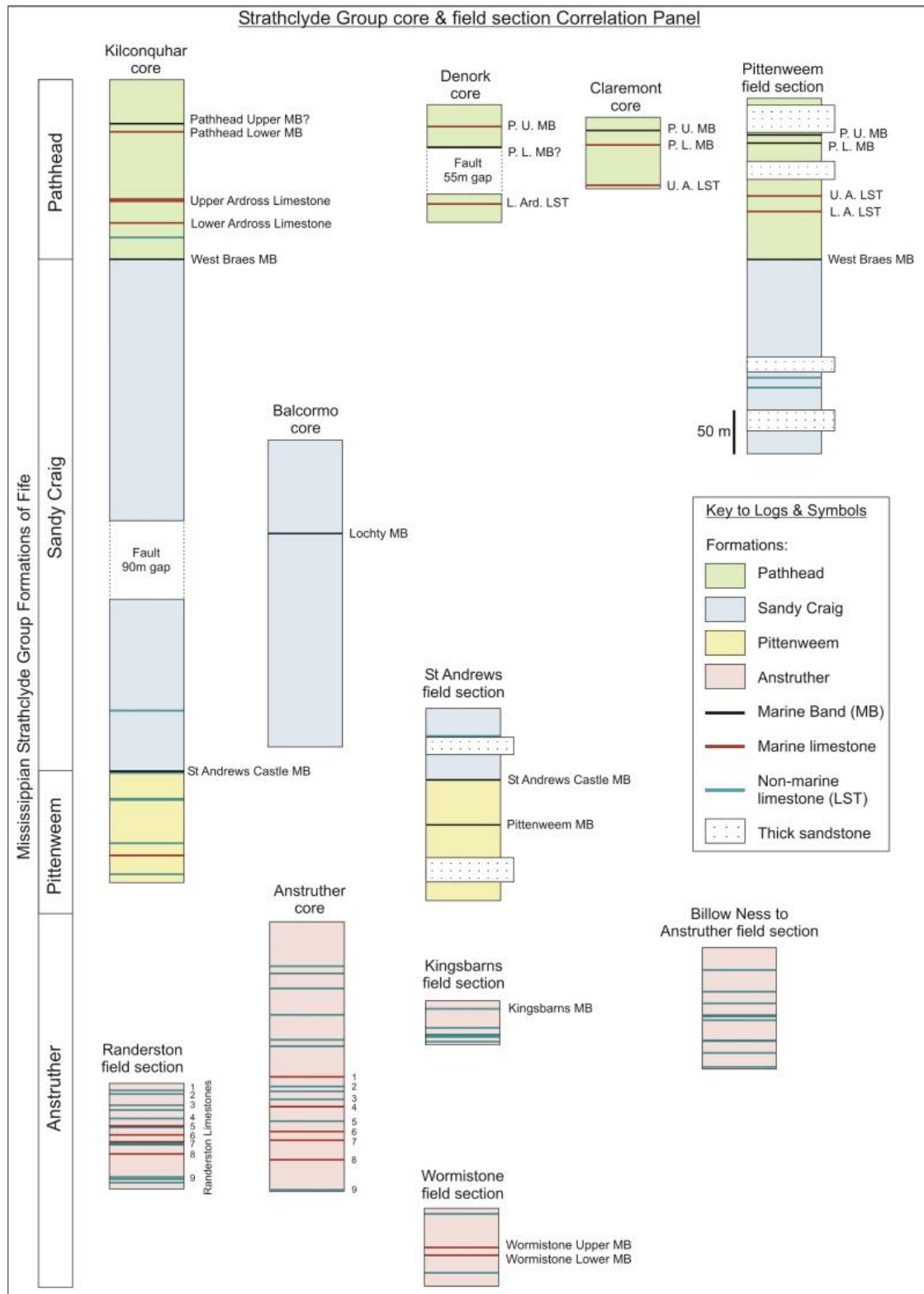


Figure 1. Borehole and field section correlation panel for the Strathclyde Group of Fife. The primary borehole and field section data comes from the British Geological Survey, but the correlation is part of this study. This figure is repeated in Chapter 4.

Carboniferous ostracods from the Strathclyde Group of Fife were obtained by field collection and from borehole samples. Survey boreholes were taken by the British Geological Survey (BGS) from 1964-1980, and core samples were taken during this time and stored at the BGS in Edinburgh (Figure 2). Sample numbers used relate to BGS numbered samples from these cores and sections. The Fife Ness Formation has not been studied, as it contains no ostracods or other fossils apart from “*Spirorbis*”. The formation only occurs as a field exposure, and its stratigraphical position and age are uncertain (Owens *et al.* 2005). A few samples from the Ballagan Formation of the Inverclyde Group were studied (Chapter 6), these were collected by the BGS from Ayrshire.

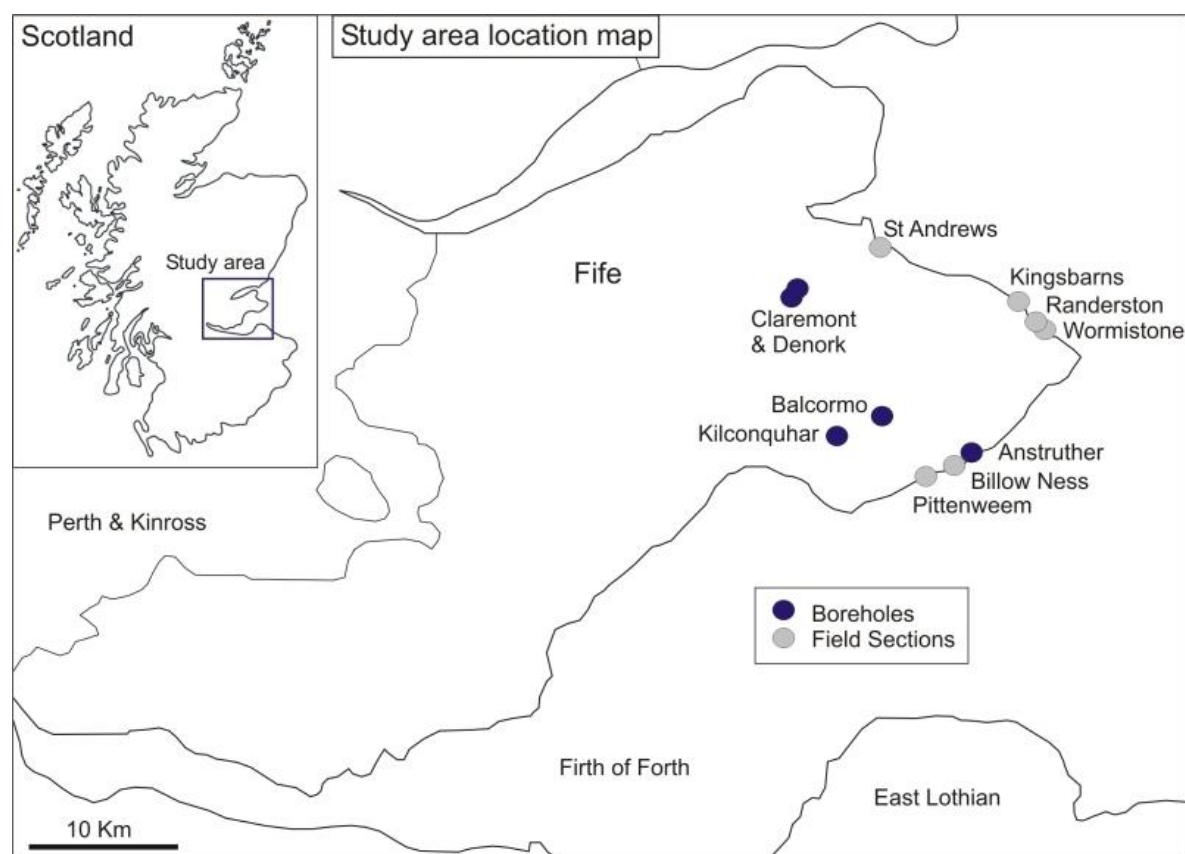


Figure 2. Location map of boreholes and field sections studied from the Strathclyde Group at Fife. BGS collection samples were taken from cores and some field sections by BGS workers from 1964-80. These samples were used in this study, with additional field samples were collected from 2005-2008.

Methodology

This is a summary of the methods employed in this study, with more detail relating to each in the relevant chapters:

- Mississippian sediments, macrofauna and ostracods were examined in hand specimen, core sample, and polished thin section. Ostracods and macrofossils were imaged by scanning electron microscopy and light microscopy, for taxonomic identification (Chapters 3 and 4).
- Palynological slides from processed samples were studied for palynofacies and algal content (Chapter 5).
- Recent ostracods were collected *in vivo* for comparison with Carboniferous specimens (Chapter 6).
- The diagenetic alteration to ostracod shell chemistry and ultrastructure was studied using light microscopy, cathodoluminescence, scanning electron microscopy and electron microprobe analysis (Chapter 6 and 7).
- The different diagenetic stages present in macrofossil and ostracod shells were examined in $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ analysis (chapter 7).

Thesis Summary

The thesis is structured so that each chapter (apart from chapter 1) can stand as an independent article for publication, or combine with a second chapter for publication. In this way figure numbering is separate for each chapter and certain important figures such as

the stratigraphic table have been reproduced. While targeted for journal publication, the chapters maintain the same formatting style.

A review of the state of knowledge of the first non-marine colonisation by ostracods is given in Chapter 2. This documents the current state of knowledge and interprets ostracod records in terms of freshwater, brackish and other non-marine environments. Chapter two is a shortened and revised version of a published article (Bennett 2008, published in *Senckenbergiana lethaea*), which is included as Appendix 1. Ostracod taxonomy from 25 ostracod species, including six new species, is presented in Chapter 3. This chapter will be combined with Chapter 4 for publication. The ostracod data are discussed in Chapter 4 in relation to the sediments and macrofauna, and brackish to freshwater palaeoenvironmental interpretations are presented. This chapter is targeted for publication in *Palaeontology* or *Geological Magazine*, while information on the algal limestones may be a small paper in the *Journal of Sedimentary Research*. An important proxy used to determine a freshwater depositional environment is algal palynomorphs. Chapter 5 describes algal palynomorphs interpreted as freshwater forms, typical palynofacies, and intriguing arthropod fragments, from samples containing non-marine ostracods and macrofossils. This chapter is targeted for publication in *Review of Palynology and Palaeobotany*.

Oxygen and carbon isotopes from fossil shells have been used to determine freshwater to marine environments. Prior to isotopic work the preservation of specimens is assessed. In Chapter 6 the carapace ultrastructure of Carboniferous ostracods is documented with reference to Recent ostracods. Carboniferous specimens preserve some structural elements of Recent specimens, despite diagenetic recrystallisation. Chapter 7 presents a new protocol for the assessment of diagenetic alteration of Carboniferous ostracods and macrofossils.

The diagenetic history is reflected in the isotope results, and any possible palaeoenvironmental interpretations are explored. Chapter 6 and 7 will be combined and targeted for publication in *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology*. The conclusions summarise the findings of the previous chapters and revisit questions as to the timing and nature of the non-marine colonisation of ostracods. An expanded version of this chapter is targeted for publication in *Palaios*, with a possible title: The colonisation of non-marine environments by ostracods: a multi-proxy approach.

Chapter 2: A review of the pioneer colonisation of non-marine environments by ostracods

Abstract

This review examines the nature and chronology of the transition of ostracods from marine to non-marine aquatic environments in the Devonian and Carboniferous. There is putative evidence of ostracods in brackish waters from the middle Silurian, but more robust evidence from the Devonian. The first putative freshwater ostracods are species of the genera *Carbonita* and *Geisina* which are found in the late Mississippian. The freshwater ostracods *Darwinula*, *Carbonita*, *Candona* and *Cypridopsis* are common in the Pennsylvanian Coal Measures. The first non-marine environments occupied by ostracods were near shoreline, influenced by marine transgressions. Adaptations needed to survive in freshwater or low salinities would include changes in osmoregulation and feeding and reproductive strategies, to enable opportunistic colonisation of temporary freshwater habitats such as seasonal pools.

Introduction

Ostracods are found today in a diverse range of aquatic environments, from freshwater ephemeral pools to deep marine waters and damp terrestrial habitats (Horne 2003) and have occupied a range of environments throughout their history (Table 1). The first true ostracods occurred in the early Ordovician, and lived in shallow marine environments (Tinn & Meidla 2004, Williams *et al.* 2008), radiating into pelagic environments by the middle Silurian (Siveter 1984, Siveter *et al.* 1991, Vannier & Abe 1992, Perrier *et al.* 2007). Carboniferous ostracods occupied a wide range of environments, from non-marine and

near-shore facies to deep marine (Bless 1983). Ostracods occur in freshwater environments by the middle Carboniferous (Pollard 1966, Sohn 1985).

The ecological radiation of Palaeozoic Ostracoda	
Permian	Carbonitoidea and most Palaeocopida extinct end Permian (9)
Carboniferous	Freshwater ostracods common in Pennsylvanian Coal-Measures e.g. <i>Carbonita</i> and <i>Darwinula</i> (8) Putative freshwater and common brackish water ostracods in the Mississippian e.g. <i>Geisina</i> (7)
Devonian	Leperditicopids in brackish water, extinct at end Devonian (6) Marginal marine ostracods e.g. <i>Sansabella</i> , <i>Cavellina</i> (5)
Silurian	Putative evidence for brackish ostracods (4) Myodocopes colonise the pelagic realm (3)
Ordovician	Leperditicopids in shallow marine and hypersaline waters (2) Palaeocopes characterise shallow marine benthic environments (1)

Table 1. The ecological radiation of Palaeozoic Ostracoda. References: 1: Tinn & Meidla 2004; 2: Berdan 1984; 3: Siveter *et al.* 1991, Perrier *et al.* 2007; 4: Clarkson *et al.* 1998; 5: Bless 1983; 6: Friedman & Lundin 1998; 7: Bless 1983; 8: Bless & Pollard 1973, Schäfer 2007; 9: Horne 2003.

Ostracods that inhabit terrestrial and freshwaters today are the podocopid superfamilies Darwinuloidea, Cypridoidea and Cytheroidea (Horne 2003). Figure 1 provides the

taxonomic classification scheme used for Recent and Palaeozoic ostracods described on referred to in this study. The Cypridoidea are the dominant freshwater ostracods today, and it is possible that they had a late Palaeozoic origin, as has been suggested for the terrestrial Terrestrialcytheroidea (Horne *et al.* 2004). Other groups of arthropods made the first moves from a marine to freshwater transition during the Ordovician-Silurian (Park & Gierlowski-Kordesch 2007). Evolutionary studies using genetic date hypothesise that in theory ostracods could have first inhabited terrestrial and aquatic non-marine environments in the early Ordovician (Newman 2005), but there is no fossil evidence to support this, and most other groups did not colonise non-marine aquatic settings until the Silurian-Devonian (Park & Gierlowski-Kordesch 2007).

Lateral valve outline, hingement, muscle scars and surface ornamentation are used to classify Carboniferous freshwater ostracods. These criteria were used, for example, to distinguish between the Pennsylvanian freshwater ostracods *Carbonita*, *Whipplella* and *Gutschickia* (Sohn 1977, 1985). Detailed muscle scars are often not preserved, leading to problems in identification. Critically, the discovery of myodocopid soft part anatomy in palaecope-like carapaces from the Silurian (Siveter *et al.* 2003, 2007, Siveter 2008), demonstrates that caution is needed in Palaeozoic ostracod taxonomy.

This study reviews the evidence for the timing and nature of the colonisation of non-marine environments by ostracods, and the physiological adaptations they would need. Here, non-marine refers to the complete range of salinities lower than that of ‘normal marine’. The different proxies used to interpret non-marine palaeoenvironments are assessed. The strongest evidence of ostracods adapting to reduced salinities is from the late Devonian and early Carboniferous.

Order PODOCOPIDA Müller, 1894	Family CYTHERELLIDAE Sars, 1866
Suborder PODOCOPINA Sars, 1866	Genus <i>Cytherella</i> Jones, 1849
Superfamily BAIRDIOIDEA Sars 1887	Family GEISINIDAE Sohn, 1961
Family BAIRDIIDAE Sars 1887	Genus <i>Geisina</i> Johnson, 1936
Genus <i>Acratia</i> Delo, 1930	<i>Knoxiella</i> Egorov, 1950
<i>Acutiangulata</i> Buschmina, 1968	<i>Jonesina</i> Ulrich & Bassler, 1908
<i>Bairdia</i> McCoy, 1844	<i>Limnoprimitia</i> Kummerow, 1949
<i>Bairdiacypris</i> Bradfield, 1935	?Superfamily KLOEDENELLOIDEA Ulrich & Bassler, 1908
<i>Bairdiolites</i> Croneis & Gale, 1939	Family UNCERTAIN
Superfamily BAIRDIOCYPRIDOIDEA Shaver in Moore, 1961	Genus <i>Glyptolichvinella</i> Posner in Gurevich, 1966
Family BAIRDIOCYPRIDIDAE Shaver in Moore, 1961	Order LEIOCOPA Schallreuter, 1973
Genus <i>Bairdiocypris</i> Kegel, 1932	Suborder PARAPARCHITICOPINA Gramm, 1975
<i>Silenites</i> Coryell & Booth, 1933	Superfamily PARAPARCHITOIDEA Scott, 1959
Superfamily CARBONITOIDEA Sohn, 1985	Family PARAPARCHITIDAE Scott, 1959
Family CARBONITIDAE Sohn, 1985	Genus <i>Chamishaella</i> Sohn, 1971
Genus <i>Carbonita</i> Strand, 1928	<i>Paraparchites</i> Ulrich & Bassler, 1906
<i>Gutschickia</i> Scott, 1944	<i>Shemonaella</i> Sohn, 1971
<i>Pruvostina</i> Scott & Summerson, 1943	<i>Shishaella</i> Sohn, 1971
Superfamily CYPROIDEA Sylvester-Bradley, 1949	<i>Shivaella</i> Sohn, 1971
Family CYPRIDAE Baird, 1845	Order PALAEOCOPIDA Henningsmoen, 1953
Genus <i>Bythocypris</i> Brady, 1880	Suborder PALAEOCOPINA Henningsmoen, 1953
Superfamily DARWINULOIDEA Brady & Norman, 1889	Superfamily HOLLINOIDEA Swartz, 1936
Family DARWINULIDAE Brady & Norman, 1889	Family HOLLINIDAE Swartz, 1936
Genus <i>Darwinula</i> Brady & Robertson, 1885	Genus <i>Gortanella</i> Ruggieri, 1966
Family SUCHONEILIDAE Mischina, 1972	Family HOLLINELLIDAE Bless & Jordan, 1971
Genus <i>Suchonella</i> Spizharsky, 1937	Genus <i>Hollinella</i> Coryell, 1928
<i>Whipplella</i> Holland, 1934	Superfamily KIRKBYOIDEA Ulrich & Bassler, 1906
Suborder SIGILLIOPINA Martens, 1992	Family AMPHISSITIDAE Knight, 1928
Superfamily SIGILLIOIDEA Mandelstam, 1960	Genus <i>Amphissites</i> Girty, 1910
Suborder CYPRIDOCOPINA Jones, 1901	Family KIRKBYIDAE Ulrich & Bassler, 1906
Superfamily CYPRIDOIDEA Baird, 1845	Genus <i>Kirkbya</i> Jones, 1859
Family CANDONIDAE Kaufman, 1900	?Superfamily KNOXITOIDEA Egorov, 1950
Genus <i>Candona</i> Baird, 1845	Family GLYPTOPLEURIDAE Girty, 1910
<i>Candonopsis</i> Vávra, 1891	Genus <i>Glyptopleura</i> Girty, 1910
<i>Fabaeformiscandona</i> Kristic, 1972	Family SANSABELLIDAE Sohn in Moore, 1961
<i>Pseudocandona</i> Kaufmann, 1900	Genus <i>Sansabella</i> Roundy, 1926
Family CYPRIDIDAE Baird, 1845	Superfamily PRIMITIOPSIDAE Swartz, 1936
Genus <i>Bradleystrandesia</i> Broodbakker, 1983	Family PRIMITIOPSIDAE Swartz, 1936
<i>Cypridopsis</i> Brady, 1868	Genus <i>Coryellina</i> Bradfield, 1935
<i>Eucypris</i> Vávra, 1891	Superfamily BEYRICHOIDEA Matthew, 1886
Suborder CYTHEROCOPINA Baird, 1850	Family BEYRICHIIDAE Matthew, 1886
Superfamily CYTHEROIDEA Baird, 1850	Genus <i>Beyrichia</i> M'Coy, 1846
Family BYTHOCYTHERIDAE Sars, 1926	<i>Copelandella</i> Bless & Jordan, 1971
Genus <i>Monoceratina</i> Roth, 1928	Superfamily UNCERTAIN
Family CYTHERIDAE Baird, 1850	Family UNCERTAIN
Genus <i>Cythere</i> Müller, 1785	Palaeocene spp. A-D
Family CYTHERIDEIDAE Sars, 1925	Suborder UNCERTAIN
Genus <i>Cyprideis</i> Jones, 1857	Superfamily UNCERTAIN
Family HEMICYTHERIDAE Puri, 1953	Family UNCERTAIN
Genus <i>Aurila</i> Pokorný, 1955	Genus <i>Sargentina</i> Coryell & Johnson, 1939
<i>Hemicythere</i> Sars, 1925	Order MYODOCOPIDA Sars, 1866
Suborder METACOPINA Sylvester-Bradley, 1961	Suborder MYODOCOPINA Sars, 1866
Superfamily HEALDIOIDEA Harlton, 1933	Superfamily UNKNOWN
Family HEALDIIDAE Harlton, 1933	Family BOLBOZOIDAE Boucek, 1936
Genus <i>Criboconcha</i> Cooper, 1941	Genus <i>Entomozoe</i> P?ibyl, 1950
<i>Healdia</i> Roundy, 1926	<i>Maternella</i> Rabien, 1954
<i>Pseudobythocypris</i> Shaver, 1958	Suborder CLADOCOPINA Sars, 1866
<i>Seminolites</i> Coryell, 1928	Superfamily unknown
<i>Velatomorpha</i> Tibert & Dewey, 2006	Family POLYCOPIDAE Sars, 1866
<i>Waylandella</i> Coryell & Billings, 1932	Genus <i>Polycope</i> Sars, 1866
Superfamily BAIRDIOCYPRIDOIDEA Shaver, 1961	Order LEPERDITICOPIDA Scott, 1961
Family BAIRDIOCYPRIDIDAE Shaver, 1961	Suborder UNCERTAIN
Genus <i>Pseudobythocypris</i> Shaver, 1958	Superfamily UNCERTAIN
Suborder PLATYCOPINA Sars, 1866	Family LEPERDITIIDAE Jones, 1856
Superfamily KLOEDENELLOIDEA Ulrich & Bassler, 1908	Genus <i>Hermannina</i> Kegel, 1933
Family BEYRICHIOPSIDAE Henningsmoen, 1965	<i>Leperditia</i> Rouault, 1851
Genus <i>Beyrichiopsis</i> Jones & Kirkby, 1886	
Family CAVELLINIDAE Egorov, 1950	
Genus <i>Cavellina</i> Coryell, 1928	
<i>Sulcella</i> Coryell & Sample 1932	

Figure 1. Taxonomic scheme for the ostracods which feature in this study. The higher taxonomy is a combination of the schemes of Horne *et al.* (2002) for Recent ostracods, and Whatley *et al.* (1993) for Palaeozoic ostracods. Exceptions are: the Superfamily Carbonitoidea (see Sohn 1985), and the Family Geisinidae (see Dewey & Fåhraeus 1987).

Determining palaeoenvironments containing ostracods

Common Carboniferous genera occupy a range of environments (Table 2). The criteria used to distinguish non-marine ostracods include comparisons with Recent ostracods and data from sedimentology, associated fossils and geochemistry. The most comprehensive studies of palaeoenvironment use a multiproxy approach (for example Schultze *et al.* 1994, Tibert & Scott 1999, Williams *et al.* 2006).

Taxonomic uniformitarianism: Some Carboniferous ostracods interpreted as freshwater such as *Darwinula*, *Candona* and *Cypridopsis* have been identified as the same genera as living freshwater Podocopida. However, as no soft part evidence exists, only the details of muscle scars in Carboniferous specimens, which are comparable to Recent ostracods with *Darwinula*, but are uncertain for the Cypridoidea (Horne *et al.* 2002, Sohn 1977). The evidence for the true Cypridoideans (*Candona* and *Cypridopsis*) in the Carboniferous is in debate: Swain (1976) and Lethiers & Damotte (1993) argue for a late Palaeozoic origin for the Cypridoidea, which Whatley & Ballent (1996) and Horne (2003) place the likely origin of the Cypridoidea in the Mesozoic. *Carbonita* have no extant relatives, but they have been compared to Recent podocopes such as *Cypridopsis* (Neale 1984). However, as with fossil darwinulids this is unconfirmed by soft part evidence and therefore the origins and affinities of the Carbonitoidea and the Darwinuloidea are still debated (Horne 2003: see *Carbonita* discussion in Chapter 3).

The principle of taxonomic and hence ecological uniformitarianism can only be applied to Palaeozoic ostracods only with caution. For example *Darwinula* in the Pennsylvanian Hamilton Konservat-Lagerstätte is described as a freshwater genus, without any discussion

of fossils and Recent comparisons (Schultze *et al.* 1993). An example of ecological uniformitarianism from within the Carboniferous is when *Carbonita* from Pennsylvanian freshwater sediments (Pollard 1966, 1969) is considered indicative of freshwater when it occurs in the Mississippian (Pollard 1985). However, *Carbonita* is found in marginal marine sediments of the early Mississippian, so may have been euryhaline (Tibert & Scott 1999). It is clear that ecological uniformitarianism is an unreliable form of evidence, considering the lack of taxonomic certainty (no soft part evidence) and ecological variability of Carboniferous ostracods and their supposed living relatives.

The environmental range of common Carboniferous ostracods				
Deep marine	Shallow marine	Marginal & Brackish	Freshwater	Hypersaline
Bairdiaceans Tricornids Entomozoaceans	<i>Acratia</i> <i>Amphissites</i> <i>Bairdia</i> <i>Bairdiacypris</i> <i>Basslerella</i> <i>Coryellina</i> <i>Cribroconcha</i> <i>Geffenina</i> <i>Healdia</i> <i>Hollinella</i> <i>Jonesina</i> <i>Kirkbya</i> <i>Monoceratina</i> <i>Polycope</i> <i>Shishaella</i> <i>Shivaella</i> <i>Youngiella</i>	<i>Beyrichiopsis</i> <i>Bythocypris</i> <i>Cavellina</i> <i>Chamishaella</i> <i>Geisina</i> <i>Glyptolichvinella</i> <i>Glyptopleura</i> <i>Knoxella</i> <i>Paraparchites</i> <i>Sansabella</i> <i>Shemonaella</i> <i>Silenites</i> <i>Sulcella</i>	Mississippian: <i>Carbonita</i> <i>Geisina</i> <i>Velatomorpha</i> Pennsylvanian: <i>Candona</i> <i>Carbonita</i> “ <i>Cypridina</i> ” <i>Cypridopsis</i> <i>Darwinula</i> <i>Gutschickia</i> <i>Hilboldtina</i> <i>Pruvostina</i> <i>Suchonella</i> <i>Whipplella</i>	<i>Beyrichiopsis</i> <i>Paraparchites</i> <i>Shemonaella</i>

Table 2. Common Carboniferous ostracod genera, grouped according to their environment, as sourced from: Becker *et al.* 1990, Benson 1955, Bless 1983, Bless *et al.* 1988, Buschmina 1959, Coen 1989, Cooper 1946, Crasquin 1985, Dewey 1987, 1988, 1989, 1992, Dewey *et al.* 1990, Dewey & Puckett 1993, Kummerow 1949, Pollard 1966, 1969, 1985, Přibyl 1960, Schäfer 2007, Schultze *et al.* 1994, Scott 1944, Scott & Summerson 1943, Sohn 1977, 1985, Tibert & Scott 1999, Vannier *et al.* 2003, Williams *et al.* 2005c, 2006. Freshwater taxa endemic to North America are *Gutschickia*, *Hilboldtina*, *Pruvostina*, *Whipplella* and *Suchonella*.

Palaeoecology: It is well documented that in living and fossil faunas restricted marine and brackish ostracods have relatively low diversity and high abundance compared to marine assemblages (see, for example, Keen 1977, Whatley 1983, Siveter 1984, Carbonel 1988). The occurrence of low diversity, high abundance ostracod faunas has been used to interpret stressed environmental conditions such as low salinity (Pollard 1985) and hypersalinity (Dewey 1987) in the Mississippian. The abundance of typically stenohaline ostracods such as bairdioideans can be informative, as in open marine conditions they often constitute up to 50% of the individuals in an assemblage (Lethiers 1981, Bless 1983, Bless *et al.* 1988).

Macrofossils: Many groups of macrofossils are good palaeoenvironmental indicators. Certain taxa are characteristic of brackish or freshwater salinities, such as the bivalves *Naiadites*, *Carbonicola* and *Anthraconaia*, from the Pennsylvanian Coal Measures of North America and Britain (Clift & Trueman 1929, Scott & Summerson 1943, Pollard 1966, Brand 1996). Spirorbiform microconchids (“*Spirorbis*”) occur in a range of non-marine environments (Taylor & Vinn 2006). However, the typical salinity range of many Carboniferous macrofossils is unknown or equivocal. For example, a fauna containing fish, spirorbids, myalinid bivalves and abundant plant matter can be interpreted as brackish or shallow marine (Pollard 1985).

Sedimentology: Hypersaline environments can be identified by the presence of evaporitic sediments such as gypsum; these environments could contain ostracods (Dewey 1987). A combination of sedimentology and fossil evidence is the most robust means for determining palaeoenvironment. In the Hamilton Konservat-Lagerstätte of Kansas (Schultze *et al.* 1994), freshwater conditions were deduced by the presence of a fluvial palaeochannel containing terrestrial flora, *Anthraconaia*, *Carbonita* and *Darwinula*.

A multi-proxy approach: Mississippian (Tournaisian) sediments from the Ballagan Formation, Midland Valley of Scotland contain multiple potential proxies (sedimentology, palynology and ostracods) that are used to deduce brackish to hypersaline palaeoenvironments (Stephenson *et al.* 2002, Williams *et al.* 2005c, 2006). The sediments contain desiccation cracks and evaporites, suggesting conditions of fluctuating salinity. Certain algal palynomorphs such as *Botryococcus* ssp. are known from brackish to freshwater conditions (Stephenson *et al.* 2004). Ostracods form low diversity assemblages, and lack typical marine species. Ostracod and mollusc shells gave a range of -3‰ to -11‰ $\delta^{18}\text{O}_{\text{VPDB}}$, interpreted as marine to more freshwater end members respectively, including a significant diagenetic overprint (Williams *et al.* 2006). This is a rare example of geochemical work on Palaeozoic ostracods (the other case being from the Ordovician: Brenchley *et al.* 2003).

The timing of non-marine colonisation by ostracods

Hypersaline waters

The Leperditicopida, a putative ostracod group (Whatley *et al.* 1993), for which no soft parts are known, occur from the Ordovician to Devonian. They are found in hypersaline waters in the Ordovician (Berdan 1984, Williams & Siveter 1996), and brackish to freshwater in the Devonian (Friedman & Lundin 1998, Knox & Gordon 1999). They commonly occur in low diversity communities, frequently associated with stromatolitic limestones (Siveter 1984, Vannier *et al.* 2001, Warshauer & Smosna 1977).

Paraparchitoidean ostracods are common in Carboniferous marine environments, and they dominate in early Carboniferous hypersaline sediments, as seen in examples from Canada

(Dewey 1983, 1987, 1988) and Scotland (Williams *et al.* 2006). They commonly occur as low diversity, high abundance assemblages, with evidence of opportunistic reproduction strategies such as supposed progenesis and parthenogenesis (Dewey 1987).

Brackish waters

The middle Silurian Straiton Grits Formation of south west Scotland contains beyrichioidean palaeocopes thought to be deposited in a brackish, coastal lagoon (Clarkson *et al.* 1998, Floyd & Williams 2003). This is the oldest putative occurrence of ostracods in reduced salinities.

The Pennsylvanian and early Devonian of Belgium contains possible brackish water ostracods (Bless 1983, Bless *et al.* 1988). The early Devonian sediments are interpreted as deltaic or brackish based on the sediments and fauna, as is another early record of brackish water ostracods (Rebske *et al.* 1985). In the Rebske (*et al.* 1985) study the ostracods *Euprimites? koeppeni* (a palaeocope) and *Rebskeella waxweilerensis* (affinity unknown), are associated with abundant plant fragments, miospores, *Modiolopsis* and the leperditicope *Hermannina*.

Carbonita is first recorded from the middle Devonian Dushan Formation of Kueichow, China (Shi 1964). This record is questionable; *Carbonita* is figured poorly and listed with common marine ostracods without details of the sediments or macrofauna to allow an environmental interpretation. This is also the case for some Mississippian records which include *Carbonita* with a list of marine ostracods (for example Buschmina 1965, Samoilova & Smirnova 1960).

The earliest record of *Carbonita* with information about macrofossils and sediments that indicates a brackish setting is from the Mississippian (Tournaisian) of Nova Scotia (Tibert & Scott 1999). It occurs with *Bairdiacypris*, *Shemonaella* and *Copelandella* in a range of environments from near-shore marine to low salinity coastal ponds. Tournaisian ostracods interpreted as marginal marine to brackish water tolerant (from the Ballagan Formation) include species of *Bythocypris*, *Cavellina*, *Glyptolichvinella*, *Sansabella* and *Sulcella* (Williams *et al.* 2005c, 2006). The Mississippian of Britain contains *Shemonaella scotoburdigalensis*, *Cavellina* and possibly *Carbonita*, interpreted to be from a brackish setting (Pollard 1985). The earliest documentation of freshwater ostracods (*Shemonaella scotoburdigalensis*) is from the Mississippian Burdiehouse Limestone of Scotland (Hibbert 1834). However, the fauna of *Shemonaella*, “*Spirorbis*”, coprolites and fish is also found in supposed brackish environments. Paraparchitoidean, platycope and bairdioidean ostracods occur in reportedly brackish settings from the Mississippian of the Maritimes Basin of Canada (Dewey 1983, 1989). Supporting evidence for brackish conditions from the macrofauna and sediments is somewhat limited.

Freshwaters

The first arthropods taxonomically ‘close’ to ostracods that have been flagged as possibly freshwater are leperditicopes. The genus *Isochilina* is recorded from lake and floodplain deposits from the Devonian Wood Bay Formation of Spitzbergen, associated with charophyte algae (Friend & Moody-Stuart 1970). Devonian leperditicopes of the Catskill Mountains, New York State, were interpreted to be from a brackish to freshwater environment (Friedman & Lundin 1998, Knox & Gordon 1999). Sediments interpreted as

freshwater are fluvial sandstones, with abundant plant and fish debris and the bivalve *Archandon catskillensis*.

The Devonian to Carboniferous boundary sediments of South China have the earliest record of putative freshwater supposed ostracods; *Leperditia* and *Gutschickia*? were used to signal a lagoonal and a freshwater environment respectively (Coen 1989). *Gutschickia*? may have been misidentified (based on the muscle scar pattern compared with that in Sohn 1977), and these ostracods are associated with stenohaline to marginal marine ostracod species. It is considered that in this case a brackish to marginal marine environment is more likely than freshwater.

Supposed freshwater ostracods, including *Carbonita*, *Darwinula*, *Gutschickia*, *Pruvostina* and *Whipplella*, are described from the late Mississippian of Virginia (Sohn 1985), in carbonaceous shales above a rooted clay, at the base of a marine transgression. Ideally, more sedimentological and macrofossil data are needed to confirm a fully freshwater setting. The Pennsylvanian Joggins Formation of Nova Scotia contains *Carbonita* associated with well-documented sediments and macrofauna. The ostracods are interpreted to be from a freshwater to brackish palaeoenvironment (Falcon-Lang *et al.* 2006, Tibert & Dewey 2006).

The Pennsylvanian Coal Measures contain the majority of Carboniferous freshwater ostracods, and were a key environment for non-marine colonisation. The Coal Measures of Northern England contain *Geisina arcuata* and species of *Carbonita* (Pollard 1966, 1969, Anderson 1970, Bless & Pollard 1973). *Carbonita* is numerically dominant over *Geisina* from the Lower to Upper Coal Measures, and this reflects an increasing freshwater

influence through time. *Carbonita* and *Geisina* are also more common in the Pennsylvanian than the Mississippian (Robinson 1978). Ostracods from the Coal Measures of North America, Europe and Russia include species of *Candona*, *Carbonita*, “*Cypridina*”, *Cypridopsis*, *Darwinula*, *Gutschickia*, *Hilboldtina*, *Pruvostina*, *Whipplella* and *Suchonella* (Scott & Summerson 1943, Scott 1944, Cooper 1946, Kummerow 1949, Buschmina 1959, Přibyl 1960, Sohn 1977, Schäfer 2007; see Table 2).

The first record of ostracods from an unequivocally freshwater setting is *Carbonita* in the Montecieu Lagerstätte (Pennsylvanian) of France (Vannier *et al.* 2003). The ostracods are associated with spinicaudant arthropods, interpreted from Recent and fossil deposits as a freshwater group. The Montecieu ostracods may have lived in an ephemeral freshwater pond in an intramountain basin, with no marine influence, in contrast to some of the Coal Measures, which have rare marine horizons.

Integrity of the fossil record of non-marine ostracods

The majority of the published fossil evidence for Carboniferous non-marine ostracods comes from North America, Canada and Western Europe, with fewer records from China and Russia (Figure 2). The data reflect ‘collections biases’ rather than an original palaeogeographic signal. This can be verified by the fact that similar marginal marine assemblages are found from Europe, Russia, North America, Canada and Africa (Bless 1983, Bless & Massa 1982). More fossil discoveries could provide evidence for the origin of freshwater ostracods in the Mississippian, and more brackish or even freshwater evidence from the late Devonian.

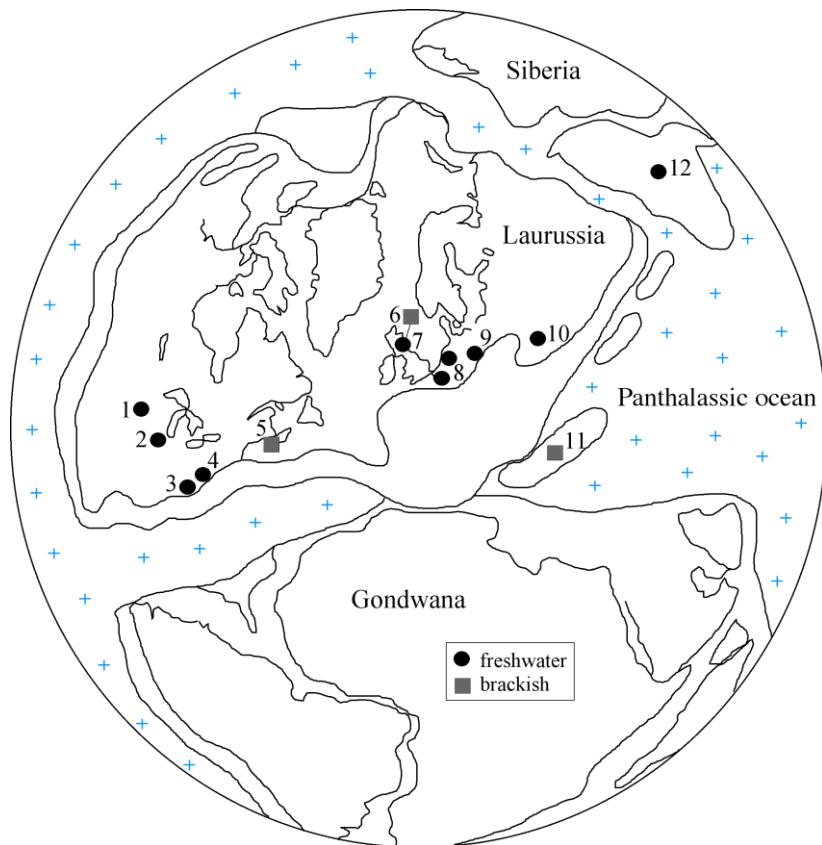


Figure 2. Distribution of Carboniferous non-marine ostracods (reconstruction of the Mississippian at 335Ma, modified from Ziegler 1989). Records that include typically non-marine genera, for example *Darwinula*, but which do not give an environmental interpretation are not included. Sources: 1: Kansas, USA: Schultze *et al.* 1994. 2: Illinois, USA: Cooper 1946. 3: Virginia, USA: Sohn 1985. 4: Southern Appalachian Coal Field, USA: Scott & Summerson 1943. 5: Nova Scotia, Canada: Tibert & Scott 1999, Dewey 1987, 1989. 6: Midland Valley of Scotland: this study, Williams *et al.* 2006. Berwickshire, Scotland: Pollard 1985. 7: Northern England: Bless & Pollard 1973, Pollard 1966, 1969. 8: Limburg, the Netherlands: Bless & Pollard 1973. Brabant Massif, Belgium: Bless 1983, Bless *et al.* 1988. Central France: Vannier *et al.* 2003. 9: South West Germany: Schäfer 2007, Ruhr region, Germany: Kummerow 1949. 10: Czech Republic: Přibyl 1960. 11: South China: Coen 1989. 12: central Kazakhstan Buschmina 1959.

Adaptations for life in non-marine environments

All the faunal groups in Palaeozoic lakes can be traced to marine origins, with estuaries acting as the main freshwater colonisation pathway (Park & Gierlowski-Kordesch 2007).

The first non-marine environments occupied by ostracods were near shoreline, and

influenced by marine transgressions (for example Schultze *et al.* 1994, Tibert & Scott 1999). The first non-marine colonisers are likely to have been euryhaline, reflecting the changeable nature of the environment. Osmoregulation is used to regulate salinity change, by gaseous exchange through the integumental circulatory system in the inner lamella (Aladin & Potts 1996, Vannier & Abe 1995). Some living ostracods such as *Cyprideis torosa* can survive in salinities of 1 to 40‰ NaCl (Aladin & Potts 1996). It has been suggested that the thick-shelled Leperditicopida may have used their larger size to cope with osmotic pressures, and their integumental circulatory system may have aided their survival in eurytopic settings (Vannier & Abe 1995, Vannier *et al.* 2001). The paraparchitoideans are the dominant group in hypersaline waters, and this adaptation may have been facilitated by a similar morphology to the Leperditicopida (their thick shells and relatively large size), thus aiding osmoregulation.

The survival of the podocope *Carbonita* over the platycope *Geisina* into the Permian may have been dictated by their feeding strategies. In the Pennsylvanian Coal Measures of northern England, *Geisina* and *Carbonita* occur in different facies (Pollard 1966). *Geisina* has been interpreted as a filter feeder, while *Carbonita* may have been a deposit feeder like the Recent *Cypridopsis* (Neale 1984, Pollard 1966). *Carbonita* was probably better adapted to freshwaters than *Geisina*, as it has a greater diversity and adapted to a wider range of sedimentary niches (Bless & Pollard 1973).

Reproductive strategies are very important to the survival of ostracods in harsh environments. The paraparchitidae show evidence of opportunistic reproduction strategies in the Carboniferous such as supposed progenesis and parthenogenesis, to survive hypersaline conditions (Dewey 1987). The strategy of producing resting eggs resistant to

desiccation and transport, as seen in the spinicaudant arthropods, may also have been used by the first freshwater ostracods, as suggested by their co-occurrence in the temporary pond environment of the Monteceau Lagerstätte (Vannier *et al.* 2003). The Cretaceous of Brazil has produced possible ostracod eggs (Smith 1999), but the only confirmed fossil ostracod eggs are from the Silurian (Siveter *et al.* 2007). The occurrence of desiccation resistant eggs would enable the survival of ostracods that lived in ephemeral water bodies such as seasonal freshwater lakes and this adaptation had been proposed for the Cypridoidea (Lethiers & Damotte 1993). The brooding of the juvenile instars inside the carapace may have been a useful adaptation, for example in waters with a low calcium content. Brooded juveniles were discovered in a Silurian myodocope (Siveter *et al.* 2007), and Recent freshwater *Darwinula* also have this adaptation (Van Doninck *et al.* 2003).

Two possible environmental pathways that ostracods could take in order to colonise freshwaters are: 1, active invasion from the sea by euryhaline ostracods; 2, passive invasion from the sea by the restriction of ostracods to isolated habitats (see Gray 1988). A driving force for active invasion may have been the abundance of land plants, which multiplied in diversity and abundance in the Carboniferous (Bateman *et al.* 1998). This is a unique feature of the late Devonian and Mississippian, and provided a nutrient rich terrestrial habitat in non-marine waters. Mississippian sediments across the globe show fluctuating sea levels due to glacial episodes (Fielding *et al.* 2008), which could result in environmental scenarios which would aid freshwater colonisation. For example, passive invasion could occur in coastal areas that were first subtidal, then rapidly exposed by falling sea levels, creating stranded saline water bodies that would freshen over time. Active invasion may have occurred if ostracods migrated up estuaries and into coastal lakes

or rivers at times of high sea level. Non-aquatic means of passive invasion have been proposed, such as transport of ostracods or desiccation resistant ostracod eggs on the body of tetrapods, or blown by humid winds (Lethiers & Damotte 1993).

Conclusions

- The ecological radiation of ostracods from marine to non-marine waters is an important step in their evolutionary history. Ostracods were adapted to brackish conditions from the Devonian onwards. The leperditicopid arthropods (putative ostracods) were adapted to a wide range of non-marine environments, including freshwater in the Devonian.
- The first undoubted ostracods found in freshwater environments occur in the late Mississippian, and consist solely of species of *Carbonita* and *Geisina*. A more diverse freshwater fauna including *Darwinula* occurs in the Pennsylvanian.
- In review of the existing records, it is clear that there is a gap in the data of Mississippian non-marine ostracods, with most of the records occurring in Western Europe, North America and Canada, which represents a collections bias.
- The recognition of palaeoenvironments of a non-marine nature requires a multi-proxy approach, incorporating data from ostracod and associated faunas, sedimentology, geochemistry and palynology.
- The first non-marine environments were probably influenced by marine waters. Ostracods adapted to euryhaline conditions through changes in osmoregulation and reproductive strategies such as parthenogenesis, as a survival strategy.

Chapter 3: The Taxonomy of the ostracods of the Strathclyde Group

Twentyfive ostracod species are described from the Strathclyde Group of Fife, four of which are new species. The ostracods are from the families Bairdiidae, Bairdiocyprididae, Carbonitidae, Cavellinidae, Geisinidae, Healdiidae, Holliniellidae, Paraparchitidae, Polycopidae, and palaeocopes of unknown affinity.

The dimensions given are the average size of adult carapaces, unless stated otherwise. The dimensions do not include large spines that project from the carapace. The stratigraphic distribution and ostracod associates of the taxa described are also noted. Stratigraphic terms are noted in Table 1 of Chapter 1. The occurrence relative to sediment types and macrofossils is discussed in Chapter 4.

Order PODOCOPIDA Müller, 1894

Suborder PODOCOPINA Sars, 1866

Superfamily BAIRDIOIDEA Sars, 1887

Family BAIRDIIDAE Sars, 1887

Genus ACRATIA Delo, 1930

Type species: *Acratia typical* Delo, 1930

Diagnosis: See Delo, 1930, p.174-175.

Acratia sp. A.

Plate 2, fig. L

Material: One specimen, sample EN 4818 (juvenile, single valve, partly broken).

Dimensions: Length 324 µm, height 135 µm.

Description: Valve elongate in lateral outline, length approximately three times the height. Dorsal margin curved, ventral margin straight, anterior and posterior margins curved. Surface smooth.

Discussion: Similar lateral outline to *Acratia acuta* (Jones & Kirkby 1895).

Distribution: Pathhead Formation; Claremont core, below the Pathhead Upper Marine Band, associated with *Cavellina valida*, *Geisina arcuata*, *Shemonaella siveteri* n. sp. and *Shemonaella ornata* n. sp.

Acratia is recorded from the Mississippian of the Maritimes Basin, Canada (Dewey & Fåhræus 1987), Alabama, USA (Dewey 1992) and Poland (Olempska 1993).

Genus ACUTIANGULATA Buschmina, 1968

Type species: *Acutiangulata acutiangulata* Buschmina, 1968

Diagnosis: carapace subelongate and ventroposterior margin squared in lateral view.

Acutiangulata sp. A.

Plate 1, figs A, D

Material: One specimen, sample EN 4885 (juvenile, carapace).

Dimensions: length 450 µm, height 265 µm, width 200 µm.

Description: Carapace subelongate in lateral outline. Dorsal margin convex, arched at the midpoint, ventral margin concave. In lateral outline anterior margin rounded, posterior margin has a distinct square outline ventroposteriorly. Surface smooth, left over right valve overlap.

Discussion: This specimen occurs in a marine band, although other British species such as *Acutiangulata aequalis* have been associated with brackish water tolerant *Shemonaella scotoburdigalensis* (Athersuch *et al.* 2009).

Distribution: Pathhead Formation; Claremont core, Pathhead Lower Marine Band, associated with *Bairdia submucronata*, *Cavellina valida* and *Shemonaella siveteri* n. sp.

This genus ranges in Britain from the Tournaisian to Lower Asbian (Robinson 1978).

Genus BAIRDIA McCoy, 1844

Type species: *Bairdia curtus* McCoy, 1844

Diagnosis: See Moore, 1961, p.202-203

Bairdia submucronata Jones & Kirkby, 1879

Plate 1, figs B, C, E, F

1879a *Bairdia submucronata*, n. sp.; Jones & Kirkby, p. 572, pl. XXIX, figs 12-18.

1978 *Bairdia submucronata* Jones & Kirkby, 1867; Robinson, p. 150, pl. 11, figs 4a (OS 7457), 4b (OS 7458).

1997 *Bairdia submucronata* Jones & Kirkby, 1879; Turner *et al.*, p. 300, fig. 4i.

Topotypes: Type specimens are not recorded in Jones & Kirkby (1879), but Jones' specimens in the Natural History Museum collections are designated herein as topotype material, particularly specimens In 42133, OS 7457, and OS 7458. The latter two specimens were figured by Jones & Kirkby (1879) and Robinson (1978).

Diagnosis: Species of *Bairdia* with a straight postero-dorsal outline (coincident with the hinge), inclined at 10° to horizontal in lateral view.

Material: 10 specimens, samples EN 4884, EN 4885 and EN 4886 (carapaces).

Dimensions: Average: length 800 µm, height 440 µm, width 320 µm.

Description: Carapace subtriangular to subrhomboidal in lateral outline, asymmetrical.

Dorsal margin convex, with the greatest height in the anterior third. Ventral margin straight, anterior margin rounded, nearly triangular in shape. Posterior margin pointed and acuminate towards the ventral; the postero-dorsal margin in lateral view is inclined at an angle of 10° to horizontal. Surface smooth, with areas of punctation; shallow circular depressions of 20 µm diameter. Left over right valve overlap, left valve larger than right.

Discussion: Sohn (1960) does not include *B. submucronata* in his revision of the Palaeozoic species of *Bairdia*, but provides a good description of the genus. *Bairdia altaica* Buschmina, 1981 and *Bairdia beedei* Ulrich & Bassler, 1906 have a similar carapace outline shape in lateral view to this species, but *submucronata* is more inflated in dorsal view. *Bairdiolites elevatus* Robinson, 1959, has a similar carapace shape in lateral view, with central punctation on the surface of the valves, but in dorsal view the valves have a different shape to *submucronata*.

Distribution: Pathhead Formation; Claremont core, Pathhead Lower Marine Band, associated with *Acutiangulata* sp. A, *Cavellina valida* and *Shemonaella siveteri* n. sp.

This species is recorded from the Asbian of Britain (Robinson 1978), and its range has been further extended by a record from the Arundian to Holkerian of the Northumberland Basin (Turner *et al.* 1997). The global distribution of the genus is from the middle Devonian to the middle Permian (Sohn 1960).

Superfamily BAIRDIOCYPRIDOIDEA Shaver, 1961

Family BAIRDIOCYPRIDIDAE Shaver, 1961

Genus SILENITES Coryell & Booth, 1933.

Type species: *Silenites lenticularis* (Knight 1928), the senior synonym of *Silenites silenites* Coryell & Booth 1933 (see Moore, 1961, p.Q387).

Diagnosis: see Moore 1961, p. Q387.

Silenites sp. A

Plate 4, figs I-L

Material: Three specimens, samples EN 5249 (right valve), EN 5250 (right valve) and SE 8411 (carapace).

Dimensions: Length 650 μm , height 440 μm , width 330 μm .

Description: Carapace subovate to subelongate in lateral outline. Dorsal margin straight to curved, ventral margin slightly convex, anterior and posterior ends slightly curved. In lateral view the posterior has a greater height than the anterior. Carapace inflated at the posterior end, with the varying degree of posterior inflation perhaps indicative of sexual dimorphism. External valve surface is reticulate; 20 μm diameter polygonal to rectangular reticulae. No valve overlap.

Discussion: The small number of specimens precludes assignment to a particular species.

Distribution: Pathhead Formation; Denork core, associated with *Cavellina* sp., palaeocene sp. A and *Shemonaella siveteri* n. sp. Sandy Craig Formation; Kilconquhar core, associated with *Paraparchites circularis* n. sp.

Silenites is recorded from the Mississippian of Britain (Robinson 1978), and western Canada (Crasquin 1985).

Superfamily CARBONITOIDEA Sohn, 1985

Family CARBONITIDAE Sohn, 1985

Genus CARBONITA Strand, 1928

Type species: *Carbonita (Carbonia) agnes* Jones 1870.

Diagnosis: See Pollard 1966, p.683.

Carbonita sp.

Plate 3, figs A, C

Material: 1000s of specimens are identified as *Carbonita* to a generic, but not a specific level, these are mostly poorly preserved carapaces.

Dimensions: Length 810 µm, height 480 µm

Description of genus: Subtriangular to subrounded in lateral outline, with the height more than half the length of the valve. Dorsal margin strongly curved, ventral margin concave to nearly straight, anterior and posterior margins rounded. Surface smooth, sometimes with faint muscle scars visible in the centre of the valve. Right over left valve overlap at the ventral margin.

Discussion of the genus: The genus *Carbonita* has a long history of taxonomic revision. The British-named genus *Carbonia* Strand, 1928 was re-named *Carbonita* (Pollard 1966) and an extensive review of *Carbonita* was carried out by Anderson (1970). Some species of *Bythocypris* have a similar carapace size and shape to *Carbonita*, and Anderson (1970) considered some species synonymous with *Carbonita*.

Other material described from the United States may belong in *Carbonita*. The North American *Whipplella* Holland, 1934 and *Gutschickia* Scott, 1944, are considered as junior synonyms of *Carbonita* (Sohn 1977). Some specimens from the present study resemble

these genera in their carapace outline in lateral view; however, the details of the muscle scar are not present, and the muscle scar of *Whipplella* is quite different from that of *Carbonita* (Sohn 1977). Tibert & Dewey (2006) included many ‘*Carbonita*’ species within their new genus of *Velatomorpha*.

Horne (2003) discussed the origins and affinities of the Carbonitoidea and concluded that they are probably polyphyletic. Using the evidence of soft part anatomy (the Zenker’s Organ in Recent Cypridocopina and Sigilliocopina) and comparisons of muscle scars and other carapace characters with Palaeozoic superfamilies, Horne (2003) hypothesises that the marine Sigillioidea may have been the ancestors of the Carbonitoidea. However, until soft part evidence is found for *Carbonita* (and other non-marine ostracods such as *Darwinula*), their phylogenetic origins remain unclear.

Distribution of the genus: *Carbonita* sp. occurs in the Anstruther Formation; Anstruther core, Sandy Craig Formation; Kilconquhar and Balcormo cores.

The genus occurs in the Mississippian (Samoilova & Smirnova 1960, Buschmina 1965, Pollard 1985, Sohn 1985, Tibert & Scott 1999). It becomes more widespread globally in the Pennsylvanian (Cooper 1946, Kummerow 1949, 1953, Přibyl 1960, Pollard 1966, 1969, Anderson 1970, Bless & Pollard 1973, Bless 1983, Bless *et al.* 1988, Schultze *et al.* 1994, Vannier *et al.* 2003, Schäfer 2007).

Carbonita bairdioides (Jones & Kirkby, 1879)

Plate 3, fig. I

1879b *Cythere?* (*Carbonia?*) *bairdioides*, n. sp.; Jones & Kirkby, p. 38, pl. III, figs 24-27.

1890 *Carbonia bairdioides* Jones & Kirkby; Jones & Kirkby, p. 4, pl. 1, figs 9, 10.

1970 *Carbonita bairdioides* (Jones & Kirkby, 1879); Anderson, p. 94, pl. XVIII, fig. 77, pl. XIX, figs 92-94, 99, 100.

2009 *Carbonita bairdioides* (Jones & Kirkby, 1879); Athersuch *et al.*, p. 129, pl. 1, figs 10, 11 (I. 2566).

Lectotype: Type specimens are not recorded in Jones & Kirkby (1879), but Jones' specimens in the Natural History Museum collections are taken to be topotype material. Specimen I 2566 is assigned herein as the lectotype (CEB1), and is figured in Athersuch *et al.* (2009).

Diagnosis: Species of *Carbonita* with an arched dorsal margin in lateral view, the highest point of the dorsal margin is at two thirds of the length of the carapace from the anterior.

Material: A few specimens, sample 6E 6562 (single valves).

Dimensions: Length 800 μm , height 450 μm .

Description: Carapace subtriangular in lateral outline, asymmetrical. In lateral view the dorsal margin is arched, with the highest point towards the posterior, two thirds of the way along the length of the valve. Ventral margin straight, anterior and posterior margins rounded near to the ventral margin, then sloping up to the dorsal margin. Carapace centrally inflated towards the posterior end. Surface smooth, with a central adductor muscle scar attachment, the details of which are not preserved. Right over left valve overlap.

Discussion: The species has previously been reported only from the Pennsylvanian (Athersuch *et al.* 2009).

Distribution: Sandy Craig Formation; Balcormo core.

This species is recorded in Britain from the Westphalian D (Athersuch *et al.* 2009).

Carbonita cf. *fabulina* (Jones & Kirkby, 1879)

Plate 3, figs D, G

? 1879b *Carbonia fabulina* Jones & Kirkby; Jones & Kirkby, p. 31, pl. II, figs 1-10.

non 1960 *Carbonita fabulina* (Jones & Kirkby, 1879); Přibyl, pl. 2, figs 1-6.

? 1970 *Carbonita fabulina* (Jones & Kirkby, 1879); Anderson, p. 80, pl. XIII, figs 13-17.

non 1970 *Carbonita fabulina inflata* (Jones & Kirkby, 1879); Anderson, p. 115, pl. XVI, figs 47-38.

? 2006 *Velatomorpha altilis* (Jones & Kirkby, 1889); Tibert & Dewey, p. 63, pl. 1, figs A-H, pl. 2, figs A-I.

Material: One specimen, sample SE 8538 (carapace).

Dimensions: Length 940 µm, height 620 µm, width 550 µm.

Description: Carapace subtriangular in lateral outline, asymmetrical. Dorsal margin strongly arched, midpoint highest a little towards the posterior end of the centre of the valve. Ventral margin straight, anterior and posterior margins rounded. Carapace centrally inflated, tapering towards the anterior. Surface smooth, lacks ornamentation, no visible muscle scars. Right over left valve overlap.

Discussion: This species has a lower height:length ratio than *Carbonita bairdioides*, with a greater dorsal arch. Tibert & Dewey (2006) synonymised *Carbonita fabulina* with *Velatomorpha altilis* (Jones & Kirkby 1889). More specimens are needed to confirm that changed combination.

Distribution: Sandy Craig Formation; Kilconquhar core.

Carbonita fabulina is recorded from the Pennsylvanian Coal Measures of Britain (Anderson 1970), Germany (Kummerow 1949) and Poland (Příbyl 1960).

Carbonita cf. *humilis* (Jones & Kirkby, 1879)

Plate 3, figs F, H

- ? 1879b *Carbonia* var. *humilis*; Jones & Kirkby, p. 31, pl. II, figs 11-14.
- ? 1966 *Carbonita humilis* (Jones & Kirkby), 1879; Pollard, p. 683, text-fig. 6a-h.
- ? 1970 *Carbonita humilis* (Jones & Kirkby, 1879); Anderson, p. 87, pl. XV, figs 32-37, pl. XIX, fig. 95.
- aff. 1970 *Cytherella foveolata* Wright (*Carbonita humilis* Jones & Kirkby sp.); Anderson, p. 113, pl. XV, fig. 37.
- ? 1975 *Carbonita humilis* (Jones & Kirkby, 1879); Bless & Pollard, p. 110, pl. II, figs 3-9.
- ? 2009 *Carbonita humilis* (Jones & Kirkby, 1879); Athersuch *et al.*, p. 129, pl. 1, figs 1, 2 (Io 2980), 3, 4 (Io 2981).

Material: Two specimens, sample SE 8476 (carapaces).

Dimensions: Length 840 µm, height 630 µm, width 500 µm.

Description: Carapace subovate to ovate in lateral outline, symmetrical. Dorsal margin curved, ventral margin slightly convex, anterior and posterior margins curved, and at near right angles to the dorsal and ventral margins. Carapace centrally inflated. External valve surface has a fine reticulation of 20 µm diameter polygons, the reticulae wall is 1-2 µm in height. Right over left valve overlap.

Discussion: *Carbonita humilis* along with *Carbonita bairdioides* has not previously been recorded from the Mississippian.

Distribution: Sandy Craig Formation; Kilconquhar core.

Carbonita humilis is recorded from the Pennsylvanian (Westphalian) Coal Measures of Britain (Pollard 1966, Anderson 1970, Athersuch *et al.* 2009). It is of the most common non-marine ostracod species in the Pennsylvanian.

Carbonita cf. inflata (Jones & Kirkby, 1879)

Plate 3, figs B, E

? 1879 b *Carbonia* Var. *inflata*; Jones & Kirkby, p. 31, pl. II, figs 15-19.

aff. 1966 *Carbonita inflata* (Jones & Kirkby), 1879; Pollard, p. 687, text-fig. 8a-d.

? 1970 *Carbonita inflata* (Jones & Kirkby, 1879); Anderson, p. 84, pl. XVI, figs 42-60, pl. XIX, figs 96-98.

aff. 1970 *Bythocypris tumidus* Upson (*Carbonita inflata* Jones & Kirkby sp.); Anderson, p. 115, pl. XVI, figs 53, 54.

aff. 1970 *Carbonita fabulina inflata* (Jones & Kirkby, 1879); Anderson, p. 115, pl. XVI, figs 47-38.

aff. 1970 *Cypridopsis fabulina* Scott & Summerson (*Carbonita inflata* Jones & Kirkby sp.); Anderson, p. 115, pl. XVI, figs 51, 52.

aff. 1970 *Gutschickia ovata* Cooper (*Carbonita inflata* Jones & Kirkby sp.); Anderson, p. 115, pl. XVI, figs 59, 60.

? 2006 *Velatomorpha altilis* (Jones & Kirkby, 1889); Tibert & Dewey, p. 63, pl. 1, figs a-h, pl. 2, figs a-i.

Material: One specimen, sample SE 8413 (carapace).

Dimensions: Length 875 µm, height 660 µm, width 525 µm.

Description: Carapace subtriangular to subrounded in lateral outline, near symmetrical.

Dorsal margin strongly arched, ventral margin straight, anterior and posterior margins rounded. Carapace centrally inflated. Surface smooth, right over left valve overlap.

Discussion: Anderson (1970) regarded *Bythocypris tumidus* Upson, *Cypridopsis fabulina* Scott & Summerson, *Gutschickia ovata* Cooper and *Whipplella cuneiformis* Holland, 1934, to be junior synonyms of *Carbonita inflata*. Pollard (1966) describes *Carbonita inflata* with

a punctate surface, which is not seen in the specimen from the current study. Tibert & Dewey (2006) synonymised *Carbonita inflata* with *Velatomorpha altilis* (Jones & Kirkby 1889).

Distribution: Sandy Craig Formation; Kilconquhar core.

Carbonita inflata is recorded from the Pennsylvanian Coal Measures of Britain (Anderson 1970, Pollard 1966).

Suborder METACOPINA Sylvester-Bradley, 1961

Superfamily HEALDIOIDEA Harlton, 1933

Family HEALDIIDAE Harlton, 1933

Genus HEALDIA Roundy, 1926

Type species: *Healdia simplex* Roundy, 1926.

Diagnosis: See Shaver in Moore, 1961, p. 361.

Healdia cf. *cuneata* Robinson, 1978

Plate 1, fig. G

aff. 1962 *Waylandella subrectangularis* Přibyl, 1962; Přibyl, p. 62, pl. 8, figs 1-4.

cf. 1978 *Healdia cuneata* Robinson, 1978; Robinson, p. 146, pl. 9, figs 6a, b.

non 1978 *Pseudobythocypris cuneola* (Jones & Kirkby 1886); Robinson, p. 144, pl. 8, figs 7a, b.

Material: One specimen, sample EN 4849 (carapace, possibly a juvenile).

Dimensions: Length 420 µm, height 260 µm.

Description: Carapace subelongate in lateral outline. Dorsal margin curved, ventral margin slightly concave; anterior margin curved, posterior margin straight, sloped at a steep angle inwards (approximately 85 degrees). Surface smooth, ornamentation is a small postero-ventral spine on the right valve, 10 µm in length, and a posterior spine on the left valve, 7

µm in length. The spines are smooth sided and triangular in shape, angled towards the posterior. Left over right valve overlap, strong at the ventral margin.

Discussion: *Healdia cuneata* lacks spines (Robinson 1978). In the specimen from sample EN 4849 the spines are far too small to assign it to any of the known spinose species such as *Healdia cornigera* (Jones & Kirkby 1867). *Pseudobythocypris cuneola* (Jones & Kirkby 1886), as figured in Robinson (1978) has no posterior spines, and a small antero-cardinal spine on the right valve, and a carapace outline in lateral view that resembles *Healdia cuneata*, except that it is rather elongate. *Waylandella subrectangularis* Přibyl, 1962 has small postero-ventral spines, but a fairly elongate carapace.

Distribution: Pathhead Formation; Claremont core, Pathhead Lower Marine Band, associated with *Cavellina valida*, *Hollinella* (*Keslingella*) *radiata* and *palaeocope* sp. C.

Healdia cuneata is recorded from the Arnsbergian to Marsdenian of Britain, and *Healdia* is common in the Carboniferous of Britain (Robinson 1978).

Suborder PLATYCOPINA Sars, 1866

Superfamily KLOEDENELLOIDEA Ulrich & Bassler, 1908

Family CAVELLINIDAE Egorov, 1950

Genus CAVELLINA Coryell, 1928

Type species: *Cavellina pulchella* Coryell, 1928

Diagnosis: Platycopids with oval carapaces in lateral view and a right over left valve overlap, the right valve is larger than the left. Domiciliar dimorphism, no external ornamentation.

Cavellina benniei (Jones, Kirkby & Brady, 1884)

Plate 2, figs A, D, G

1884 *Cytherella benniei*, sp. nov.; Jones, Kirkby & Brady, p. 70, pl. VI, figs 3a, b, 4a, b, 5a, b, 7a, b, pl. VII, figs 12a-d.

1884 *Cytherella concinna* Sp. nov.; Jones, Kirkby & Brady, p. 71, pl. VI, figs 9, 12a, b, 19a, b.

1884 *Cytherella recta* Sp. nov.; Jones, Kirkby & Brady, p. 71, pl. VI, figs 6a, b, 11a, b.

1978 *Cavellina benniei* (Jones, Kirkby & Brady, 1884); Robinson, p. 132, pl. 2, fig. 1a (OS 7339), b (OS 7340).

Topotypes: Type specimens not recorded in Jones, Kirkby & Brady (1884), but Jones' specimens in the NHM collections are designated herein as topotype material. Specimens OS 7339 and OS 7340 from the collection were figured in Jones, Kirkby & Brady (1884), and Robinson (1978).

Diagnosis: Species of *Cavellina* with a subquadrate carapace outline in lateral view and nearly parallel dorsal and ventral margins.

Material: Four specimens, samples EN 4841 (adult, carapace) and EK 9601 (two adults, one carapace, one single valve; one juvenile, single valve).

Dimensions: Length 700 µm, height 420 µm.

Description: Carapace subquadrate in lateral outline, anterior and posterior ends are near symmetrical in lateral view. Dorsal and ventral margins straight and nearly parallel to each other, anterior and posterior margins curved. The valves are fairly flat, with some inflation at the centre of the carapace. Surface smooth, right over left valve over reach around the entire margin.

Discussion: Specimens referred to *Cythere superba* in the NHM ("Jones collection") slide I. 1725, are considered synonymous with *Cavellina benniei*, and were collected from Billow Ness in Fife, the same locality as some specimens from the current study.

Distribution: Anstruther Formation; Billow-Ness to Anstruther section, associated with *Cavellina valida*. Pathhead Formation; Claremont core, Pathhead Lower Marine Band, associated with *Cavellina valida*, *Hollinella (Keslingella) radiata* and *palaeocope* sp. A. *Cavellina* is recorded from the Mississippian of Britain, abundant from the Holverian to Lower Asbian, and declining in abundance from the Uppermost Brigantian to Arnsbergian (Robinson 1978).

Cavellina valida (Jones, Kirkby & Brady, 1884)

Plate 2, figs B, C, E, F, H, I

1884 *Cytherella valida*. Sp. nov.; Jones, Kirkby & Brady, p. 70, pl. VI, fig. 2a-c.

1968 *Cavellina valida* sp. nov.; Bushmina

1978 *Cavellina* cf. *taidonensis* Bushmina; Robinson, p. 132, pl. 2, fig. 5a (OS 7346), b (OS 7347).

Topotypes: Type specimens are not recorded in Bushmina (1968), but Jones' specimens in the NHM collections are assigned herein as topotypes. Specimens OS 7346 and OS 7347 from the collection were figured in Jones, Kirkby & Brady (1884), and Robinson (1978), and these are comparable to Russian and Siberian forms.

Diagnosis: Species of *Cavellina* with a steep slope of the posterior end (approximately 85 degrees) in lateral view.

Material: 1000s of specimens, mostly carapaces, many are juvenile instars.

Dimensions: Length 600 µm, height 380 µm, width 260 µm

Description: Carapace subovate to subelongate in outline. Dorsal margin curved, ventral margin straight, anterior and posterior margins rounded. Posterior end higher and more inflated than anterior end. The posterior end is sloped at a steep angle inwards

(approximately 85 degrees). Varying posterior inflation in adult specimens indicates possible domiciliar sexual dimorphism. Smooth surface, right over left valve over reach around the entire margin.

Discussion: Along with *Shemonaella siveteri* n. sp., this species is one of the most abundant of the Strathclyde Group.

Distribution: This species occurs throughout most of the Strathclyde Group, with the best preservation in core samples. Sandy Craig Formation; Kilconquhar core. Pathhead Formation; Claremont and Denork cores, commonly associated with a high diversity of ostracods.

The species is recorded in Britain from the Chadian to the Arundian (Robinson 1978).

Family GEISINIDAE Sohn, 1961

Genus GEISINA Johnson, 1936

Type species: *Jonesina gregaria* Ulrich & Bassler, 1906.

Diagnosis: See Johnson, 1936, p. 21-22.

Geisina arcuata (Bean, 1836)

Plate 3, fig. K

1836 *Cypris arcuata*; Bean, p. 377, fig. 55.

1874 *Beyrichia* sp.; Jones, Kirkby & Brady, p. 71, pl. VII, figs 16a-c.

1886 *Beyrichia arcuata* (Bean); Jones & Kirkby, p. 438, pl. 12, figs 12-14.

non 1889 *Beyrichia arcuata* (Bean); Jones, p. 381, pl. 17, fig. 7a-c.

1932 *Sansabella arcuata* (Bean), 1836; Latham, p. 366, fig. 12.

1943 *Jonesina arcuata* (Bean); Scott & Summerson, p. 672, pl. 1, figs 12-15, 19, 21.

1946 *Geisina arcuata* (Bean); Cooper, p. 110, name only.

non 1949 *Limnoprimita arcuata* (Bean, 1836); Kummerow, p. 49, fig. 1.

1953 *Limnoprimita arcuata* (Bean, 1836); Kummerow, p. 15, pl. 1, fig. 7.

1966 *Geisina arcuata* (Bean, 1836); Pollard, p. 678, text-fig. 4a-f.

aff. 1978 *Sargentina* cf. *williamsae* Sohn, 1975; Robinson, p. 154, pl. 13, fig. 1a, b.

1987 *Geisina arcuata/subarcuata*; Bless *et al.*, p. 356, fig. 8, A-F.

2006 *Limnoprimita arcuata* (Bean, 1836); Adamczak, p. 297, fig. 11, 1a-d.

2009 *Geisina arcuata* (Bean, 1836); Athersuch *et al.*, p. 129, pl. 1, figs 13, 14 (In 4596 lectotype).

Type specimens: Type specimens are not recorded in Bean (1836), but Jones' specimens in the NHM collections have previously been assigned as type material. From slide In 43596, specimen 12 was assigned as a lectotype, and specimens 1-7, 10 and 18-23 as paratypes, by Pollard (1966). The lectotype is figured in Athersuch *et al.* (2009).

Diagnosis: Species of *Geisina* with a shallow adductorial sulcus compared to other geisinids, and a strong right over left valve overlap.

Material: Six specimens, samples EN 4818 (single valve), EN 4827 (carapaces), EN 5257 (single valve, crushed), EK 9591 (single valve) and EL 5272 (cast).

Dimensions: Length 1100 µm, height 685 µm, width 500 µm.

Description: Carapace subovate in lateral outline, preplete. Dorsal margin straight, ventral margin curved, strongly convex. Anterior and posterior margins rounded, flattened at the edges. The dorsoposterior corner has a right-angled appearance in lateral view, while the anteroposterior edge has a more gentle slope. A prominent to shallow adductorial sulcus (S2) situated dorso-medially and towards the anterior of the midpoint. There is a slight suggestion of a shallow anterior sulcus (S1). The two areas of the valve on either side of the adductorial sulcus are slightly lobate in the dorsal region. The anterior lobe is slightly lower down the valve from the dorsal margin than the posterior lobe. Surface smooth, strong right

over left valve overlap at the ventral, posterior, anterior margins and the cardinal angles, obscuring the dorsal margin in lateral view.

Discussion: This species was described in Pollard (1966), but those specimens differ from those of this study in that they have a surface ornament of polygonal pitted reticulation. The extensive synonymy list in Pollard (1966) was examined and added to for this study.

Distribution: Anstruther Formation: Billow Ness – Anstruther field section, associated with *Carbonita* sp. and *Cavellina valida*. Pathhead Formation; Claremont core, Pathhead Lower Marine Band, associated with *Acratia* sp. A, *Cavellina valida*, *Shemonaella siveteri* n. sp. and *Shemonaella ornata* n. sp. Denork core, associated with *Shemonaella siveteri* n. sp.

The species is recorded in the Pennsylvanian Coal Measures of Belgium (Bless *et al.* 1987). *Geisina* sp. is recorded from the Mississippian of Nova Scotia (Dewey & Fåhræus 1987, Sohn 1985).

?Superfamily KLOEDENELLOIDEA Ulrich & Bassler, 1908

Family UNCERTAIN

Genus GLYPTOLICHVINELLA Posner in Gurevich, 1966

Type species: *Glyptolichvinella spiralis* (Jones & Kirkby 1885)

Diagnosis: Elongate carapace in lateral outline, ribbed ornament, including a marginal rib.

Glyptolichvinella spiralis (Jones & Kirkby, 1880)

Plate 2, fig. J

1880 *Kirkbya spiralis* Jones & Kirkby; Kirkby p. 564, 568, 578, 588, name only.

1885 *Kirkbya spiralis* Jones & Kirkby; Jones & Kirkby, p. 184, pl. III, fig. 11.

1932 *Glyptopleura spiralis* (Jones), 1884; Latham, p. 373, text-fig. 22.

1978 *Glyptolichvinella spiralis* (Jones & Kirkby 1884); Robinson, p. 138, pl. 5, fig. 4 (OS 7384).

1987 *Glyptolichvinella spiralis* Jones & Kirkby; Lundin, p. 139, fig. 1a-3b.

2005 *Glyptolichvinella* cf. *spiralis* (Jones & Kirkby); Williams *et al.* 2005c, p. 86, pl. 2, figs 1-3.

Lectotype: Type specimens are not recorded in Jones & Kirkby (1880) or Jones (1885), but Jones' specimens in the NHM collections are considered as topotype material. Specimen OS 7384 from the NHM collection was figured in Jones & Kirkby (1885) and Robinson (1978), and is assigned herein as the lectotype (CEB2).

Diagnosis: Species of *Glyptolichvinella* with a distinctly spaced spiral pattern of costae, and a larger carapace size than other species of the genus.

Material: One specimen, field sample 20 (left valve).

Dimensions: Length 1100 μm , height 700 μm .

Description: Valve subtriangular to subovate in lateral outline. Dorsal margin curved, highest at the midpoint, ventral margin slightly concave, anterior and posterior margins rounded. Costae on the surface of the valve form a ridge around the valve margin, an inner spiral which begins at about 150 μm inwards of the margin and a horizontal ridge at the centre. When viewed from ventral to dorsal margin, the costae number five curved horizontal lines. Surface between the costae appears smooth.

Discussion: The species is distinguished from *Glyptolichvinella annularis* (Kummerow, 1939), which has the same pattern of spiral costae, by its larger size. The taxonomic position of *Glyptolichvinella* in terms of its kloedenelloidea affinity and its links to Recent platycopes is poorly understood.

Distribution: Anstruther Formation; Kingsbarns section.

This species is described from the Arundian - Brigantian of Britain, and may range into the Namurian (Robinson 1978).

Order LEIOCOPIDA Shallreuter, 1973

Suborder PARAPARCHITICOPINA Gramm, 1975

Superfamily PARAPARCHITOIDEA Scott, 1959

Family PARAPARCHITIDAE Scott, 1959

Genus PARAPARCHITES Ulrich & Bassler, 1906

Type species: *Paraparchites humerosus* Ulrich & Bassler, 1906.

Diagnosis: See Dewey & Fåhræus 1987, p.108.

Paraparchites armstrongianus (Jones & Kirkby, 1886)

Plate 2, fig. K

1867 *Leperditia armstrongiana*, Jones & Kirkby; Jones & Kirkby, p.219 (name only).

1886 *Leperditia armstrongiana* Jones & Kirkby; Jones & Kirkby, p. 253, pl. VII, figs 1a, b.

1895 *Leperditia armstrongiana* Jones & Kirkby; Jones & Kirkby, p. 453, 454, 457 (text only).

1932 *Paraparchites armstrongianus* (Jones & Kirkby), 1886; Latham, p. 356, text-fig. 4.

1978 *Shivaella* cf. *okeni* (Münster 1830); Robinson, p. 150, pl. 11, figs 7a (OS 7463), b (OS 7609).

Type specimens: Type specimens are not recorded in Jones & Kirkby (1886), but the specimen figured in Jones & Kirkby (1886) from slide I. 1756 of Jones' NHM collection is assigned herein as the lectotype (CEB3).

Diagnosis: Species of *Paraparchites* with an antero-cardinal spine that is one third the length of the carapace.

Material: Eight specimens, samples EN 5188 and EN 5197 (mainly single valves or disarticulated carapaces), plus external moulds from another four samples.

Dimensions: Length 1800 µm, height 1000 µm.

Description: Carapace subovate in lateral outline, subamplete to postplete. Dorsal margin straight, ventral, anterior and posterior margins curved. Large carapace size, thick valves, carapace inflated centrally. A large hollow spine in the antero-cardinal position on each valve, length of spine is one third the carapace length. The spine is broadest at the base and tapers outwards, with a curved end angled towards the posterior. Surface smooth, valve overlap relationships not seen.

Discussion: Many species of *Shishaella* and *Shivaella* have the same carapace size and dimensions as this species, but have much smaller cardinal spines: for example, *Shishaella moreyi* Sohn, 1975, *Shishaella suborbiculata* (Münster 1830), *Shivaella macallisteri* Sohn, 1972 and *Shivaella okeni* (Münster 1830).

Distribution: Pathhead Formation; Denork core, above Pathhead Upper Marine Band, associated with *Shemonaella siveteri* n. sp.

This species is recorded from the Mississippian of Scotland (Latham 1932).

Paraparchites circularis n. sp.

Plate 3, figs J, L-P

Holotype: Specimen CEB4, a left valve; length 800 µm; Plate 3, fig. L.

Derivation of name: The latin *circularis*, “circular”, referring to the valve outline shape in lateral view.

Type locality: Sample SE 8411, at 363.2 m core depth, Kilconquhar borehole; the Sandy Craig Formation, Fife (grid reference NO 4844 0304).

Diagnosis: Species of *Paraparchites* with a subcircular carapace outline in lateral view, except for a straight dorsal margin. The carapace has a high height:length ratio of 1:1.1.

Material: 1000s of specimens, samples SE 8410, 8411 and 8412 (single valves and carapaces).

Dimensions: Length 840 μm , height 740 μm , width 420 μm .

Description: Carapace subcircular in lateral outline, amplete, symmetrical. Dorsal margin straight, two thirds the length of the carapace, ventral, anterior and posterior margins rounded. Height slightly less than length, strong central inflation. External surface of the valves have shallow circular punctae, each approximately 12 μm in diameter, and a smooth central muscle scar spot. Internal moulds have anastomosing structures radiating from a central muscle spot, which may reflect part of the circulatory system. Right over left valve overlap, to give a ridge around the free margins of the valve.

Discussion: *Paraparchites circularis* n. sp. has a semicircular lateral carapace outline, with a valve height:length that is greater than other large paraparchitoideans which also have the same outline shape. This includes common Mississippian species such as *Chamishaella suborbiculata* (Münster 1830), *Paraparchites carbonaria*, *Paraparchites scotoburdigalensis* (Hibbert 1836) and *Shemonaella scotoburdigalensis* (Hibbert 1836). *Paraparchites discus* Williams *et al.*, 2005c, has an incised dorsum and smaller height:length ratio than this species.

Distribution: Sandy Craig Formation; Kilconquhar core, commonly in monospecific assemblages or associated with rare *Carbonita* cf. *inflata* and *Silenites* sp. A.

Species of *Paraparchites* are recorded from the Mississippian of the Midland Valley of Scotland (Latham 1932, Williams *et al.* 2005), Canada (Dewey 1988), and the USA (Benson 1955, Sohn 1971).

Type species: *Shemonaella dutroi* Sohn, 1971.

Diagnosis: See Dewey & Fåhraeus 1987, p.109.

Shemonaella ornata n. sp.

Plate 4, figs C, F, G, H

Holotype: Specimen CEB6, a carapace; length 1600 µm; Plate 4, figs C, F.

Derivation of name: The latin *ornata*, “ornate”, referring to the distinctive pitted ornament.

Type locality: Sample EN 4804, at 11.53 m core depth, Claremont borehole; the Pathhead Formation, Fife (grid reference NO 4518 1419).

Diagnosis: Species of *Shemonaella* with an ornament of 10 µm diameter circular pits.

Material: Six specimens, samples EN 4818 (four single valves) and EN 4804 (two carapaces).

Dimensions: Length 1450 µm, height 920 µm, width 500 µm.

Description: Carapace subovate in lateral outline, postplete. Dorsal margin straight, length approximately 60% of the length of the carapace. Ventral margin straight, sloping towards the anterior; anterior and posterior ends rounded. The posterior end is distinctly higher than the anterior end. Carapace large for the genus, with a symmetrical central inflation. External surface of the valves have a circular pits 10 µm in diameter. A 120 µm diameter muscle scar is situated at the midpoint, with a smooth surface. Right over left valve overlap.

Discussion: This species has the same outline shape in lateral view as other species of *Shemonaella*, but it has a larger carapace size and a unique ornament. The dorsal margin is shorter than that of *Shemonaella siveteri* n. sp. Specimens of *Leperditia youngiana* Jones & Kirkby, from the NHM “Jones collection” have a similar carapace outline in lateral view, size and ornament. However, the specimens have an ornament of 5 µm diameter pits, not the 10 µm diameter pits that are diagnostic of this new species.

Distribution: Pathhead Formation; Claremont core, above the Pathhead Upper Marine Band. Occurs in abundance, associated with *Acratia* sp. A, *Cavellina taidoneisis*, *Cavellina* sp., *Geisina arcuata*, palaeocope sp. A, and *Shemonaella ornata* n. sp.

Shemonaella siveteri n. sp.

Plate 4, figs A, B, D, E

Holotype: Specimen CEB7, a left valve; length 1200 µm; Plate 4, fig. A.

Derivation of name: The name *siveteri*, derives from the surname of Professor David J Siveter, a Palaeozoic ostracod expert.

Type locality: Sample EN 4805, at 11.53 m core depth, Claremont borehole; the Pathhead Formation, Fife (grid reference NO 4518 1419).

Diagnosis: Species of *Shemonaella* with a long dorsal margin (80% of the carapace length), and a high height:length ratio of 1:1.6.

Material: 1000s of specimens from many samples, carapaces and single valves.

Dimensions: Length 1200 µm, height 760 µm.

Description: Carapace subovate to semicircular in lateral outline, subamplete to postplete. Dorsal margin straight, length approximately 80% of the length of the carapace. Ventral

margin curved, anterior and posterior margins rounded. Carapace large, inflated centrally and towards the posterior. Surface smooth, internal moulds have anastomosing structures radiating from a central muscle spot, which may preserve the circulatory system. Left over right valve dorsal overreach.

Discussion: Many paraparchitoideans have the same carapace size, outline shape in lateral view and lack of external ornamentation as *Shemonaella siveteri* n. sp. These include the postplete forms of *Shemonaella* sp. A of Williams *et al.*, 2005c, *Paraparchites inornatus* McCoy, 1844, *Paraparchites superbus* (Jones & Kirkby), 1886, and *Shishaella sohnella* Crasquin, 1985. This also applies to the preplete forms of *Leperditia okeni* Münster (Jones & Kirkby 1865), *Paraparchites nicklesi* (Ulrich 1891), *Paraparchites okeni* Münster, 1830, and *Shishaella nanaformis* Crasquin, 1985. However, they are all more centrally inflated, with a shorter carapace height, and a much narrower dorsal margin to carapace length.

Distribution: One of the most common species in the Strathclyde Group, occurs in all formations, often in high abundance assemblages.

The genus is recorded from the Mississippian of Britain (Robinson 1978), Germany (Coen 1990) and Canada (Crasquin 1985, Dewey 1993, Dewey & Fåhræus 1987).

Order PALAEOCOPIIDA Henningsmoen, 1953

Suborder PALAEOCOPIINA Henningsmoen, 1953

Superfamily HOLLINOIDEA Swartz, 1936

Family HOLLINELLIDAE Bless & Jordan, 1971

Genus HOLLINELLA Coryell, 1928

Subgenus HOLLINELLA (KESLINGELLA) Bless & Jordan, 1970

Type species: *Hollinella (Keslingella) pumila* Kesling, 1952.

Diagnosis: See Bless & Jordan 1970, p.84.

Hollinella (Keslingella) radiata (Jones & Kirkby, 1886)

Plate 5, figs A-L, Plate 6, figs A-F

1867 *Beyrichia radiata* Jones & Kirkby; Jones & Kirkby, p. 8 (name only).

1886 *Beyrichia radiata* Jones & Kirkby; Jones & Kirkby, p. 257, pl. viii, figs 1, 2a, b.

1906 *Beyrichia ? radiata* Jones & Kirkby; Ulrich & Bassler, p. 156, text, pl. XI, fig. 5.

1932 *Hollina avonensis* n. sp.; Latham, p. 360, fig. 9.

1932 *Hollina radiata* (Jones & Kirkby), 1886; Latham, p. 359-360, fig. 8 (GSE 4957).

1970 *Hollinella (Keslingella)* nov. subgenus; Bless & Jordan, p. 84 (text only).

non 1972 *Hollinella (Keslingella) radiata* (Jones & Kirkby, 1886); Bless & Jordan, p. 122, pl. 19, figs 1-5, (I 1782), p. 124, pl. 20, figs 1-7.

1978 *Hollinella (Keslingella) radiata* (Jones & Kirkby, 1886); Robinson, p. 130, pl. 1, fig. 3 (OS 7331).

non 1987 *Hollinella (Keslingella)* ex. gr. *radiata* (Jones & Kirkby, 1886); Bless *et al.*, p. 353, fig. 5, k, l.

Type specimens: Type specimens are not recorded in Jones & Kirkby (1886), but Jones' specimens in the NHM collections are considered to be topotype material. Specimen OS 7331 (a heteromorph) is figured in Jones & Kirkby (1886), and Robinson (1978), and may be an original type specimen. However, specimens from slide I. 1782 of the Jones collection (figured in Bless & Jordan 1972) have a different shaped histium, and are not considered to be the same species.

Diagnosis: Species of *Hollinella (Keslingella)* with a large postero-dorsal bulb.

Material: At least 20 specimens, fifteen samples (all carapaces).

Dimensions: Length 950 µm, height 620 µm, width 530 µm.

Description: Carapace semicircular in lateral outline, preplete. Dorsal margin straight, ventral margin convex, anterior and posterior margins rounded. Small node antero-dorsally, a large bulb postero-dorsally. Some specimens have two small antero-dorsal nodes. A sulcal pit is situated between the node and the bulb, dorso-medially. A histium fringes the anterior and ventral margins. It starts at the base of the posterior margin, is widest at the ventral, narrows towards the antero-dorsal, and terminates at the dorsal margin. Tooth and socket closure of the valves at the ventral margin, no valve overlap.

The histium flares outwards from the ventral margin to form two symmetrical ridges. The histium is distinctly wider in some specimens, up to 140 μm , compared to specimens where it is only 50 μm wide; this is indicative of dimorphism. There is an inflated mid-ventral region in the heteromorphs. One juvenile instar of 710 μm length has two adventral spines.

An external surface ornament of tubercles and spines occurs in both dimorphs. Tubercles are 10 – 25 μm in diameter, approximately 10% of the tubercles are pores. A row of closely-spaced porate tuberculae is present at the commissure of each valve. Turreted spines are clustered at the edges of the valves, pointing towards the margins. The spines have a hollow centre, and range from 20 – 30 μm diameter at the base. The histium has a ridge of small, fairly flat pores along the outer margin, and the edge is finely ridged on a micron scale.

Discussion: Adventral spines in juvenile instars are typical of the subgenus *Keslingella* (Bless & Jordan 1970). Heteromorphs and tecnomorphs have been assigned based on the width of the histium (Kellett 1936). Heteromorphs have a histium at least twice the width

of tecnomorphs, and a wider carapace. Carapace length and ornament are the same in both dimorphs.

Distribution: Pathhead Formation; Claremont core, Pathhead Lower Marine Band, associated with *Cavellina benniei*, *Cavellina valida*, *Healdia* cf. *cuneata*, palaeocope sp. A, C and *Shemonaella siveteri* n. sp.

Hollinella is widespread from the mid Silurian to lower Permian, and *Hollinella* (*Keslingella*) occurs from the mid Silurian to Namurian A-B (Bless & Jordan 1970).

Hollinella (*Keslingella*) *radiata* ranges from the Chadian – Marsdenian in UK (Latham 1932, Robinson 1978). It is also recorded from the Pennsylvanian of Kansas, USA (Ulrich & Bassler 1906) and the Tournaisian of Belgium (Bless *et al.* 1987).

Superfamily UNCERTAIN

Family UNCERTAIN

Genus UNCERTAIN

Palaeocope sp. A.

Plate 7, figs A-D

Material: 100s of specimens (carapaces and single valves).

Dimensions: Length 760 µm, height 390 µm.

Description: Carapace subelongate in lateral outline, preplete to amplete. Dorsal margin straight, ventral margin convex; anterior and posterior margins curved, anterior end higher than posterior end. Quadrilobate, with a large posterior lobe and three smaller lobes that start near the dorsal margin and end one third down the height of the carapace. Prominent adductor sulcus in the middle of the lobes, situated towards the anterior. Inflated posterior end and adventral region. The posterior lobe is strongly inflated in some

specimens, often separated from the rest of the carapace by a depression. This may represent the heteromorph domatium. Surface smooth, right over left valve overlap.

Discussion: This palaeocope is always found in association with other ostracods such as *Shemonaella siveteri* n. sp.

Distribution: Pathhead Formation; Denork and Claremont cores, most frequently associated with *Shemonaella siveteri* n. sp. and *Cavellina valida*. Sandy Craig Formation; Balcormo core, associated with *Shemonaella siveteri* n. sp.

Palaeocope sp. B

Plate 7, figs E-H

Material: Five specimens, samples EN 4805 (three single valves), EN 4807 (carapace), and EL 5791 (single valve).

Dimensions: Length 770 μm , height 450 μm .

Description: Carapace subovate in lateral outline, preplete. Dorsal margin straight, ventral margin convex, anterior and posterior margins rounded, the anterior is higher than the posterior. Trilobate, lobes that start near the dorsal margin and end one third down the height of the carapace. Adductor sulcus, and smaller sulcus between the anterior and preanterior lobes. Spines of 20 μm or less in length present on anterior and posterior free margins, or only on the anterior margin. The spines have different forms in different specimens: 1; Clavellate (widens distally), 2; Wide, flat, narrows distally, 3; Rounded-end, triangular shaped, 4; small, closely spaced, rounded-end, triangular. 5: closely-spaced, needle-like. These differences may be indicative of variation within the species. Surface smooth. No valve overlap.

Discussion: *Jonesina fastigiata* (Jones & Kirkby 1867), figured in Robinson (1978) is the closest to this new species; trilobate, with a straight dorsal margin and an adventral frill of closely-spaced spines. It differs in that it has lobes that are distinctly spherical in shape, so is not considered the as synonymous with *Palaeocope* sp. B.

Distribution: Anstruther Formation; Anstruther core. Pathhead Formation; Claremont core, associated with *Cavellina* sp., *palaeocope* sp. A and *Shemonaella siveteri* n. sp.

Palaeocope sp. C.

Plate 7, figs I-K

Material: 3 specimens, samples EN 4848 (crushed carapace), EN 4849 (carapace) and EN 4856 (carapace, juvenile).

Dimensions: Length 640 μm , height 430 μm , width 300 μm .

Description: Carapace subovate in lateral outline, preplete to amplete. Dorsal margin straight, ventral margin straight to convex; anterior margin curved, the upper half slopes inwards; posterior margin curved, posterior higher than anterior. Trilobate, with a small anterior lobe, a large bulb-like post-anterior lobe, a broad inflated posterior lobe and a large adductorial sulcus. A postero-cardinal spine on the posterior lobe, triangular shaped, 30 μm in length. The posterior end is greatly inflated in one specimen, nearly spherical in dorsal view. Surface smooth. No valve overlap.

Discussion: In two of the three specimens the postero-cardinal spine has broken off. Due to the poor preservation (crushed carapaces) and the small number of specimens, the species remains in open nomenclature. With more specimens it may be possible to recognise sexual dimorphism of the posterior domatium, as this is greatly inflated in one specimen.

Distribution: Pathhead Formation; Claremont core, Pathhead Lower Marine Band, associated with *Cavellina valida*, *Healdia* cf. *cuneata*, *Hollinella* (*Keslingella*) *radiata* and *Shemonaella siveteri* n. sp.

Palaeocope sp. D.

Plate 7, fig. L

Material: One specimen, sample EN 4787 (carapace, specimen now lost).

Dimensions: Length 700 µm, height 440 µm.

Description: Carapace subovate in lateral outline, preplete. Dorsal margin straight, ventral margin straight, anterior and posterior margins curved. The anterior end is greater in height than the posterior end, with the maximum curve just below midpoint. Trilobed, lobes start near the dorsal margin and end one third down the height of the carapace. Wide and deep adductorial sulcus (S2), with a smaller sulcus (S1) between the first and second lobes. Flattened free margin forming ridge along the anterior, posterior and ventral margins, adventral bulge, no spines. External valve surface strongly reticulate, polygonal reticulae are approximately 20 µm in diameter, and cover entire surface except the flattened free margin. No valve overlap.

Discussion: This species is similar in carapace size, outline and lobate ornamentation to *palaeocope* sp. B, but without the fringing spines.

Distribution: Pathhead Formation; Claremont core, associated with *Cavellina* sp., *palaeocope* sp. A and *Shemonaella siveteri* n. sp.

Order MYODOCOPIDA Sars, 1866

Suborder CLADOCOPINA Sars, 1866

Superfamily UNCERTAIN

Family POLYCOPIDAE Sars, 1866

Genus POLYCOPE Sars, 1866

Type species: *Polycope orbicularis* Sars, 1866.

Diagnosis: See Sars, 1928, p.29-30.

Polycope elegans n. sp.

Plate 1, figs H-K

Non 1874 *Polycope youngiana* Jones & Kirkby; Jones, Kirkby & Brady, p. 56

Holotype: Specimen CEB5, a carapace; length 1800 µm; Plate 1, figs H, I.

Derivation of name: The latin *elegans*, “beautiful/elegant”, referring to the beautiful, fine reticulate ornamentation.

Type locality: Sample EN 5329, at 74.93 m core depth, Denork borehole; the Pathhead Formation, Fife (grid reference NO 4540 1409).

Diagnosis: Species of *Polycope* with a large carapace size and a unique radial pattern of hexagonal (at the valve centre) to rectangular (at the valve edge) reticulation.

Material: 26 specimens, samples EN 5329 (10 carapaces, 10 moulds), EN 5328 (two carapaces, two single valves), EN 5327 and EN 5326 (one mould in each).

Dimensions: Length 1800 µm, height 1580 µm, width 1250 µm: CEB4.

Description: Carapace subcircular in lateral outline, subspherical in shape, postplete.

Dorsal margin straight, one-third of carapace length. Ventral, anterior and posterior margins rounded. Carapace large, thick shelled, tumid, strongly inflated centrally. External surface

ornament of 40 µm diameter reticulae, arranged in a radial pattern from the midpoint. The pattern of reticulation changes from hexagonal or polygonal in the centre of the valve, to rectangular or square shaped at the edges of the valve. No valve overlap.

Discussion: Few species of *Polycope* have been recorded from the Mississippian. Of these *Polycope sphaerula* (Gründel), and *Polycope spinula* Dewey & Fåhraeus 1987, have a smaller carapace size compared to this new species, and a different ornamentation.

Polycope youngiana Jones & Kirkby, 1874 resembles the new species in size, hinge and shape, but it has an ornament of concentrically ringed grooves that is distinctly different.

Distribution: Pathhead Formation; Denork core, below the Lower Ardross Limestone. The four samples that contain *Polycope elegans* n. sp. are each spaced at least a metre apart.

Other species of *Polycope* have been described from the Devonian/Carboniferous of Germany (Becker *et al.* 1993), the Mississippian of Northumberland (Dewey 1993) and the Maritimes Basin of Canada (Dewey 1988, Dewey & Fåhraeus 1987).

Ostracod plates

Sample numbers relate to British Geological Survey borehole samples. All images are Scanning electron micrographs or light photographs.

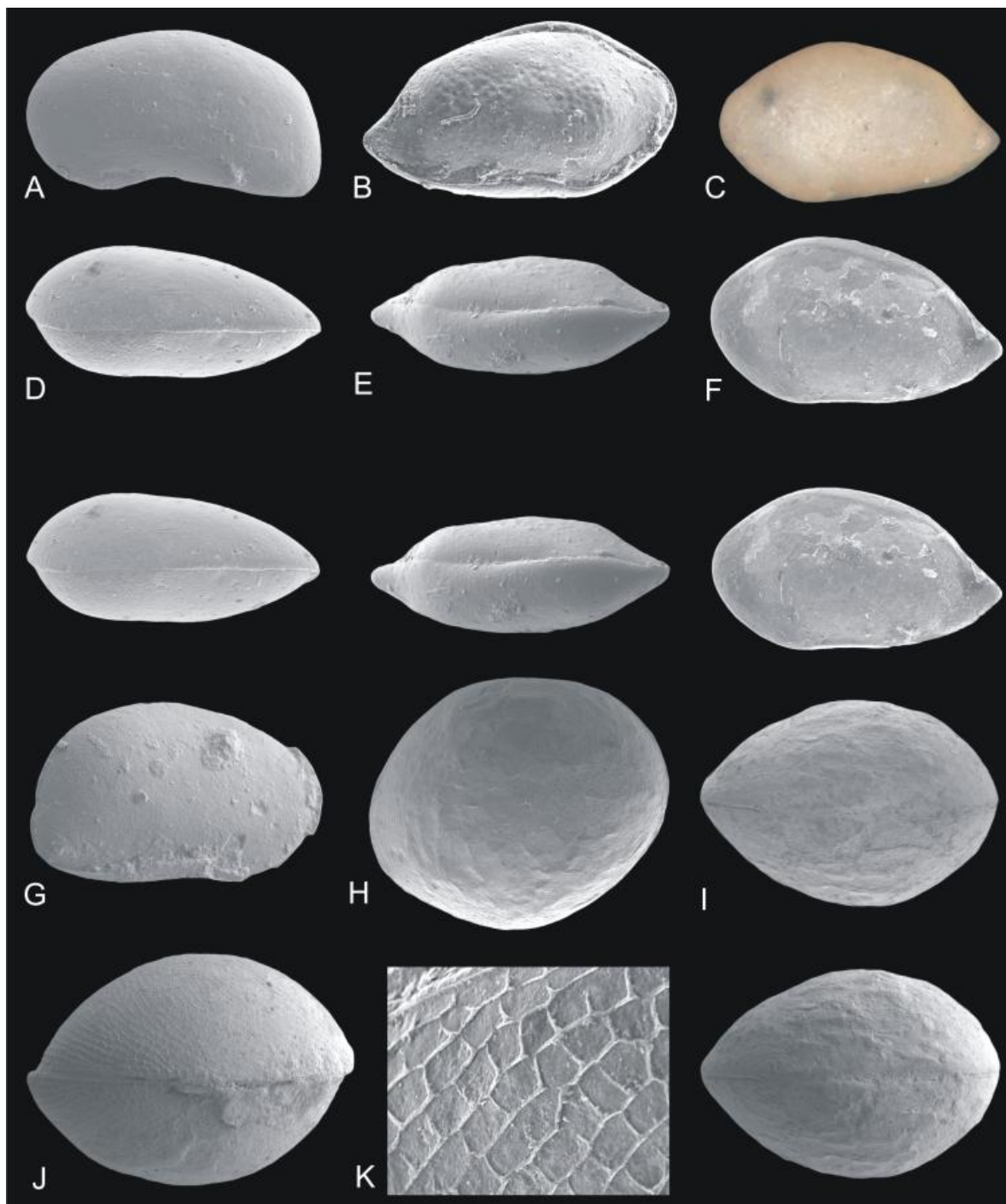


Plate 1: *Acutiangulata*, *Bairdia*, *Healdia* and *Polycope*.

Acutiangulata sp. A.

A, D: carapace (EN4885; length 440 μm), left lateral and dorsal (stereo pair) views, x100.

Bairdia submucronata Jones & Kirkby, 1879.

B, E, F: carapace (EN 4885; length 830 μm), right lateral and dorsal (stereo pair) and left lateral (stereo pair) views x60.

C: carapace (EN 4886; length 800 μm), left lateral view x54.

Healdia cf. *cuneata* Robinson, 1978.

G: carapace (EN 4849; length 420 μm), right lateral view x110.

Polycope elegans n. sp.

H, I: carapace (EN 5329; holotype; CEB5; length 1800 μm), right lateral and dorsal view (stereo pair), x26.

J, K: carapace (EN 5329; length 1550 μm), subdorsal view (x33), and rectangular reticulation (image 230 μm wide; x187).

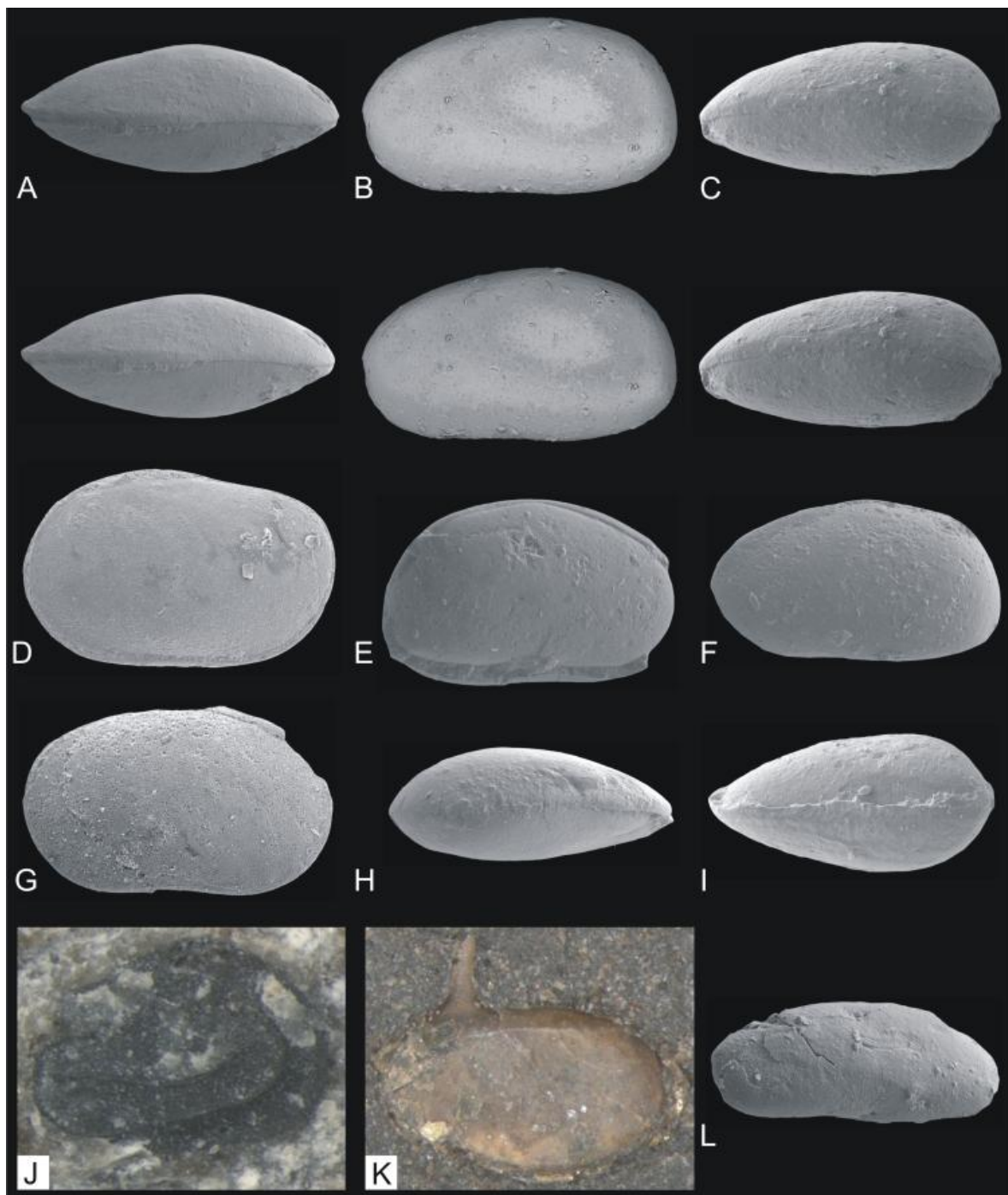


Plate 2: *Cavellina*, *Glyptolichvinella*, *Paraparchites* and *Acratia*.

Cavellina benniei (Jones, Kirkby & Brady, 1884), sample EK 9601.

A, D: carapace (large juvenile; length 540 μm) left lateral and dorsal (stereo pair) views, x91.

G: carapace (length 665 μm), right lateral view, x72.

Cavellina valida (Jones, Kirkby & Brady, 1884), sample EN 4885.

B, C: carapace (length 570 μm), left lateral and dorsal view (stereo pairs), x84.

E, H: carapace (juvenile; length 500 μm), right lateral and dorsal views, x87.

F, I: carapace (length 540 μm), left lateral and ventral views, x81.

Glyptolichvinella spiralis (Jones & Kirkby, 1880)

J: left valve (field sample 20; length 1000 μm), lateral view, specimen partly obscured by dolomite crystals, x46.

Paraparchites armstrongianus (Jones & Kirkby, 1886)

K: left valve of a disarticulated carapace (EN 5188; length 1600 μm), lateral view, x29.

Acratia sp. A

L: single valve (EN 4818; length 324 μm), lateral view, x133.

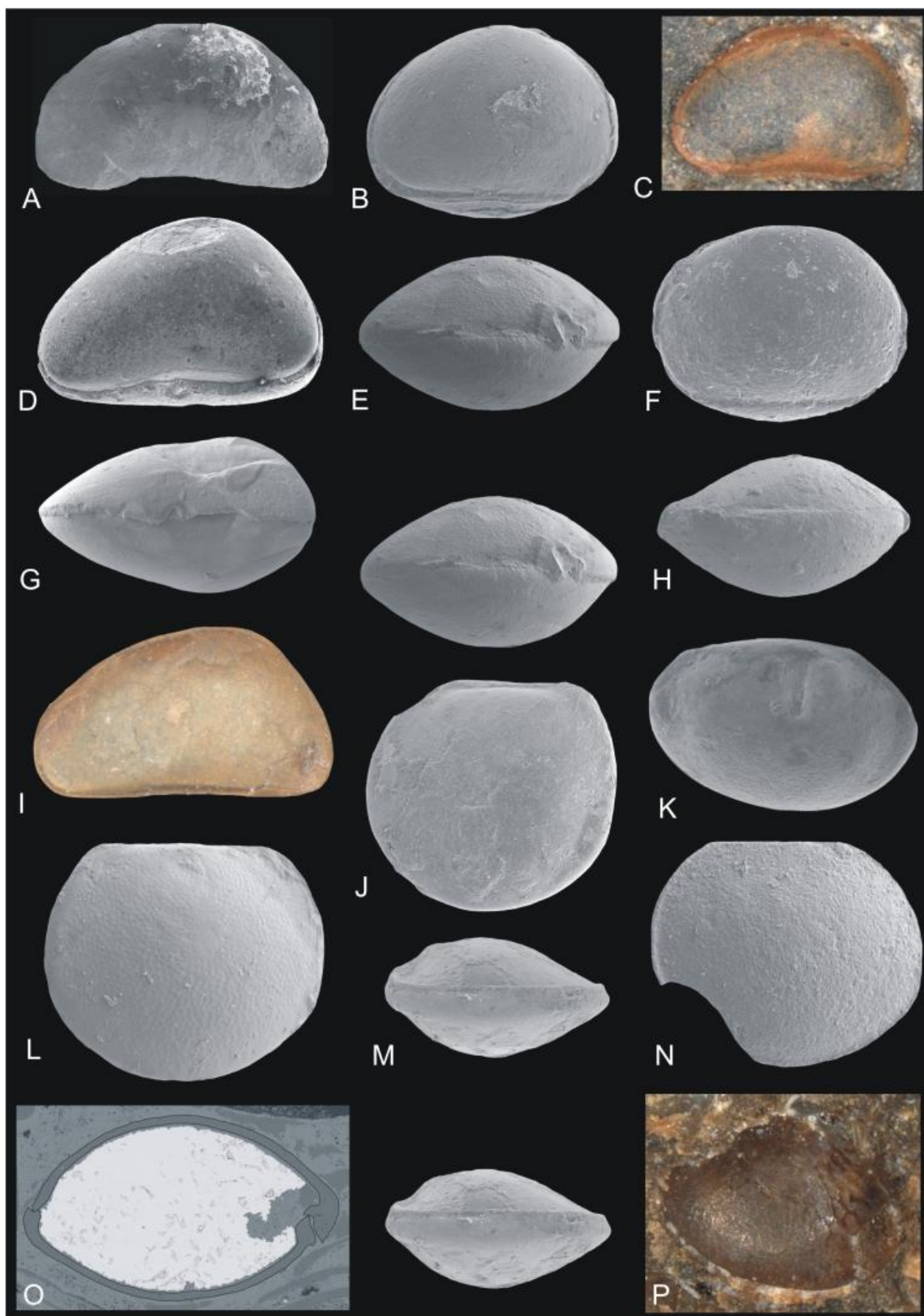


Plate 3: *Carbonita*, *Geisina* and *Paraparchites*.

Carbonita sp.

A: carapace (6E 6658; length 800 μm), left lateral view, x63.

C: left valve (6E 6517; length 900 μm), lateral view, the valve is partly dissolved, x46.

Carbonita cf. *inflata* (Jones & Kirkby, 1879).

B, E: carapace (SE 8413; length 875 μm), left lateral and dorsal (stereo pair) views, x48.

Carbonita cf. *fabulina* (Jones & Kirkby, 1879).

D, G: carapace (SE 8538; length 940 μm), left lateral and ventral views, x51.

Carbonita cf. *humilis* (Jones & Kirkby, 1879).

F, H: carapace (SE 8476; length 840 μm), left lateral and ventral views, x50.

Carbonita bairdioides (Jones & Kirkby, 1879).

I: carapace (6E 6562; length 800 μm), left lateral view, x63.

Geisina arcuata (Bean, 1836).

K: carapace (EN 4827; length 610 μm), right lateral view, x74.

Paraparchites circularis n. sp.

L: left valve (SE 8411; holotype; CEB4; length 800 μm), lateral view, x58.

J, M: carapace (juvenile; SE 8411; length 850 μm), left lateral and ventral (stereo pair) views, x49.

N: right valve (SE 8411; length 720 μm), lateral view, x64.

O: carapace (juvenile; SE 8412; thin section; length 600 μm), the valves are outlined in black, the hinge is to the left, x87.

P: carapace (SE 4812; image 800 μm wide), oblique view of an internal skeinkern, central muscle spot and anastomosing structures, x54.

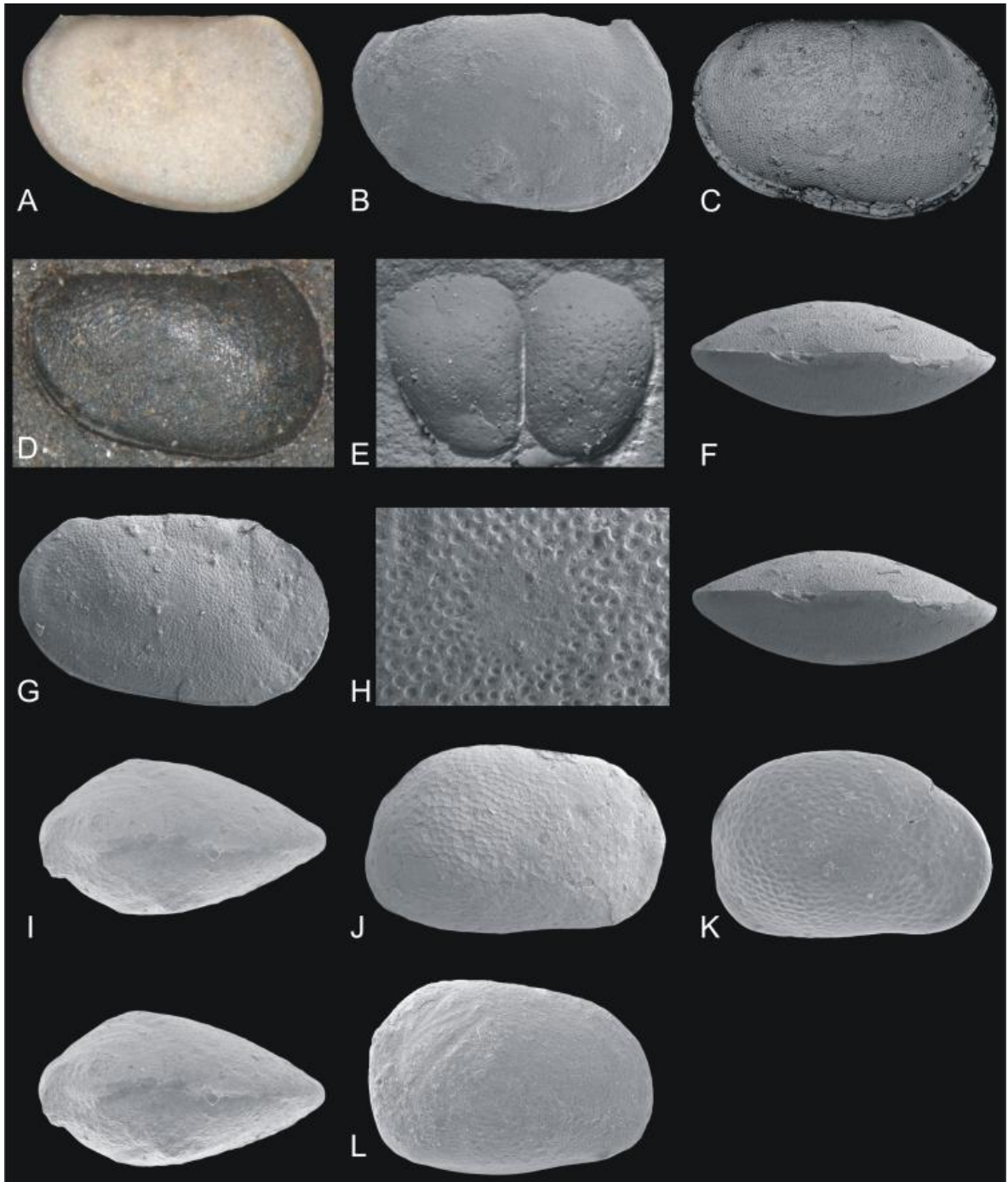


Plate 4: *Shemonaella* and *Silenites*.

Shemonaella siveteri n. sp.

A: left valve (EN 4805; holotype; CEB7; length 1200 μm), lateral view, x39.

B: left valve (EN 4787; length 1220 μm), lateral view, specimen broken at the dorsal margin, x41.

D: right valve (EN 4805; length 1000 μm), internal mould, with anastomosing structures, x48.

E: carapace (juvenile; 6E 6514; height of valve 385 μm), silicon rubber cast, x73.

Shemonaella ornata n. sp.

C, F: carapace (EN 4804; holotype; CEB6; length 1600 μm), left lateral and ventral (stereo pair) views, x30.

G, H: left valve (EN 4818; length 1400 μm), lateral view (x34), and external view of the adductor muscle scar (120 μm diameter, x131).

Silenites sp. A.

I, L: carapace (SE 8411; length 690 μm), right lateral and dorsal (stereo pair) views, x65.

J: right valve (EN 5250; length 680 μm), lateral view, x68.

K: right valve (EN 5249; length 600 μm), lateral view, x72.

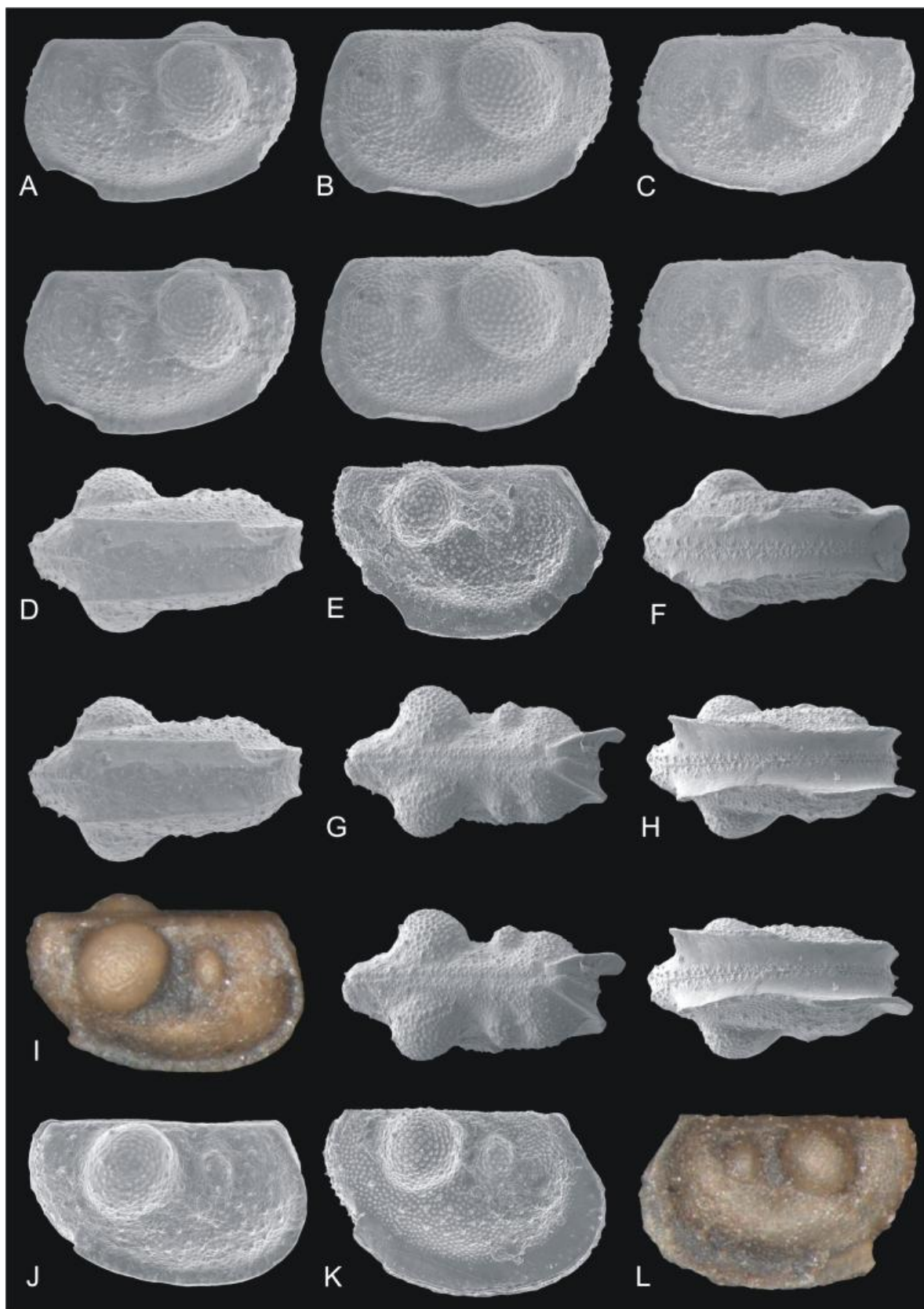


Plate 5: *Hollinella (Keslingella) radiata* (Jones & Kirkby, 1886).

Tecnomorphs:

A, D, I, J: carapace (EN 4858; length 875 μm), left lateral (stereo pair), right ventral (stereo pair) and right lateral views, x54.

B: carapace (EN 4855; length 975 μm), left lateral view (stereo pair), x51.

C: carapace (EN 4851; length 1200 μm), left lateral view (stereo pair), x40.

Heteromorphs:

E, F: carapace (EN 4830; length 920 μm), right lateral and ventral views, x51.

G, H, K: carapace (EN 4840; length 1000 μm), right lateral, dorsal (stereo pair) and ventral (stereo pair) views, x48.

L: carapace (EN 4859; length 900 μm), left lateral view, x53.

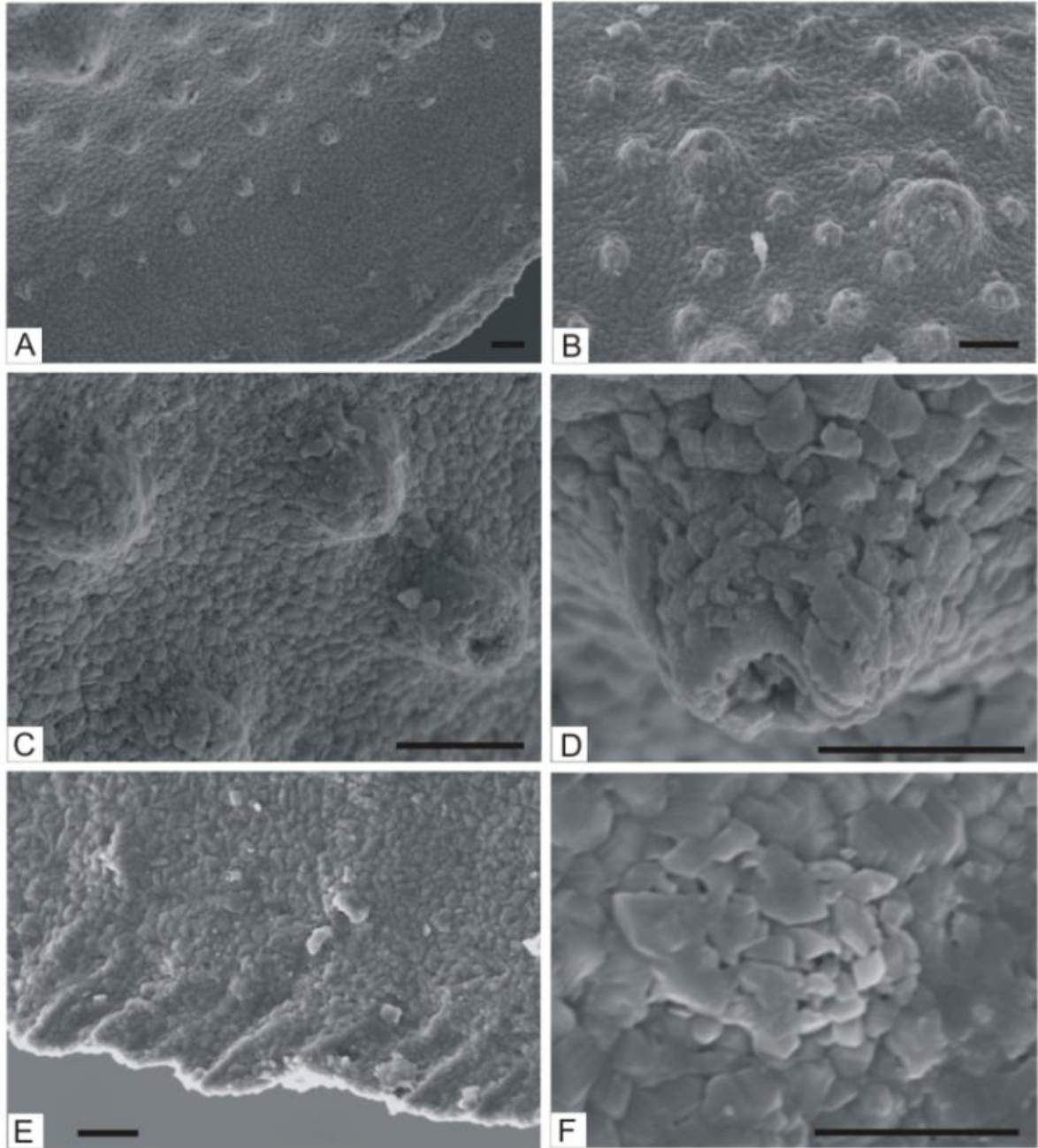


Plate 6: *Hollinella* (*Keslingella*) *radiata*.

A: Spines and tubercles at the ventral margin, EN 4855. B: Tubercles and spines near the dorsal margin, EN 4840. C: Tubercles and tuberculate pores near the ventral margin, EN 4855. D: A short spine near the ventral margin. E: Ridges at the edge of the histium, EN 4829. F: A flat pore on the histium, EN 4840. A-F: scale bar 10 μm .

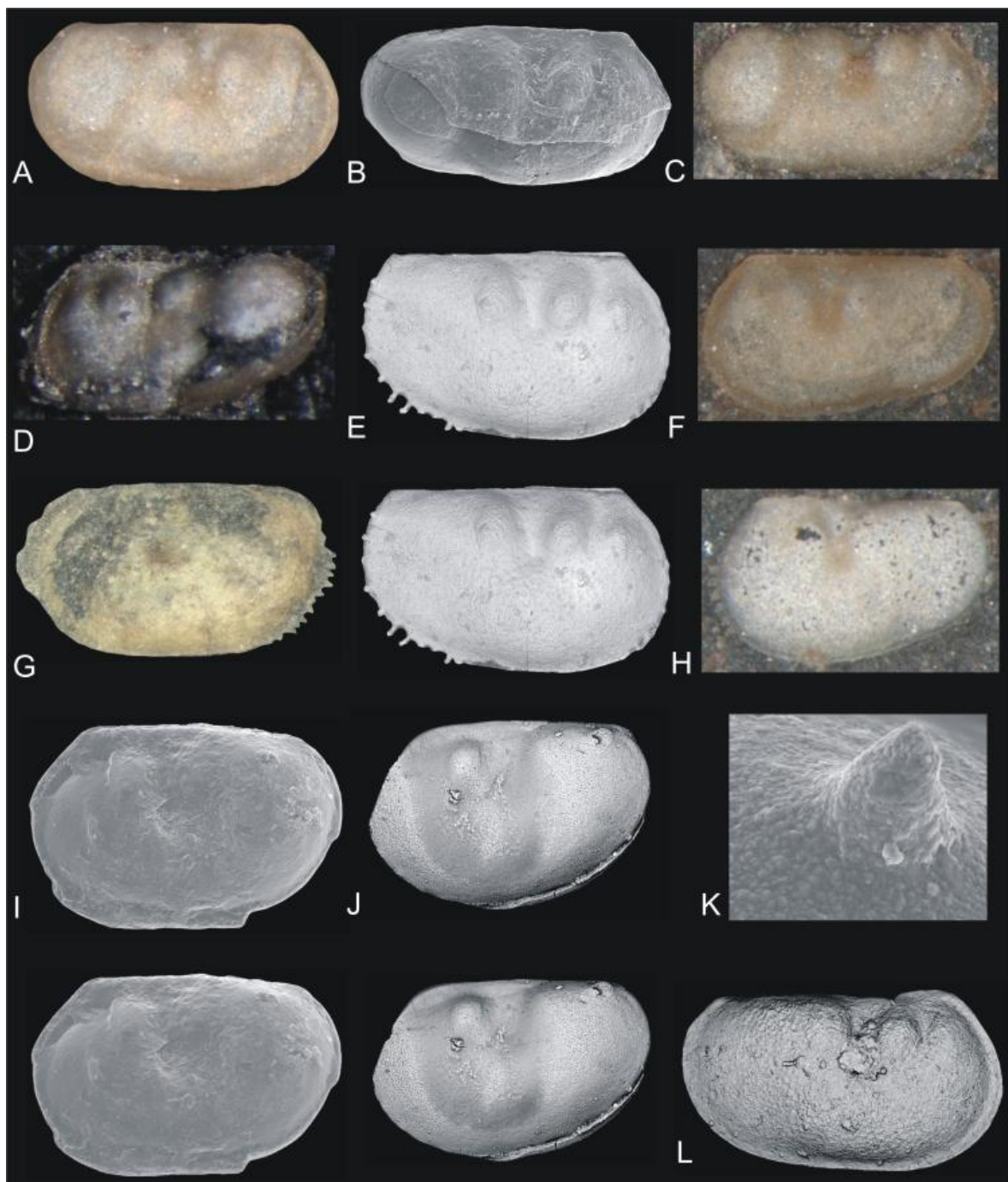


Plate 7: Palaeocopes

Palaeocope sp. A

A: right valve (EN 4805; length 850 μm), lateral view, x58.

B: right valve (EN 5266; length 725 μm), lateral view, x66.

C: right valve (EN 4804; length 870 μm), lateral view, x54.

D: carapace (EN 4796; length 730 μm), left lateral view, x63.

Palaeocope sp. B

E: carapace (EN 4807; length 630 μm), right lateral view (stereo pair), x75.

F: left valve (EN4805; length 700 μm), lateral view, x66.

G: left valve (EL 5791; length 700 μm), lateral view, flattened specimen, x70.

H: left valve (juvenile; EN 4805; length 500 μm), lateral view, x92.

Palaeocope sp. C.

I: carapace (EN 4849; length 600 μm), left lateral view (stereo pair), x82.

J: carapace (juvenile; EN 4856; length 350 μm), left lateral view (stereo pair), x129.

K: postero-dorsal spine (juvenile; EN 4848; spine 30 μm at base), lateral view, x800.

Palaeocope sp. D.

L: carapace (EN 4787; length 700 μm), right lateral view, x71.

Chapter 4: Ostracods from freshwater and brackish environments of the Mississippian Midland Valley of Scotland

Abstract

Ostracods are a diverse group of arthropod crustaceans with a geological record from the Ordovician. Their radiation from marine to non-marine environments is a key step in the evolution of the group. The Midland Valley of Scotland contains some of the earliest non-marine ostracods from the early Mississippian. The Strathclyde Group of Fife contains sediments from a range of depositional systems: shallow marine, deltaic, estuarine, lagoonal, lacustrine, fluvial and swamps. Using assemblage occurrence data macrofossils are assigned to marine, marginal marine, brackish and freshwater environments. The environmental tolerance of the ostracods is interpreted in terms of their macrofaunal and sedimentological associations. Marine macrofauna are associated with the ostracods *Acutiangulata* sp. A, *Bairdia submucronata*, *Healdia* cf. *cuneata*, *Hollinella* (*Keslingella*) *radiata*, *palaeocope* sp. C and *Polycope elegans* n. sp. Marginal marine macrofossils are the bivalves *Schizodus* and *Sanguinolites*, and the brachiopod *Lingula*. Marginal marine to freshwater macrofossils are associated with the eurytopic ostracods *Cavellina benniei*, *Cavellina valida*, *Paraparchites armstrongianus*, *Shemonaella siveteri* n. sp. and various palaeocopes. Important brackish to freshwater macrofauna are the bivalves *Naiadites* and *Curvirimula* and the microconchid “*Spirorbis*”, associated with *Geisina arcuata*, *Paraparchites* n. sp, *Shemonaella ornata* n. sp. and *Silenites* sp. A. Freshwater macrofauna are the bivalves *Anthraconaia*, *Carbonicola* and *Cardiopteridium*, conchostracan crustaceans and fish. The oldest freshwater ostracods are species of *Carbonita*; important

brackish ostracods are *Geisina arcuata* and *Paraparchites circularis* n. sp. Swamps, lakes, temporary pools and estuaries are brackish to freshwater environments colonised by ostracods. This study adds primary knowledge to the first colonisation of non-marine environments by ostracods.

Introduction

Ostracod crustaceans are one of the most abundant animals in the fossil record, and are found at least back to the early Ordovician (Siveter 2008). The ecological migration of the Ostracoda from marine to freshwater aquatic environments occurred during the Carboniferous, and the most successful non-marine genus was *Carbonita* Strand, 1928 (Bennett 2008). This study records *Carbonita* in what are interpreted as freshwater sediments from the early Mississippian. The earliest records of *Carbonita* from a brackish environment are from the early Mississippian of Nova Scotia (Tibert & Scott 1999) and the Ballagan Formation of the Midland Valley of Scotland (Williams *et al.* 2006). *Carbonita* is commonly found in freshwater to brackish environments in the late Mississippian (for example Pollard 1966, Anderson 1970, Bless & Pollard 1973, Sohn 1985). In the Pennsylvanian this group of ostracods are found in freshwater deposits globally (for example as reported in Schultze *et al.* 1994, Vannier *et al.* 2003 and Schäfer 2007), along with *Darwinula*, extant examples of which occur in freshwater. However the lack of soft part evidence and phylogenetic uncertainty surrounding *Carbonita* limit the use of taxonomic and ecologic uniformitarian parallels.

The colonisation of the land by plants and non-marine waters on land by animals is one of the major evolutionary events. From the late Silurian to Devonian a non-marine lacustrine

fauna became established, which included freshwater fish and arthropods (Buatois *et al.* 1998, Halstead 1985). The diversity of lacustrine fauna significantly increased in the Devonian, and by the Carboniferous all nonmarine environments were colonised (Maples & Archer 1989). The timing of invertebrate colonisation can be linked to the evolution of land plants; for example, there was an increase in the diversity of detritus-feeding epifauna in the Carboniferous (Buatois *et al.* 1998), which can be directly linked to the increased availability of plant foods.

This study distinguishes marine, brackish and freshwater palaeoenvironments of the Strathclyde Group of Fife, by using sedimentological and palaeontological data.

Macrofossils are assigned to an environment based on their faunal associations and known environmental tolerance. Environments of deposition are interpreted from the sedimentology and palaeontology. The ostracod environmental tolerances are interpreted in terms of their association with macrofossils and other ostracods. The strong palaeoenvironmental bias in the ostracod occurrences rules out their use as biostratigraphic tools. A spatial and temporal palaeoenvironmental interpretation of the Strathclyde Group incorporates data from the sediments, macrofossils and ostracods.

Geological background

During the Mississippian the Midland Valley of Scotland was situated on the southern edge of Laurussia at the equator, within a restricted marine seaway. Deposition was of predominantly siliciclastic sediment sourced from the surrounding highlands (Browne *et al.* 1999). A shallow marine basin formed, with restricted to non-marine estuaries, lagoons, lakes and swamps. The sediments usually form in a pattern of upward coarsening deltaic

cycles (Browne *et al.* 1999), with marine and lacustrine deltaic deposition. Non-marine limestones are of historical importance; for example, the Burdiehouse Limestone which contains ostracods, plant and fish debris and coprolites (Hibbert 1834).

The evidence for early Mississippian hypersaline and brackish water ostracods was established by a multi-proxy analysis of the Tournaisian Ballagan Formation (Table 1), including isotope, ostracod and palynological studies (Stephenson *et al.* 2002, 2004, Williams *et al.* 2005, 2006).

The formations of the Strathclyde Group that are exposed in Fife have the best ostracod preservation and range of environments in which to investigate Mississippian non-marine ostracods. These formations are correlated with other sediments across the Midland Valley using distinctive marine horizons (Browne *et al.* 1999, Forsyth & Chrisholm 1977, Wilson 1989). Contemporaneous volcanism, present as small dolerite intrusions and tuffs, and abundant palynomorphs also provide robust dating tools (Monaghan & Parrish 2005, Owens *et al.* 2005, Stephenson *et al.* 2004).

System	Series	Stage	Paly. Zones	Midland Valley of Scotland Lithostratigraphy				Group
				Central Coalfield & Ayrshire	Fife	West Lothian	East Lothian	
Mississippian	Viséan	Brigantian	VF	Lawmuir Fm	Pathhead Fm	West Lothian Oil Shale Fm	Aberlady Fm	Strathclyde Group
		Asbian	NM	Kirkwood Fm	Sandy Craig Fm			
		Holkerian	TC	Clyde Plateau Volcanic Fm	Pittenweem Fm			
		Arundian	TS		Anstruther Fm	Gullane Fm		
		Chadian	Pu		Fife Ness Fm			
	Tournaisian	Ivorian		Clyde Sandstone Fm				Inverclyde Group
			CM	Ballagan Fm				
		Hastarian	PC	Kinneswood Fm				

Table 1. Mississippian stratigraphy of the Midland Valley of Scotland, showing the Strathclyde Group formations of Fife. Adapted from Browne *et al.* (1999).

Glacial and interglacial episodes in the late Mississippian resulted in eustatic sea level changes, the transgressions of which are observed globally (Fielding *et al.* 2008, Ross & Ross 1985). These global marine transgressions may correlate with those at the top of the Pathhead and Sandy Craig Formations. Each of the formations at Fife has different degrees of marine influence, but all have cyclothem-like cycles of sedimentation. This pattern is seen throughout other Mississippian sediments of Scotland (Andrews *et al.* 1991, Browne *et al.* 1999, Kassi *et al.* 1998, 2004) and England (Barnett *et al.* 2002).

Methods

Rock samples and polished thin sections were analysed for their sedimentology, macrofauna and ostracod content. The ostracod specimens were picked from the bedding planes of samples using a needle, for imaging under a light microscope or the Scanning Electron Microscope (SEM). Delicate samples were kept on the bedding plane and imaged at the Natural History Museum using the AxioCam light photography method. Ostracod carapaces were mounted on SEM stubs using PVA glue mixed with distilled water, and then gold coated using an Emitech Sputter Coater K500X. Specimens were analysed at high vacuum on a Hitachi S-3600N Scanning Electron Microscope, using a secondary electron (SE) detector. Polished thin sections were cut to a standard thickness of 30 µm.

The Strathclyde Group of Fife

Carboniferous ostracods from Fife were obtained from borehole samples and field collections (Figure 1). Survey boreholes were taken by the British Geological Survey (BGS) from 1964-1980. Core samples were recorded and stored at the BGS in Edinburgh. A sedimentary log and a list of macrofauna were described from these core samples by

BGS workers. The sample numbers used relate to BGS numbered samples. Field samples were collected as part of this study from 2005-2008. The Fife Ness Formation has not been studied; it is known to contain “*Spirorbis*” macrofossils but not ostracods, and critically its stratigraphical position and age are uncertain (Owens *et al.* 2005).

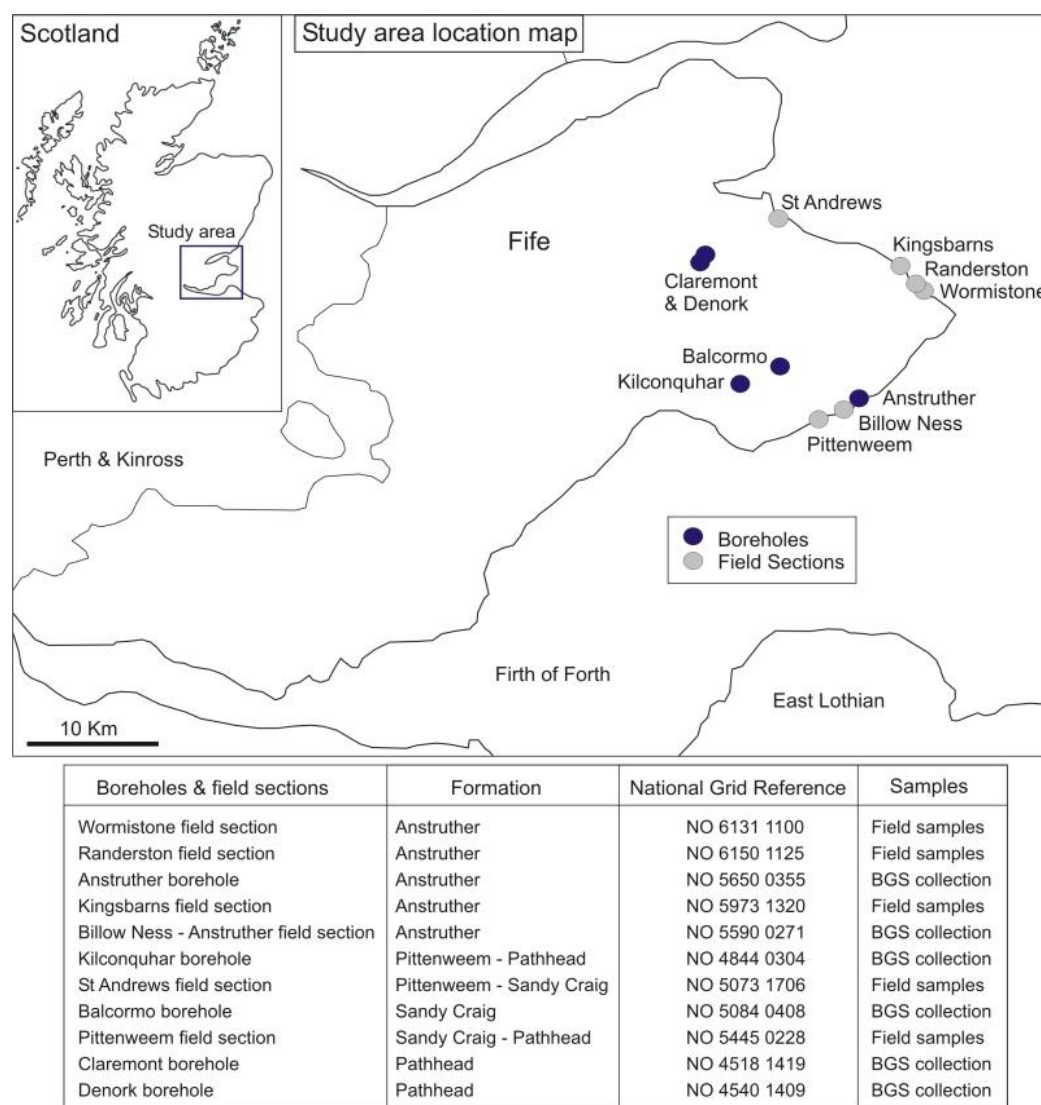


Figure 1. Location map and table of boreholes and field sections studied from the Strathclyde Group of Fife. National Grid Reference points for field sections are taken at the base of the section.

The Fife sections are correlated by using key marine horizons or non-marine limestone beds (Figure 2). Siliciclastic sediments comprise about 70% of the sediment volume; some sections have sandstone units over 20 m in thickness (Figure 2).

Each of the formations has a different sedimentological and faunal signature. The Anstruther Formation has the most non-marine limestones of the Strathclyde Group (Figure 2); non-marine ostracods are common. The Pittenweem Formation contains numerous fully marine and marginal marine horizons; ostracod preservation is poor. The Sandy Craig Formation is dominantly composed of non-marine mudstones, silts, shaley coals, black-banded ironstones and coals; non-marine ostracods are common. The Pathhead Formation contains several fully marine horizons, with a high diversity of ostracods and macrofauna.

Taphonomy

To assess the ecological ranges and true sedimentary environments of different ostracod species an assessment of the taphonomy is important. The terminology used (thanatocoenosis and taphocoenosis) relates to that of Boomer *et al.* 2003: a thanatocoenosis represents a well preserved community (the “autochthonous” assemblage of Whatley 1983, 1988), and a taphocoenosis represents an assemblage altered by taphonomic processes (an “allochthonous” assemblage). All macrofossil and ostracod assemblages detailed here represent a thanatocoenosis unless otherwise stated. In the case of ostracods the criteria for a thanatocoenosis are determined by the preservation of adults and juveniles (of different instars), with a high proportion of carapaces to single valves. The criterion for a taphocoenosis is a high proportion of single valves to carapaces (especially broken valves), random or stacked valves, a valve size bias and a large

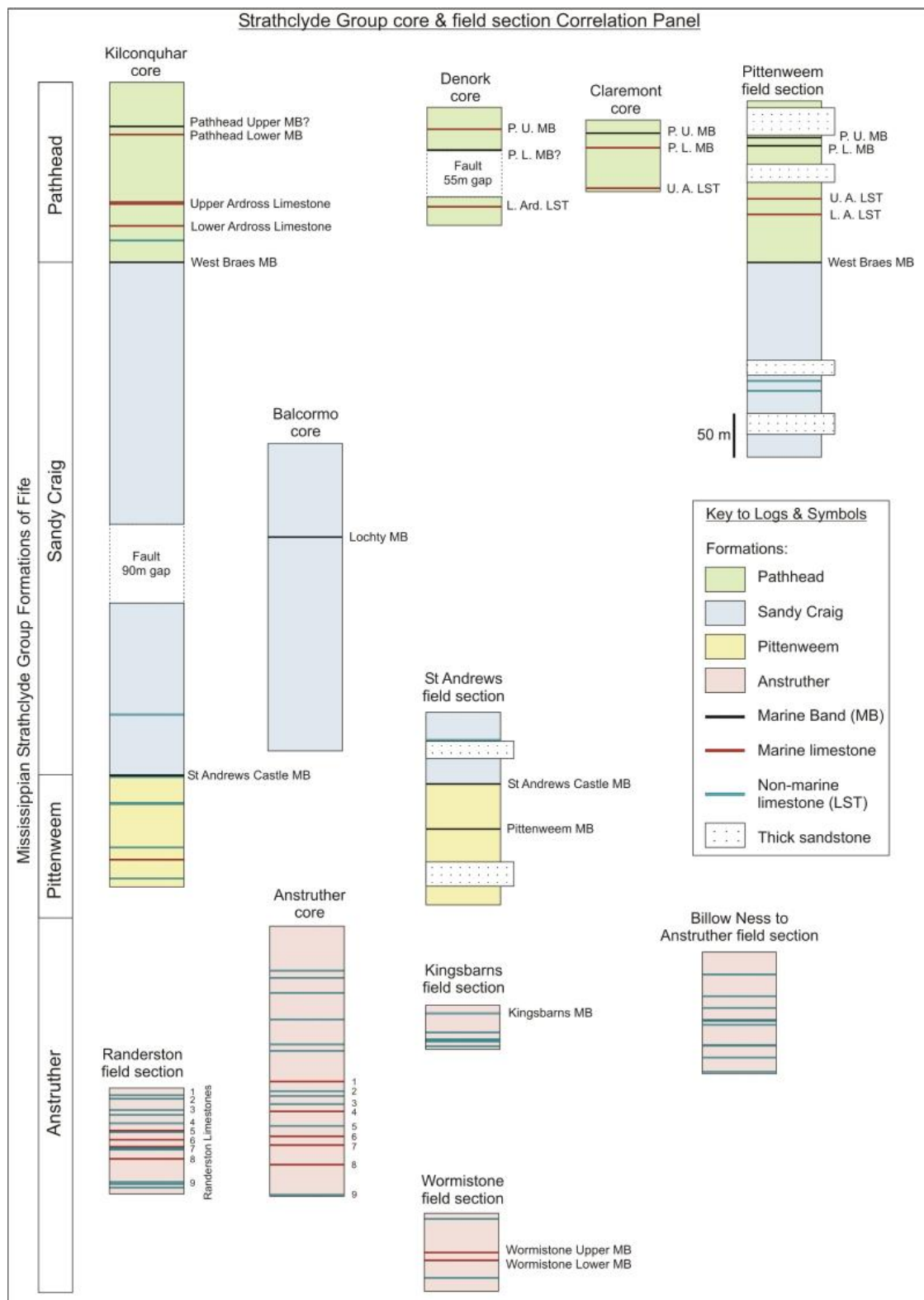


Figure 2. Borehole and field section correlation panel. Marine limestones, non-marine limestones and key marine bands are used to correlate the sections. Sandstone units with a thickness greater than 20 m are highlighted.

abundance of ostracods. A taphocoenosis characteristic of macrofossils is the *Naiadites* “*mussel bands*” that are sediments densely packed with broken and disarticulated valves. Appendix 2 contains some ostracod and macrofossil taphonomic information. Most of the macrofossils except for the *Naiadites* “*mussel bands*” are interpreted to represent a thanatocoenosis. The exception to this interpretation is in the graphical sedimentary logs and the faunal associations graphs, where all occurrences of a particular fauna are noted and the taphonomy is not assessed. To counteract the taphonomic bias inherent in this the taphonomy is closely considered when assigning individual ecological ranges to ostracod species or macrofossil groups.

Macrofaunal associations: indicators of palaeoenvironment

The macrofauna and ostracods present in the Strathclyde Group are listed in Table 2. There is a greater diversity of marine fossils compared to those interpreted as marginal or non-marine. To distinguish the different environments present an assemblage-based approach of associated fauna is used for macrofauna and ostracods. For example the environment of the brachiopod *Lingula* is interpreted in terms of its frequency of occurrence with other macrofauna of known environmental tolerance. It is important to note that there is a preservational bias when interpreting the environment from faunal associations. To help address this problem the evidence for the environmental tolerances of non-marine macrofossils in the literature is examined. Many macrofossils occur in several different environments; they may have an authentic wide-salinity tolerance, or they are dominant in one environment and occur only rarely in others.

MARINE		MARGINAL MARINE	FRESHWATER
Ostracoda	Brachiopoda	Ostracoda	Ostracoda
<i>Acutiangulata</i> sp. A	<i>Crunithyris</i>	<i>Cavellina</i> sp.	<i>Carbonita</i> sp.
<i>Bairdia submucronata</i>	<i>Echinocorihus</i> cf. <i>purictatus</i>	<i>Geisina arcuata</i>	<i>Carbonita bairdioides</i>
<i>Cavellina benniei</i>	<i>Lingula squariformis</i>	palaeocope sp. A	<i>Carbonita</i> cf. <i>fabulina</i>
<i>Cavellina valida</i>	<i>Lingula mytilloides</i>	palaeocope sp. B	<i>Carbonita</i> cf. <i>humilis</i>
<i>Healdia</i> cf. <i>cuneata</i>	<i>Lingula</i>	<i>Paraparchites armstrongianus</i>	<i>Carbonita</i> cf. <i>inflata</i>
<i>Hollinella</i> (<i>Keslingella</i>) <i>radiata</i>	<i>Orbiculoidea cincta</i>	<i>Shemonaella siveteri</i> n. sp.	<i>Cavellina benniei</i>
palaeocope sp. A	<i>Orbiculoidea</i>	Bivalvia	<i>Cavellina valida</i>
palaeocope sp. C	<i>Orthotetoid</i>	<i>Myalina</i>	<i>Cavellina</i> sp.
<i>Paraparchites armstrongianus</i>	<i>Pleuropugnoides</i>	<i>Naiadites crassus</i>	<i>Geisina arcuata</i>
<i>Polyclope elegans</i> n. sp.	<i>Productus</i>	<i>Naiadites obesus</i>	palaeocope sp. A
<i>Shemonaella siveteri</i> n. sp.	<i>Punctospirife</i>	<i>Naiadites</i>	palaeocope sp. B
Bivalvia	<i>Schizophoria</i>	<i>Sanguinolites clavatus</i>	<i>Paraparchites circularis</i> n. sp.
<i>Actinoptera persulata</i>	<i>Spirife</i>	<i>Sanguinolites costellaters</i>	<i>Shemonaella siveteri</i> n. sp.
<i>Actinopteria</i>	<i>Spiriferellina</i>	<i>Sanguinolites plicatus</i>	<i>Shemonaella ornata</i> n. sp.
<i>Aviculopecten plicatus</i>	<i>Trigonoglossa scotica</i>	<i>Sanguinolites variabiles</i>	<i>Silenites</i> sp. A
<i>Aviculopecten planoclathratis</i>	<i>Trigonoglossa</i>	<i>Sanguinolites</i>	Bivalvia
<i>Aviculopecten</i> cf. <i>subconoideus</i>	Gastropoda	<i>Schizodus pentlandicus</i>	<i>Anthraconaia?</i> <i>Kirki</i>
<i>Aviculopecten</i>	<i>Donaldina</i>	<i>Schizodus</i>	<i>Carbonicola antiqua?</i>
<i>Cypriocardella</i> cf. <i>rectangularis</i>	<i>Euphemites</i>	Brachiopoda	<i>Carbonicola elegans</i>
<i>Cypriocardella</i>	<i>Globroingulara</i>	<i>Lingula squamiformis</i>	<i>Carbonicola</i>
<i>Edmondia senilis</i>	<i>Meekospira</i>	<i>Lingula mytilloides</i>	<i>Cardiopteridium</i>
<i>Edmondia</i>	<i>Murchisonid</i>	<i>Lingula</i>	<i>Curvirimula</i> cf. <i>scotica</i>
<i>Hemipecten</i>	<i>Naticopsis scotoburdigalensis?</i>	Vertebrata	<i>Curvirimula</i>
<i>Leiptera</i>	<i>Naticopsis</i>	fish fragments indet.	<i>Naiadites obesus</i>
<i>Limipecten</i>	<i>Pseudozygopleura</i> cf. <i>rugifera</i>	Others	<i>Naiadites</i>
<i>Linoprotonia</i>	<i>Pseudozygopleura</i>	<i>Coprolites</i>	Branchiopoda
<i>Lithophaga lingualis</i>	<i>Retispira decurrata</i>	Ichinolites	<i>Estheria</i>
<i>Lithophaga</i>	<i>Retispira striata</i>	<i>Arenicolites</i>	<i>Euestheria</i>
<i>Modiolus sublamellosa</i>	<i>Retispira</i>	<i>Chondrites</i>	<i>Leaia</i>
<i>Myalina</i>	Scaphopoda	<i>Diplocraterion</i>	Vertebrata
<i>Nuculoid</i>	<i>Dentalium</i>	<i>Monocraterion</i>	fish fragments indet.
<i>Nucleopus gibbosa</i>	Cnidaria	<i>Palaeophycus</i>	actinoptergian jaw
<i>Palaeolima</i>	<i>Lithostrotion junceum</i>	<i>Planolites</i>	Others
<i>Palaeoneilo brevisstrom</i>	Bryozoa	<i>Skolithos</i>	<i>Coprolites</i>
<i>Palaeoneilo laevisstrom</i>	<i>Fenestella trepostome</i>	<i>Teichichnus</i>	" <i>Spirorbis</i> "
<i>Palaeoneilo luiniformis</i>	<i>Rhabdomason</i>		stromatolites
<i>Palaeoneilo mansonii</i>	Echinodermata		Plants
<i>Paleyoldia maegregori</i>	<i>Archaeocidaris</i>	BRACKISH	Spinose megaspores
<i>Parallelodon</i>	Crinoid columnals	Ostracoda	<i>Sphenopteris affinis</i>
<i>Permopecten sowerbii</i>	<i>Echinocidaris</i>	<i>Carbonita</i> sp.	<i>Telangium affinae</i>
<i>Permopecten</i>	Arthropoda	<i>Cavellina benniei</i>	
<i>Permopectinella</i>	Trilobite fragment indet.	<i>Cavellina taidonensis</i>	
<i>Polenomorphia minor</i>	Cephalopoda	<i>Cavellina</i> sp.	ENVIRONMENT UNCERTAIN
<i>Polenomorphia</i>	<i>Beyrichoceratoides</i>	<i>Geisina arcuata</i>	Ostracoda
<i>Polidevica attenuata</i>	Goniatite fragments indet.	palaeocope sp. A	<i>Acratia</i> sp. A
<i>Punctospyrifa</i>	<i>Stroboceras</i>	palaeocope sp. B	<i>Glyptolichvinella spiralis</i>
<i>Sanguinolites clavatus</i>	Nautiloid indet.	<i>Paraparchites circularis</i> n. sp.	palaeocope sp. D
<i>Sanguinolites costellaters</i>	Orthocones indet.	<i>Shemonaella siveteri</i> n. sp.	
<i>Sanguinolites variabiles</i>	Others	<i>Shemonaella ornata</i> n. sp.	
<i>Sanguinolites</i>	<i>Conularid</i>	<i>Silenites</i> sp. A	
<i>Schizodus</i>	<i>Paraconularia</i>	Bivalvia	
<i>Sedgwickia gigantea</i>	<i>Serpulites carbonius</i>	<i>Curvirimula</i>	
<i>Sedgwickia</i>	<i>Serpulites</i>	<i>Curvirimula</i> cf. <i>scotica</i>	
<i>Solenomorpha</i> cf. <i>minor</i>	Ichinolites	<i>Naiadites crassus</i>	
<i>Solenomorpha</i>	<i>Chondrites</i>	<i>Naiadites obesus</i>	
<i>Streblochondria elliptica</i>		<i>Naiadites</i>	
<i>Streblochondria</i>		Vertebrata	
<i>Streblopteria ornata</i>		fish fragments indet.	
<i>Wilkingia maxima</i>		Others	
<i>Wilkingia</i>		<i>Coprolites</i>	
Porifera		" <i>Spirorbis</i> "	
<i>Hyalostelina</i>		stromatolites	

Table 2. The macrofossils and ostracods from the Strathclyde Group. The distinction between marine and non-marine faunas is based on their macrofaunal associations.

Marine macrofauna: Crinoids, orthocones, bryozoans, brachiopods, trilobites, goniatites, gastropods and certain bivalves are indicators of a marine conditions. Marine macrofossils usually occur in a high diversity assemblage with most of the aforementioned groups. The faunal elements are mainly benthic (brachiopods, bivalves, bryozoans, corals, echinoids, trilobites and gastropods), but there are also rare planktonic (crinoids) and nektonic elements (cephalopods; goniatites, nautiloids and orthocones) (Figure 3).

In the Ballagan Formation orthocones occur with encrusting “*Spirorbis*”, ostracods and rare brachiopods in what is interpreted as a marginal marine to brackish environment (Stephenson *et al.* 2004). However, the orthocones from the Strathclyde Group are not encrusted by “*Spirorbis*”, and are usually associated with a high diversity assemblage of marine macrofauna.

Marginal marine macrofauna: Macrofuana attributed as marginal marine are species of *Lingula*, certain bivalves (*Myalina*, *Schizodus*, *Sanguinolites*) and fish (Table 2).

Brachiopods: *Lingula* is sometimes associated with a diverse marine macrofauna (of gastropods, crinoids, brachiopods and bryozoans), and in other deposits with non-marine fauna such as the bivalve *Naiadites*. *Lingula squamiformis* was interpreted from the Mississippian of the Midland Valley as a brackish species (Ferguson 1962). *Lingula* occurs in the highest frequency with marine macrofauna, and more rarely with groups considered as brackish or freshwater; *Naiadites*, “*Spirorbis*”, fish, freshwater bivalves and Spinicaudata (Figure 4A). From these faunal associations *Lingula* is interpreted as a marginal marine, rather than a brackish element.

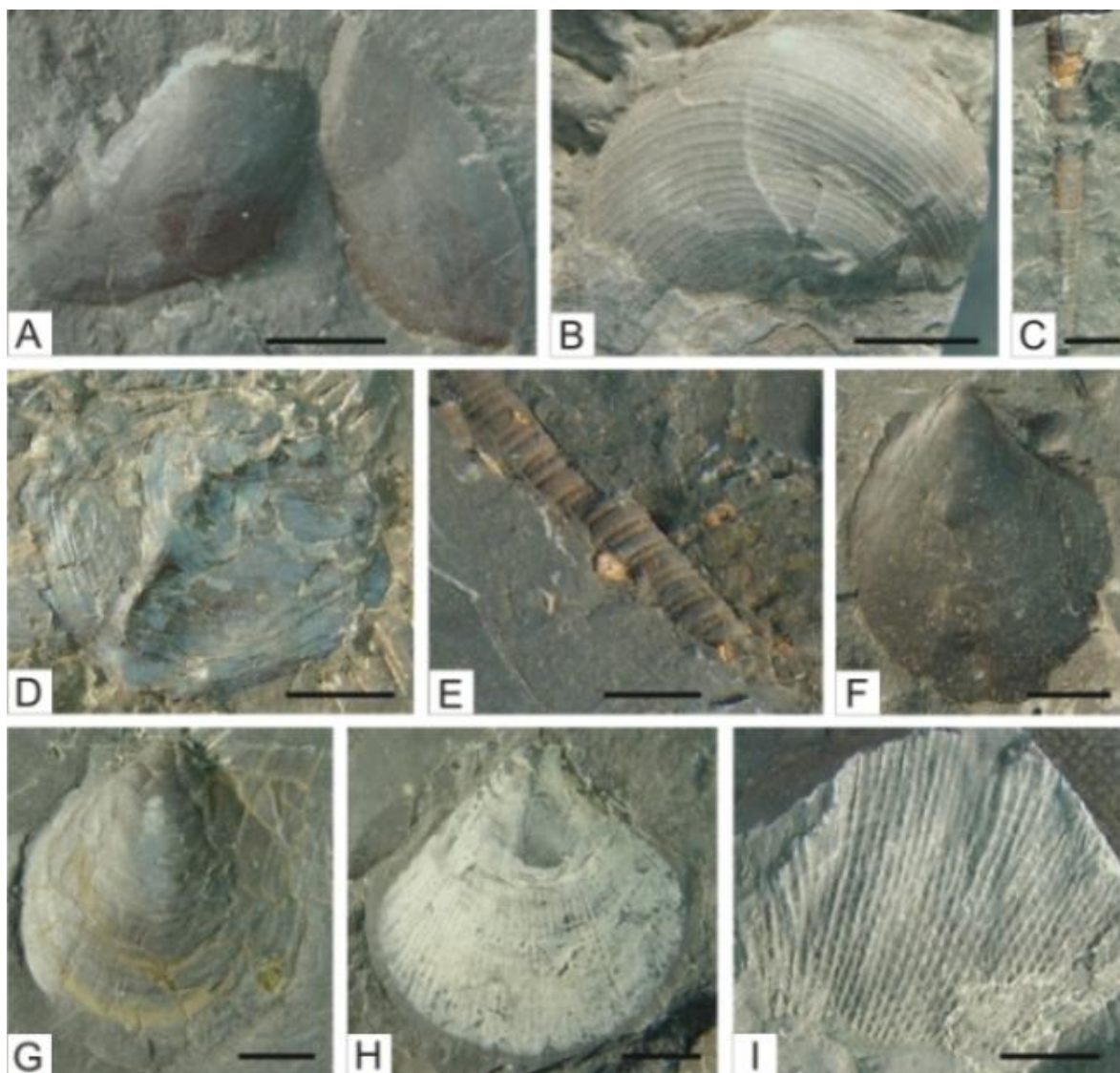


Figure 3. Marine macrofossils of the Strathclyde Group. A: *Palaeoneilo* cf. *brevisstrom*, sample SE 8859. B: *Retispira striata*, EN 4907. C: Orthocone, SE 8250. D: *Orbiculoidea* sp., SE 8717. E: Crinoid columnals, a rare example of an articulated specimen, SE 8195. F: *Streblochondria* sp., SE 8179. G: *Streblopteria ornata*, EN 5313. H: *Aviculopecten* cf. *subconoideus*, EN 5225. I: *Fenestella* sp., SE 8231. Scale bars 5 mm, light photographs.

Bivalves: The common bivalves *Schizodus* and *Sanguinolites* are interpreted as marginal marine; they follow a similar faunal association trend to that of *Lingula* (Figure 4A).

Myalina is recorded as a common freshwater bivalve from the Mississippian of Scotland

(Ferguson 1962); however in the current study it is rare, is associated with marine macrofossils and *Lingula*, and is therefore regarded as a marginal marine element.

Brackish macrofauna: The macrofauna interpreted as brackish water tolerant includes *Curvimirula* and *Naiadites*, “*Spirorbis*” and fish (Figure 5).

Bivalves: *Naiadites* and *Curvimirula* are discussed below (under ‘freshwater’).

“*Spirorbis*”: Spirorbids are frequently found in association with plant and fish fragments, *Naiadites* and *Curvimirula* (Figure 4B). They have been recorded from other sections of the Mississippian of the Midland Valley of Scotland in a range of sediments from marine to brackish (Wilson 1989). In the current study they are most often found in mudstones and are interpreted as a brackish to freshwater tolerant fauna. An example of a rare marine association is a bivalve-rich packstone from the Anstruther Formation, where “*Spirorbis*” encrusts the surface of *Schizodus* bivalves.

“*Spirorbis*” is common in non-marine sediments. Specimens have the form of prostrate discoidal tubes, which are planispiral, evolute, coiled and calcareous, ranging from 230-2000 µm in diameter (Figure 5D). Transverse growth bands are present on the tube, and the aperture is the widest part of the tube.

Recent *Spirorbis* is a polychaete worm, but Palaeozoic spirorbids are considered to be more closely related to the Microconchida, an extinct order of lophophorates (Taylor & Vinn 2006). Although recent *Spirorbis* is stenohaline, Palaeozoic spirorbids are most commonly found in freshwater, brackish and hypersaline environments (Taylor & Vinn 2006). The lifestyle is similar to modern *Spirorbis* in that they encrust hard substrates,

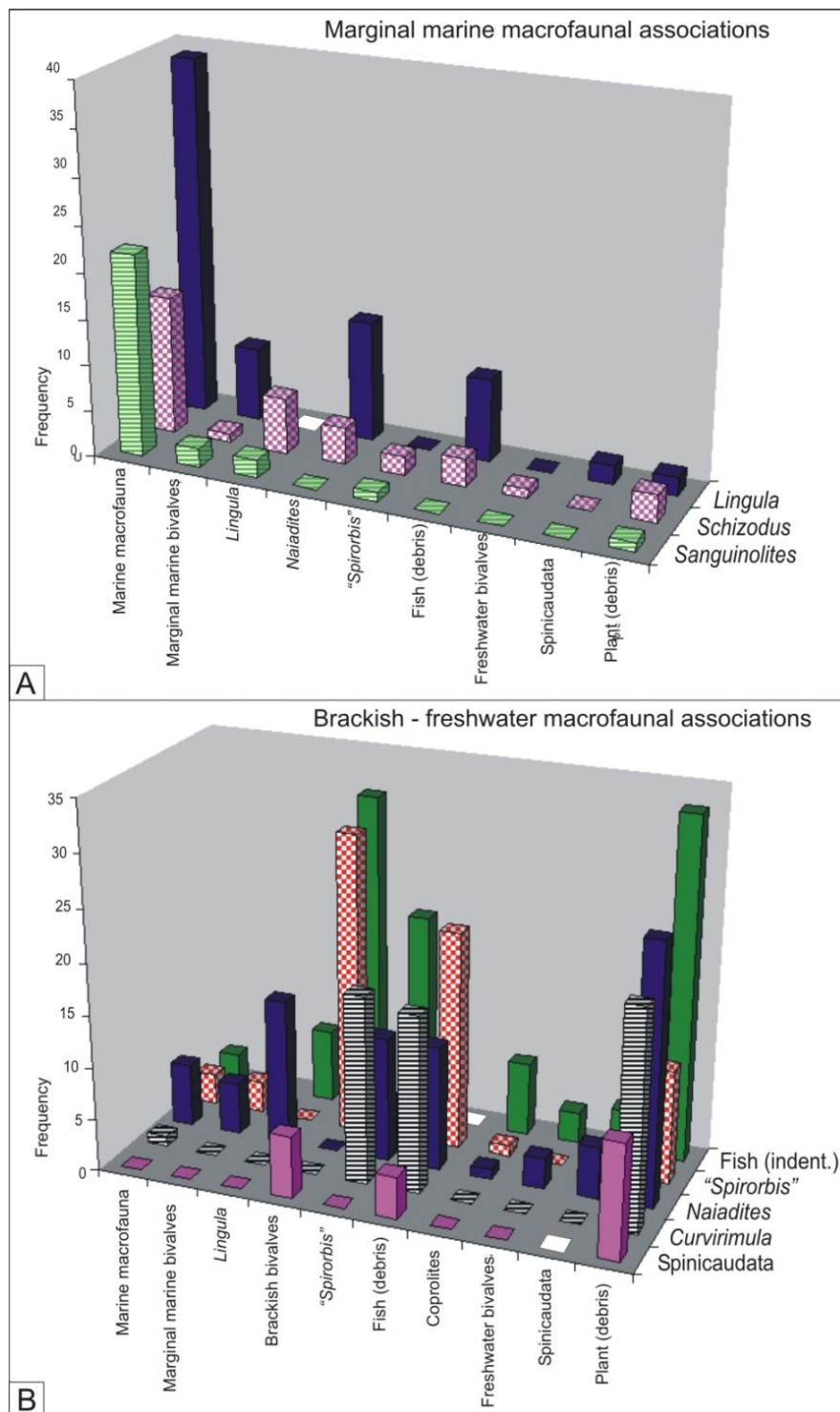


Figure 4. Histograms of macrofaunal associations for (A) marginal marine and (B) brackish to freshwater faunas. The frequency of different faunal associations is used to interpret the environmental tolerance of key non-marine fauna. The key fauna analysed are on the z axis, for example *Lingula*, *Schizodus* and *Sanguinolites* in A. On the x axis the faunal associations, from left to right, are: marine, marginal, brackish and freshwater. Appendix 2 and 3 contain the data used in this figure.

and were probably suspension feeders. Some known from the Mississippian encrust skeletal and non-skeletal stromatolites (Burchette & Riding 1977).

Freshwater macrofauna: The macrofossils interpreted as freshwater are the bivalves *Anthraconaia*, *Carbonicola* and *Cardiopteridium*, and Spinicaudata (Table 2). Some faunal elements have a brackish to freshwater tolerance, such as *Curvirimula*, *Naiadites*, fish and “*Spirorbis*”.

Bivalves: *Anthraconaia*, *Carbonicola* and *Cardiopteridium* are interpreted as freshwater bivalves. They commonly occur as low diversity assemblages associated with *Naiadites*, plant and fish debris. *Naiadites* and *Curvirimula* have an association with marine to freshwater macrofauna, but occur only rarely with marine or marginal marine macrofossils (Figure 4B). Their most common occurrence is in brackish to freshwater assemblages, associated with plant and fish debris. Of the two genera *Naiadites* more commonly occurs with marginal marine elements (Figure 4B). In all formations *Naiadites* is commonly present as the sole macrofossil in a sample, and in this case the environment is interpreted as either freshwater or brackish.

Anthraconaia, *Carbonicola* and *Naiadites* are commonly found in the Pennsylvanian Coal Measures of North America and Britain, and are interpreted as freshwater faunas (Cliff & Trueman 1929, Scott & Summerson 1943, Jenkins 1960, Pollard 1966, Hartley 1993, Brand 1996, Eagar & Belt 2003). *Naiadites* and *Curvirimula* are described from Pennsylvanian Joggins Formation of Canada, in freshwater lacustrine, palaeudal and near-shore brackish water sediments (Brand 1994, Falcon-Lang 2005, Falcon-Lang *et al.* 2006).

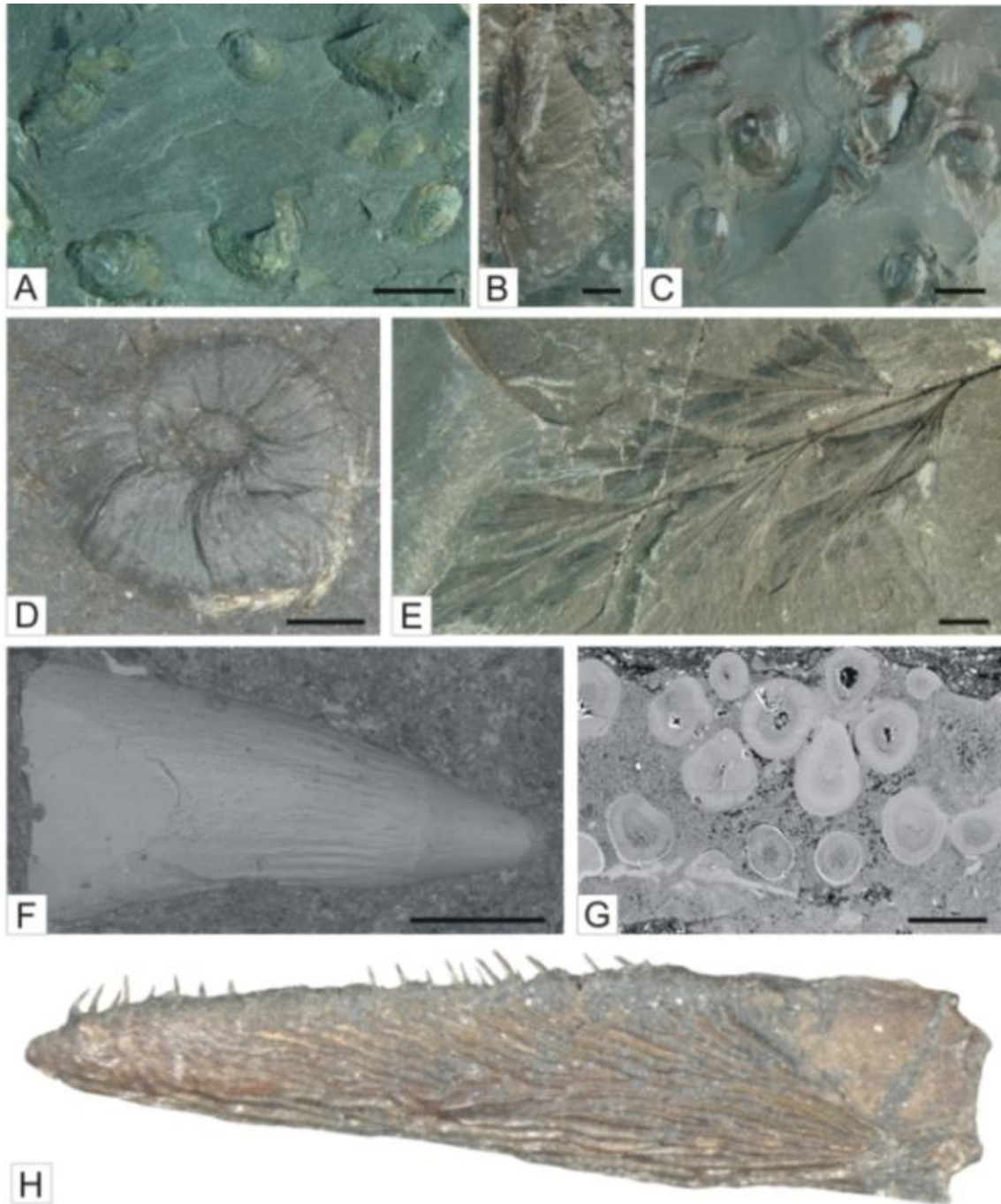


Figure 5. Non-marine macrofossils of the Strathclyde Group. A: *Curvirimula* cf. *scotica*, pyritised, 6E 6526. B: *Myalina* sp., SE 8260. C: *Naiadites obesus*, SE 8591. D: “*Spirorbis*”, SE 8729. E: *Telangium affinae*, SE 8509. F to H: fish fragments that are associated with ostracods. F: large, broad, fish tooth, EL 5476. G: thin section of a fish jaw showing cross sections across the teeth, 6E 6669. H: Fish toothed jaw plate, probably from an actinopterygian, EN 5193, jaw is 10.5 mm long. A-C, E: scale bar 5 mm. D: scale bar 0.5 mm. F: scale bar 400 μ m. G: scale bar 100 μ m. Light photographs.

Anthraconaia, *Carbonicola* and *Naiadites* are rarer in the Mississippian, and their marine to freshwater colonisation probably occurred at that time (Ballèvre & Lardeux 2005).

Mississippian examples of brackish-water *Naiadites* occur in France (Ballèvre & Lardeux 2005) and the Midland Valley of Scotland (Trueman & Weir 1946). *Carbonicola* and *Naiadites* have been described from the Randerston section, and other localities of Fife in non-marine sediments, together with “*Spirorbis*”, fish, ostracods and *Anthraconaia? kirki* (Bennison 1960, 1961). The present study records many more specimens of *Carbonicola* and *Naiadites* from sediments interpreted as freshwater.

Curvimula scotia is described from microbial limestones of the Sandy Craig Formation that are interpreted as lacustrine (Guirdham *et al.* 2003). *Curvimula* is commonly associated with *Anthraconaia* or *Naiadites* in Pennsylvanian coal deposits (see, for example, Eagar & Peirce 1993, Anderson *et al.* 1999, Falcon-Lang *et al.* 2006).

Spinicaudata: The Spinicaudata are an order of Branchiopod arthropods also called the Conchostraca (Vannier *et al.* 2003): *Euestheria*, *Estheria* and *Leaia* are present in mudstones, associated with plants, fish and *Naiadites* (Figure 4B), and rarely with *Shemonaella siveteri* n. sp. and *Cavellina valida* Buschmina, 1968 ostracods. Mudstones stratigraphically a few centimeters above or below Spinicaudata-bearing samples contain “*Spirorbis*”, *Curvimula* and *Carbonita* sp. ostracods. The chitinous carapace is poorly preserved, often occurring as an impression or thin organic layer.

Extant conchostracans typically live in freshwater, but can tolerate low salinities (up to 6‰ NaCl). Spinicaudata are typically found in freshwater to brackish sediments by the Devonian, for example the Catskill deltaic complex (Knox & Gordon 1999; for a review of

lacustrine references refer to Park & Gierlowski-Kordesch 2007). Freshwater conchostracans are most common in the Pennsylvanian; for example in a limnetic setting in France (Vannier *et al.* 2003), and from Ireland in a freshwater (possibly brackish) coal-forming environment (Orr & Briggs 1999). Continental lakes from the Pennsylvanian and Permian of Morocco contain conchostracans and ostracods indet. (Hmich *et al.* 2006).

Leaid conchostracans from the Carboniferous and Permian of Australia are usually recorded in brackish to freshwater estuarine and coastal-plain water bodies such as temporary pools (Jones & Chen 2000 and references within). A late Palaeozoic record of brackish water Spinicaudata is reported as representing a taphocoenosis (Webb 1979).

Fish: Fish debris (fragments, scales and teeth) are found throughout the Strathclyde Group, most frequently in association with plants, “*Spirorbis*”, *Curvirimula* and *Naiadites* (Figure 4B). Other associates include coprolites (which may be of fish origin), *Lingula*, Spinicaudata, *Schizodus*, marine macrofossils, *Carbonicola*, *Anthraconaia* and the ostracods *Carbonita*, palaeocope sp. A and *Shemonaella siveteri* n. sp. The associated fauna suggests a brackish to freshwater interpretation. The most complete specimen is a small fish jaw (Figure 5C), that may be an actinopterygian, with affinities to *Rhadinichthys ferrox* Traquair (Zerina Johanson pers. comm.).

There are many cases of freshwater actinopterygians and sarcopterygians recorded from the Late Devonian and Carboniferous (for example, Daeschler 2000, Turner *et al.* 1999).

Freshwater fish are recorded in lakes from the Midland Valley of Scotland from Devonian times (Trewin & Davidson 1996). Although no complete specimens were found in this study, Mississippian age deposits containing fish from other areas of the Midland Valley

are interpreted as non-marine. The Wardie Shales in Lothian contain actinopterygians (including *Rhadinichthys ferrox*) and elasmobranchs, from a deep lagoonal environment; the Foulden Beds contain sarcopterygians and actinopterygians from a semi-permanent lake within an alluvial coastal plain (Dineley & Metcalf 1999).

Ichnofauna

The ichnofauna includes polychaete vertical dwelling traces; *Monocraterion*, *Arenicolites*, *Diplocraterion*, *Skolithos* and *Teichichnus*, horizontal feeding traces; *Palaeophycus* and *Planolites*, and the feeding-dwelling trace *Chondrites*. These forms typically occur in low-diversity or monospecific assemblages, which is characteristic of brackish estuarine conditions in the Carboniferous (Archer & Maples 1984, Buatois *et al.* 2005). *Chondrites* is an indicator of normal marine salinity when it occurs with other typically marine ichnofauna (such as *Rosselia*, *Scolocia* and *Helminthopsis*), but not when it occurs in a monospecific, or low-diversity assemblage (Buatois *et al.* 2005). Here it mainly occurs in marine bands, associated with *Diplocraterion* and *Teichichnus*, or in sandstones with a range of other vertical and horizontal polychaete traces. In general the low ichnodiversity and low degree of bioturbation is characteristic of brackish water conditions.

The sedimentary environments of the Strathclyde Group

Marine – evidence

The Anstruther Formation has sparse marine sediment content, with marine limestones, sandstones or mudstones overlain by non-marine sandstones and coals. Marine sediments are most often limestones, with bivalves, brachiopods, bryozoans, gastropods, orthocones,

rare crinoid debris and poorly preserved ostracods. The Randerston limestone 6 is a typical example of a marine limestone from the Anstruther Formation. It is a dolomitised biosparite packstone containing bivalves, brachiopods, gastropods, cephalopods, fish and ostracods (Figure 6). Marine macrofossils (brachiopods and gastropods) are present in the mudstones, silts and sandstones between the limestones, but in low diversity.

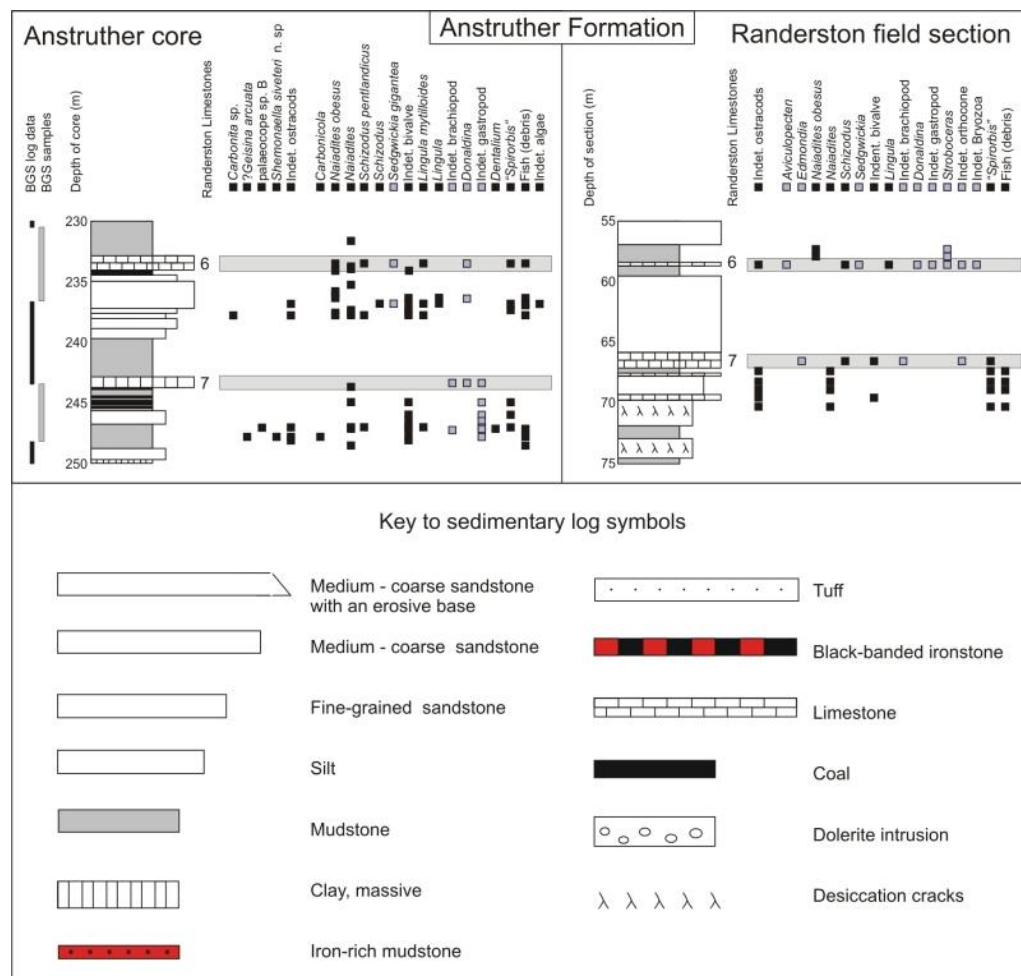


Figure 6. Sedimentary log correlation of the Randerston core and field section, Anstruther Formation. The limestones 6 and 7 are marine, and have a slightly different fauna in the core and field section. They are highlighted by a grey background box. The Randerston field section is from the east limb of the Randerston syncline. In all the logs marine fauna are represented by a grey colour square, those interpreted as non-marine by a black square. The sedimentary log key includes some symbols that are used in other figures. Appendix 4 contains sedimentary logs from all the sections in this study.

Marine sediments are more common in the Pittenweem Formation. The sequence of marine sediments are 1; limestones within marine mudstones (in a sequence of up to 8 m in thickness), or 2; isolated mudstone horizons overlain by non-marine silts and sandstones (in a coarsening upwards pattern). There is a diverse macrofauna of bivalves, brachiopods, bryozoans, echinoids, gastropods, orthocones and common crinoid debris (usually crinoid columnals).

The Sandy Craig Formation contains the fewest marine sediments, in the form of mudstones overlain by non-marine silts and sandstones (in a coarsening-upwards pattern). The macrofauna is low diversity: bivalves, brachiopods, gastropods and orthocones, associated with ostracods.

Marine sediments are the most common in the Pathhead Formation, in the form of mudstones in a coarsening upward sequence, or as marine limestones within a sequence of marine mudstones, which can be up to 10 m thick (Figure 7). The macrofaunal diversity is high, consisting of bivalves, brachiopods, bryozoans, echinoids, gastropods, orthocones, trilobites, common crinoid and goniatite debris. Dolomitised bioclastic wackstones are usually crinoidal (Searl 1990), for example the Upper Ardross Limestone (Figure 7). The Pathhead Lower Marine Band contains an abundant fauna of 30 macrofossil and 10 ostracod species (Figure 8).

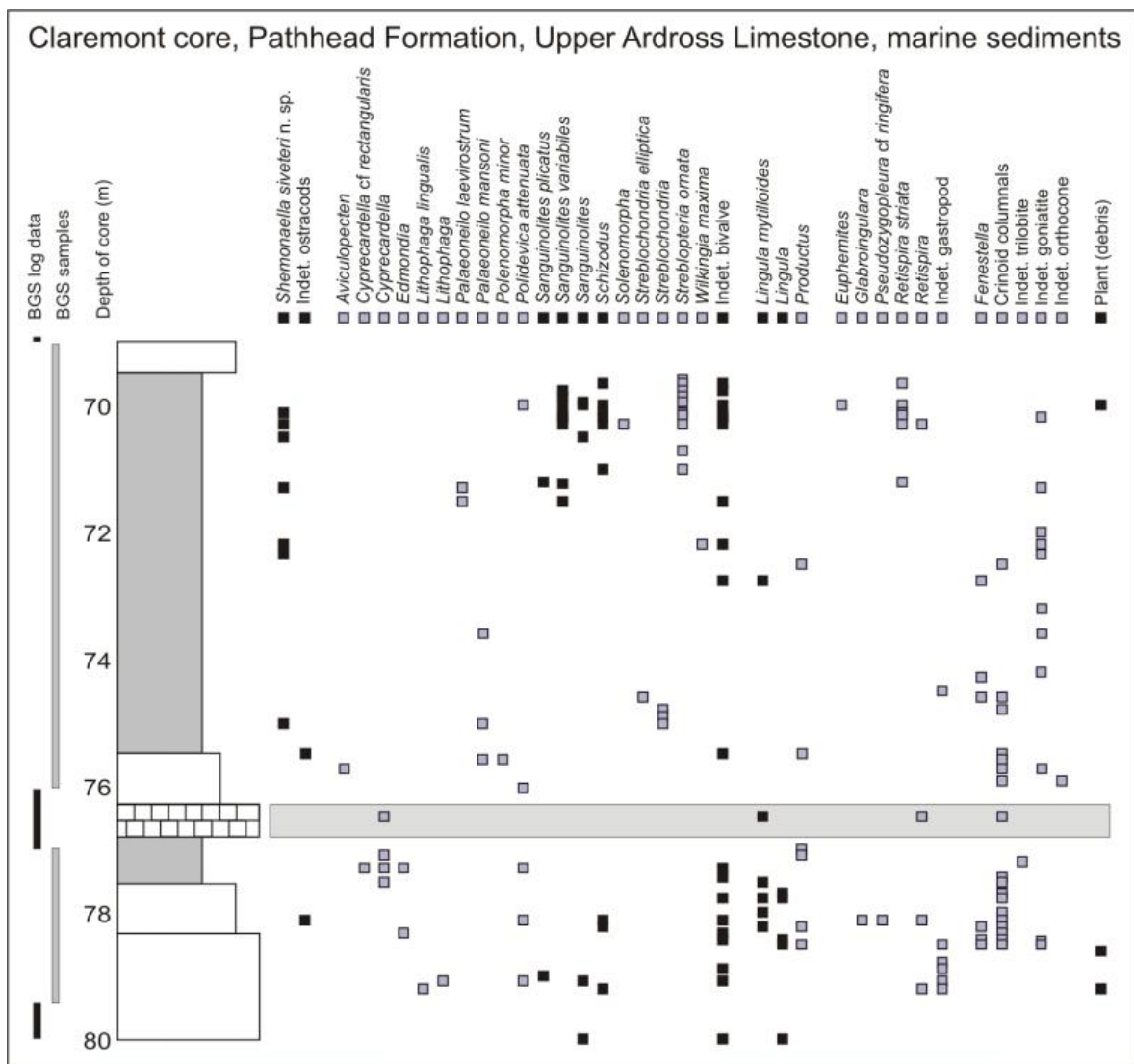


Figure 7. Sedimentary log of a marine crinoidal limestone from the Pathhead Formation, with surrounding marine mudstones and sandstones that also have a diverse marine macrofauna.

Ostracods associated with marine sediments are *Acutiangulata* sp. A, *Bairdia submucronata* Jones & Kirkby, 1879, *Cavellina benniei* Jones, Kirkby & Brady, 1874, *Cavellina taidonensis*, *Geisina arcuata* (Bean, 1836), *Healdia* cf. *cuneata* Robinson, 1978, *Hollinella* (*Keslingella*) *radiata* (Jones & Kirkby, 1886), palaeocope sp. A and C,

Paraparchites armstrongianus (Jones & Kirkby, 1886), *Polycope elegans* n. sp.,
Shemonaella siveteri n. sp. and *Shemonaella ornata* n. sp.

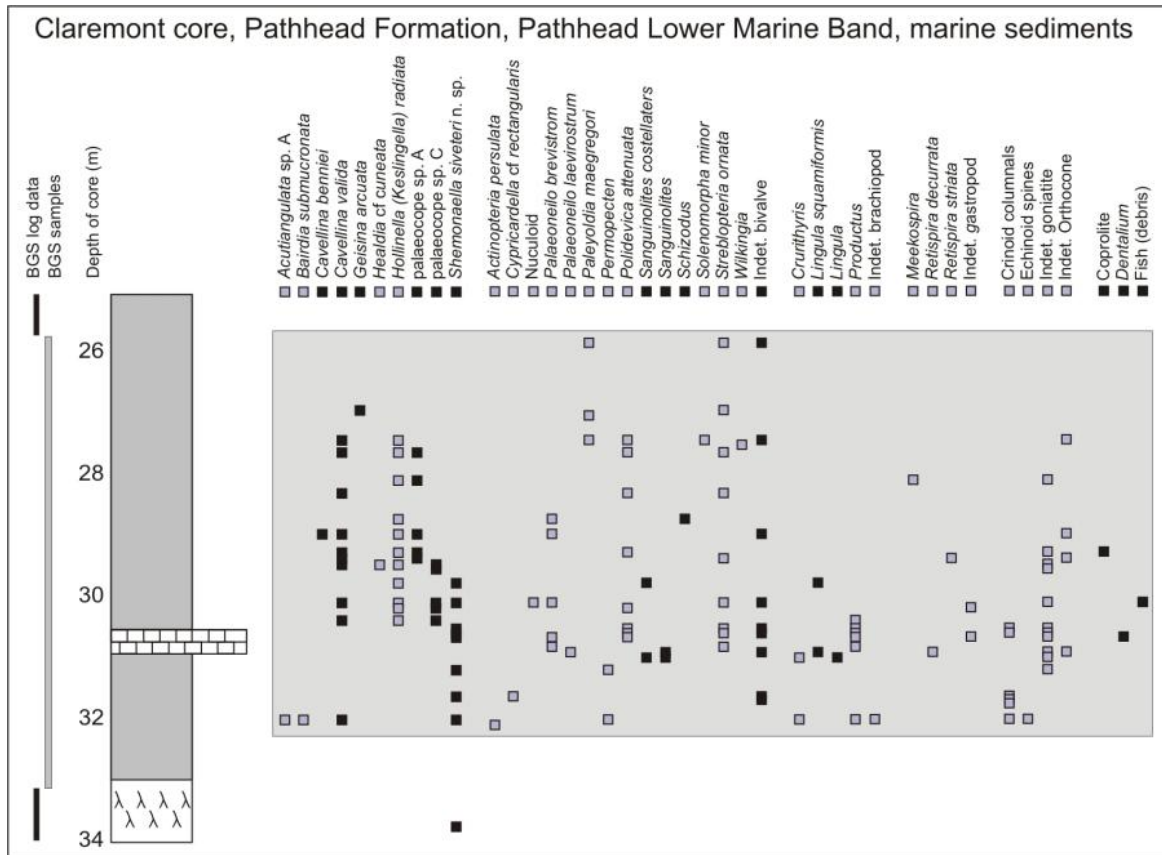


Figure 8. Sedimentary log of the Pathhead Lower Marine Band, highlighted by a grey box in the background. The marine bands of the Pathhead Formation have the highest diversity of ostracods and macrofossils in the Strathclyde Group.

Marine – interpretation

The marine sediments are interpreted as continental shelf, near-shore, shallow water deposits. This is represented by the dominance of benthic faunas representing a thanatocoenosis. Pelagic faunas such as goniatites are only found as fragments, so may have been washed in from deeper waters. The exception is orthocones, which are commonly articulated, and their presence may indicate more open marine conditions. The

deposits of marine limestones occurring within meters thickness of marine mudstones shows that at certain times there were open marine conditions for a substantial time. The lower diversity of marine fauna in some formations indicates a more restricted basin. The style of sedimentation represents rapidly shallowing-up sedimentary cycles, rather than prolonged open marine conditions. There is no evidence of hypersalinity, as is seen in the Ballagan Formation (Williams *et al.* 2006).

Marginal marine - evidence

Marginal marine sediments contain *Lingula*, *Schizodus*, *Sanguinolites* and *Naiadites*, or a reduced diversity of marine macrofauna. They are present in all of the formations, most commonly in the Pathhead and Pittenweem formations. The most common faunal element is *Lingula* in low-diversity assemblages. Based on the macrofauna, some of the named marine bands are re-interpreted as marginal marine: The Pittenweem Harbour Lingula Band contains abundant *Lingula*, plant and fish debris. The Kilconquhar Marine Band has a lower diversity of marine macrofauna, which may be an indicator of marginal conditions (Figure 9). From the Pathhead Formation the Ardross Lingula Band and the West Braes Marine Band are also interpreted as marginal marine on the basis of the restricted fauna of *Lingula*, plant and fish (debris).

Ostracods associated with marginal marine sediments are *Cavellina* sp., *Geisina arcuata*, palaeocope sp. A, *Paraparchites armstrongianus* and *Shemonaella siveteri* n. sp.

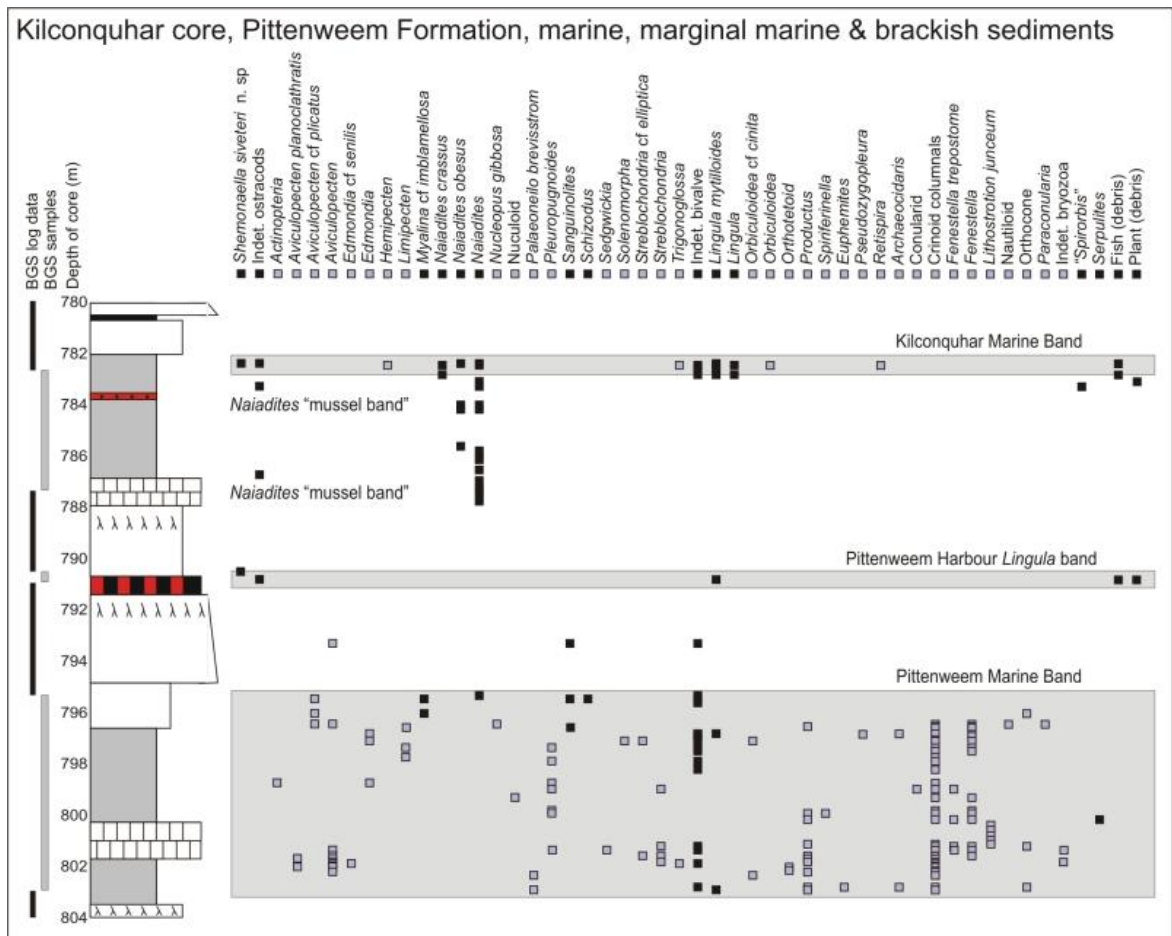


Figure 9. Sedimentary log of marine, marginal marine and brackish sediments of the Pittenweem Formation, Kilconquhar core. The Pittenweem Marine Band has a high macrofaunal diversity and is considered as fully marine. The Kilconquhar Marine Band is interpreted as marine to marginal marine. The Pittenweem Harbour Lingula band is marginal marine. *Naiadites* "mussel bands" are interpreted as brackish.

Marginal marine – interpretation

Marginal marine sediments are more common in formations which have a greater marine influence. The faunas that are assigned to a marginal marine tolerance are also present in marine or brackish sediments, so these are likely to be euryhaline species. Marginal marine environments could have formed in lagoons, embayments or estuaries where there was a lowered salinity. It is important to note that the interpretation of some sediments as

marginal marine may be influenced by poor fossil preservation; for example the West Braes Marine Band, as fauna may be more typically marine in other areas of the Midland Valley.

Deltaic to fluvial - evidence

Thick sandstone successions (greater than 20 m) with cross-bedding and convolute bedding are present in all but the Anstruther Formation (Figure 2). Two – four meter thick root-bearing and bioturbated sandstones are common in all the formations. These are usually a white, medium-grained quartz arenite. Sedimentary structures include channel forms, sigmoidal surfaces, trough cross-bedding, planar cross-bedding, convolute bedding and current ripples. Sandstones are often interbedded with mudstones on a centimeter to millimeter scale. *Stigmara* roots are the most common faunal element, and some of the tops of the beds are desiccated. The tops and bases of sandstone beds are in some cases bioturbated: *Arenicolites*, *Chondrites*, *Diplocraterion*, *Monocraterion*, *Palaeophycus*, *Planolites*, *Skolithos* and *Teichichnus* are present. Macrofossils are rare and consist of *Naiadites*, fish, plants, “*Spirorbis*”, *Lingula*, Spinicaudata and marginal marine bivalves. In rare cases a marine macrofauna is present in the sandstones (Figure 7). The sedimentary sequence is variable within and between the sections and formations. The ostracods found in the sandstones are only poorly preserved indeterminate forms.

Deltaic to fluvial – interpretation

The large tens of meters thickness of sandstone units, with convolute bedding and channel forms indicate deltaic deposition. The presence of a marine macrofauna indicates deltaic deposition in marine waters, such as at the delta front. The absence of these sediments in the Anstruther Formation provides evidence for lake-deltaic cycles. The majority of the

sandstones that are on a meter scale of thickness and contain cross-bedding, ripples and sigmoidal surfaces, are interpreted as fluvial in origin. The most common fauna in these sediments (*Naiadites*, fish, plants and ichnofauna) indicates brackish to freshwater conditions. Sandstones that are finely interbedded with mudstones and contain *Stigmaria* plant roots are interpreted as overbank deposits.

Brackish - evidence

Coquina of packed valves of *Naiadites* termed *Naiadites* “mussel bands” are common in the Anstruther and Pittenweem Formations (Figure 9). They occur in mudstones, more often in limestones, and can reach tens of centimeters in thickness. The majority of the “mussel bands” are associated with fresh to brackish water macrofauna, especially the mudstones; 14% of the “mussel band” limestones contain marine macrofauna. “Mussel bands” are no longer present above the base of the Sandy Craig Formation, as the dominant bivalve changes from *Naiadites* to *Curvirmula*, a genus that does not occur in coquina deposits.

Naiadites is the most common non-marine macrofossil. It is common in silts and mudstones in lower abundances, with articulated valves resting on the bedding planes. For example in the Randerston section (Anstruther Formation) *Naiadites* is associated with *Lingula*, *Schizodus* and plant debris, which are interpreted as brackish water. In other areas of this section *Naiadites* is associated with sediments interpreted as freshwater (Figure 10).

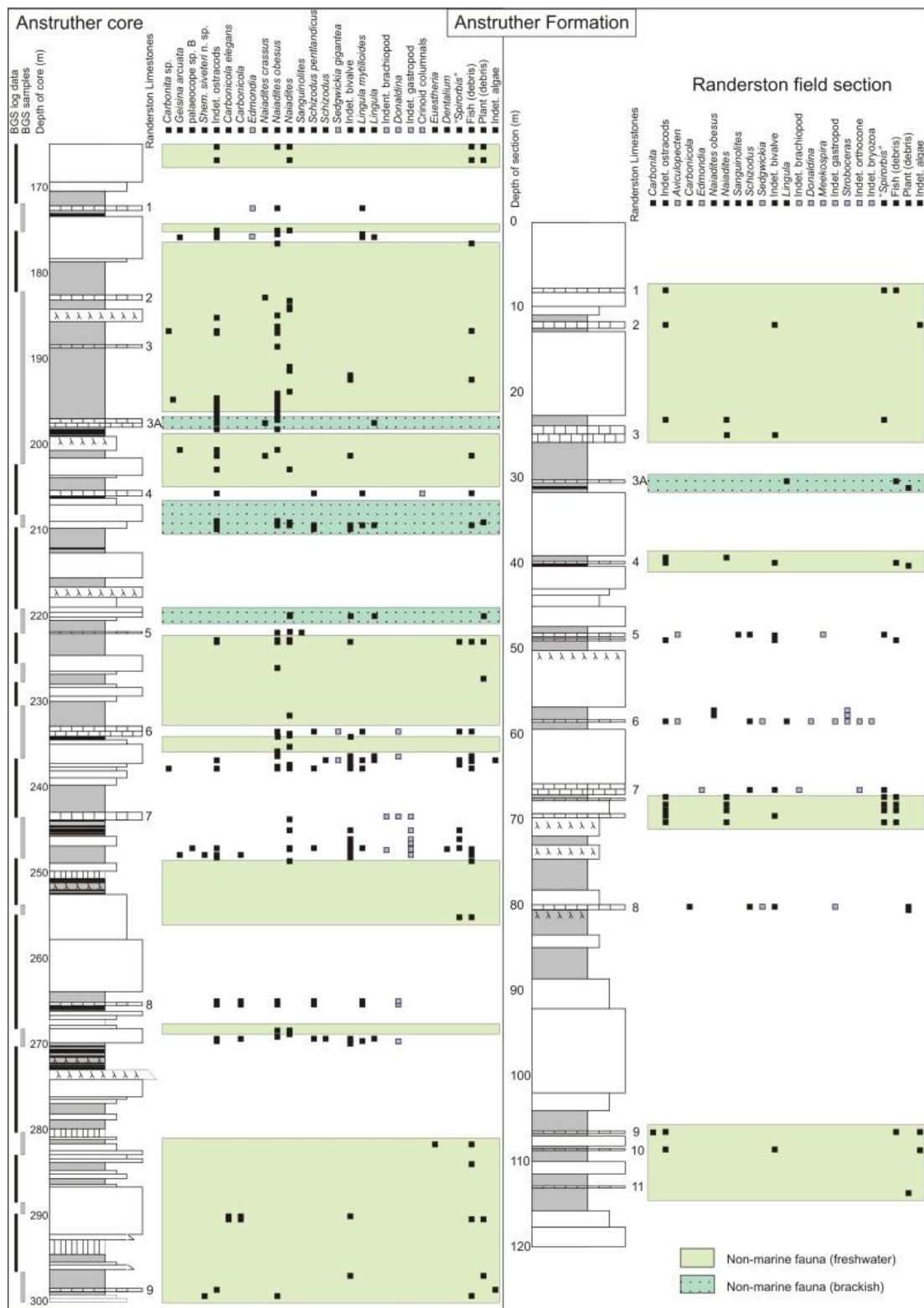


Figure 10. Sedimentary logs of the Randerston section. Sediments interpreted as brackish or freshwater are highlighted by background boxes. Sediments with no faunal content or with a marine fauna are not highlighted.

Ostracods associated with brackish sediments are *Carbonita* sp., *Cavellina benniei*, *Cavellina valida*, *Cavellina* sp., *Geisina arcuata*, palaeocope sp. A and B, *Paraparchites circularis* n. sp., *Shemonaella siveteri* n. sp., *Shemonaella ornata* n. sp. and *Silenites* sp. A.

Brackish – interpretation

The packstones and mudstones of *Naiadites* “mussel bands” indicate post-depositional transport by currents and wave action. The high degree of broken valves intimates a taphocoenosis. Bivalve and oyster shell bands are recorded in a shallow marine environment in the Jurassic (Wakefield 1995). In the current study *Naiadites* is commonly associated with brackish macrofauna, or as a mono-specific assemblage. Its occurrence in association with marine macrofauna may be due to taphonomic processes.

Siltstones and mudstones interpreted as brackish are associated with a fauna typified by *Curvirimula*, *Naiadites* and “*Spirorbis*”. As the exact palaeoenvironmental conditions of *Naiadites* (and some of its associated fauna such as “*Spirorbis*”) are unknown, there is a degree of uncertainty regarding a brackish or a freshwater interpretation. The change from *Naiadites* to *Curvirimula* dominance from the bottom of the Sandy Craig Formation may signify a change in water conditions from brackish to more freshwater. However, there is no change in other macrofauna to support this. Brackish environments could have formed in estuaries, restricted embayments or lakes with a partial marine connection.

Freshwater - evidence

The Anstruther Formation and Sandy Craig Formation contain common mudstones, carbonaceous shales, silts and sandstones associated with a macrofauna of Spinicaudata,

Carbonicola, *Curvirimula*, *Naiadites*, “*Spirorbis*”, coprolites, fish and plant (debris). These macrofossils represent a freshwater assemblage, and are associated with ostracods (Figures 10, 11A, 11B, 12). Marginal marine bivalves and brachiopods do not occur with these faunas. The Pittenweem Formation contains *Naiadites* in “mussel bands”, but few other freshwater fossils.

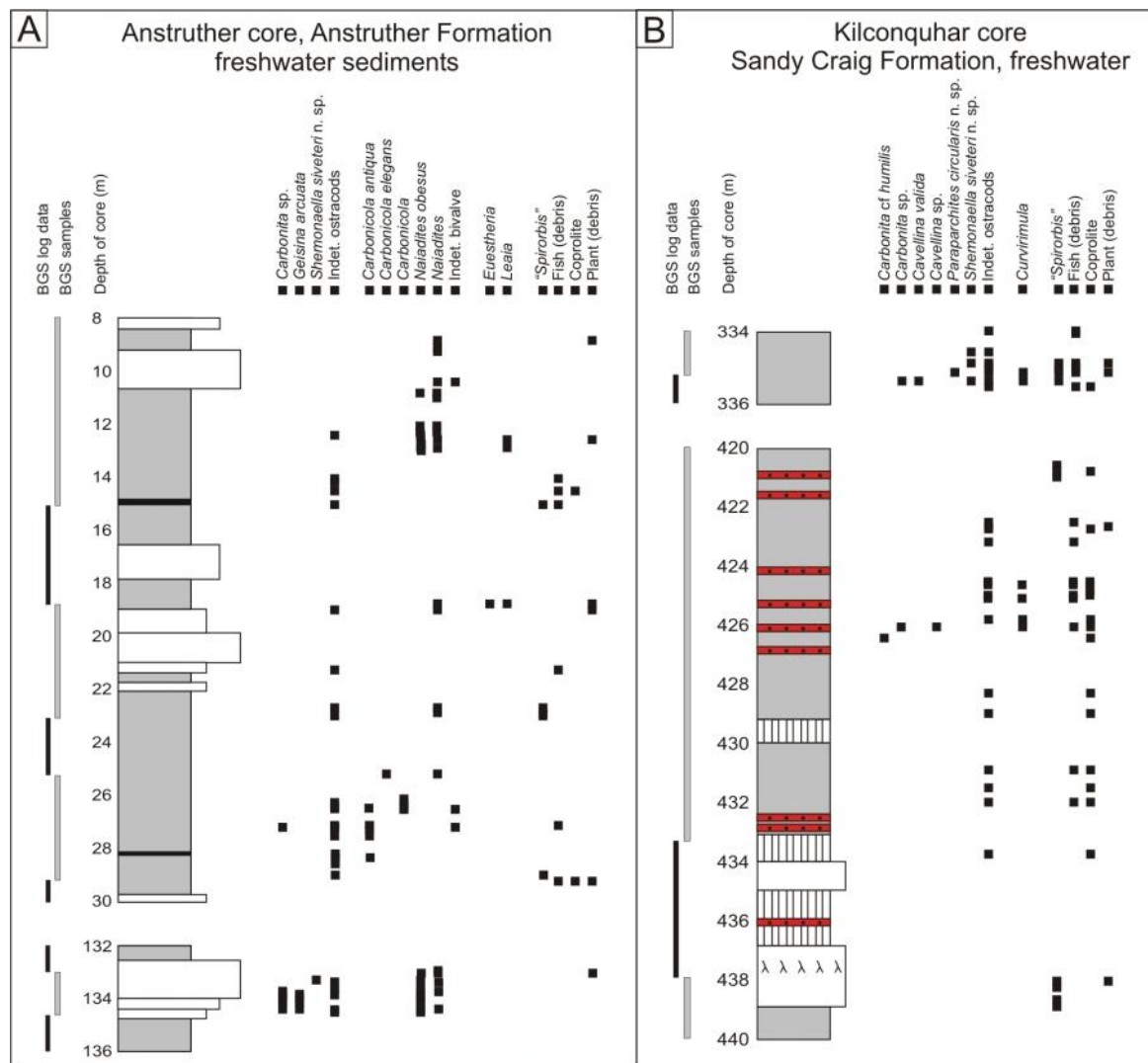


Figure 11. Sedimentary logs of freshwater sediments and ostracods of selected intervals from (A) the Anstruther core and (B) the Kilconquhar core. In the Kilconquhar core *Carbonita*, *Cavellina* and *Paraparchites* ostracods are associated with bivalves, Spinicaudata, “*Spirorbis*”, fish and plant debris. Mudstones contain the most fauna compared to other sediment types.

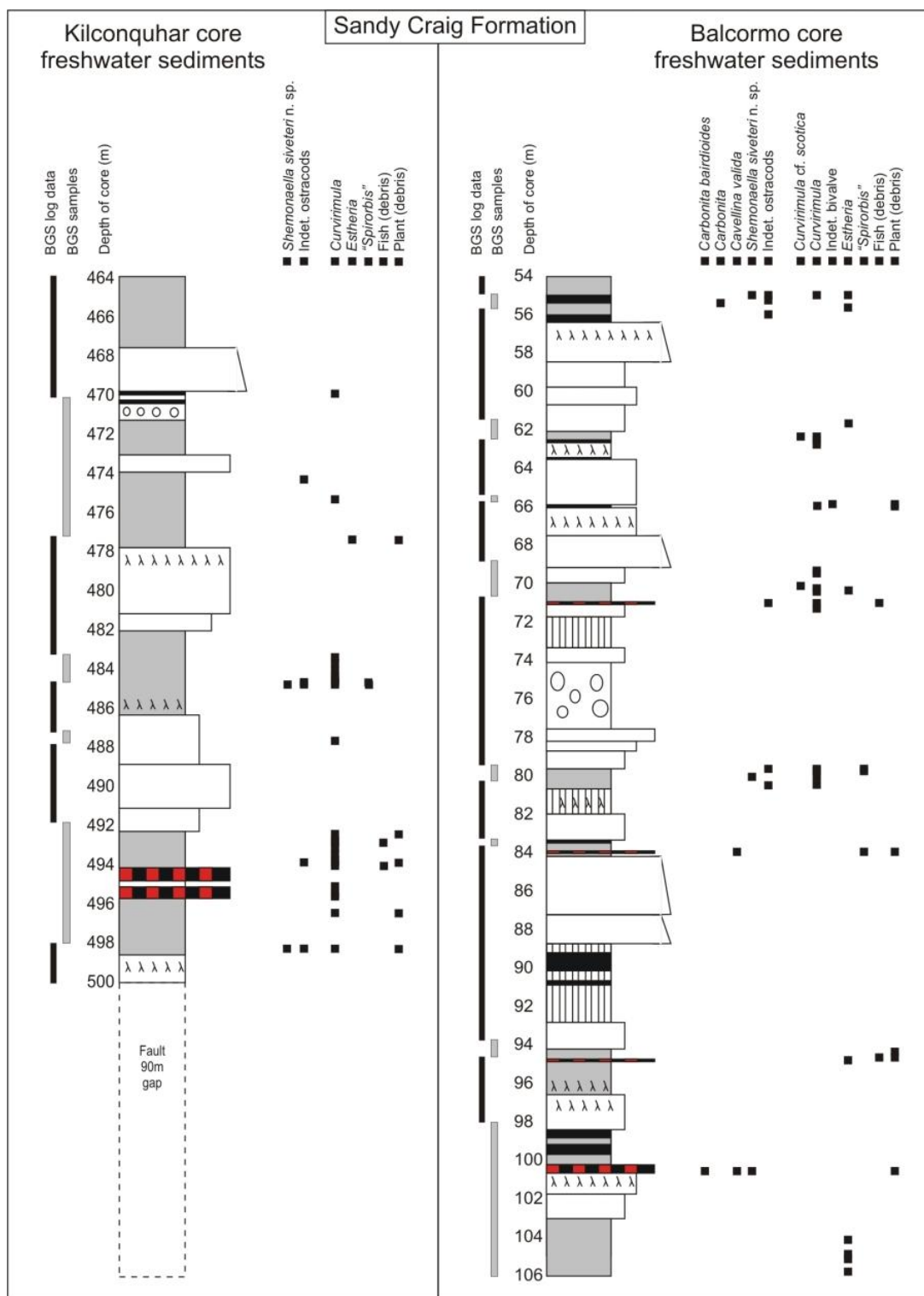


Figure 12. Freshwater sediments and fauna of the Kilconquhar and Balcormo cores, Sandy Craig Formation. Key freshwater sediments are black-banded ironstones.

Black-banded ironstones: Ostracods from the Sandy Craig Formation are most abundant in beds of black-banded ironstone (BBI). These consist of alternating laminations of iron-rich (siderite) mudstone and a black carbonaceous layer of mudstone, so abundant in plants it appears coalified. The laminae are bioturbated in some cases. This lithology is most common in the Sandy Craig Formation (Figure 12), but is also present in the Pathhead and Pittenweem formations. The fauna associated with BBIs are Spinicaudata, *Lingula*, *Curvirimula*, fish, “*Spirorbis*”, and four ostracod genera (Figure 13). From the macrofaunal associations the sediments are interpreted as freshwater; for example, a BBI of the Kilconquhar core (Pathhead Formation) contains carapaces of *Cavellina valida*, *Estheria*, “*Spirorbis*” and plant (debris). Ostracods are present on both the black plant-rich and the orange iron-rich mudstone laminae, and in most cases represent a thanatocoenosis.

The most abundant ostracod in monospecific assemblages is the podocopid *Paraparchites circularis* n. sp. It occurs within a 20 cm thick interval of BBI from the Sandy Craig Formation. The associated fauna are abundant plant debris, rare fish and rare *Carbonita* cf. *inflata* and *Silenites* sp. A. The ostracods are mainly adult carapaces, but there are also some juveniles and single valves. The random orientation of the carapaces, and their occurrence in abundance represents a thanatocoenosis (Figure 13). *Paraparchites* is known in the Carboniferous for its occurrence in hypersaline environments (Dewey 1983, 1987, 1988, Williams *et al.* 2004, 2006). In the deposits studied evidence of hypersalinity, such as desiccation cracks, gypsum or haline crystals, is lacking. The other occurrence of *Paraparchites circularis* n. sp. in the Strathclyde Group is in mudstones containing *Curvirimula*, “*Spirorbis*”, fish and plant debris that are interpreted as freshwater or possibly brackish.

Ostracods associated with argillaceous freshwater sediments are species of *Carbonita*, *Cavellina*, *Geisina*, *Paraparchites*, *Shemonaella*, *Silenites* and certain palaeocopes.



Figure 13. Black-banded ironstone (BBI) summary table of associated fauna (macrofossils and ostracods) and thin section scan of an ostracod-rich sample. The BBI sediments are most commonly associated with Spinicaudata. The thin section is of a BBI from the Sandy Craig Formation (Kilconquhar core, 363.37 m, SE 8412), which contains abundant *Paraparchites* n. sp ostracods. Scale bar 5 mm.

Algal limestones containing ostracods: Limestones interpreted as non-marine are most numerous in the Anstruther Formation (Figure 2). Some of these limestones contain algal bodies such as stromatolites or oncoids, with some of the oldest ostracods in the Strathclyde Group. The fauna in algal limestones consists of "*Spirorbis*", fish and plant (debris), coprolites, *Naiadites*, *Carbonita* sp., rare *Glyptolichvinella spiralis* (Jones & Kirkby, 1880), *Shemonaella siveteri* n. sp. and common ostracods indet. The ostracod-bearing algal limestones fit into two types:

Type 1. Stromatolitic and oncoidal limestones

Stromatolites and oncoids are organo-sedimentary structures of detrital sediment particles bound together by an algal film. The microbial structures and the sediment inbetween contain fish fragments and abundant ostracods. They occur in the Anstruther to Sandy Craig Formations and are classified into two sub-types: Type 1a: Discrete, vertically stacked hemispheroids (stromatolites). Type 1b: Concentrically stacked spheroids (oncoids).

Type 1a: The vertically stacked hemispheroidal algal forms have *Cryptozoon* like club-shaped or columnar shapes in outline (Logan *et al.* 1964). There is a space between each of the stromatolitic forms that is filled with oncoids or detrital sediment (Figure 14A). For each hemispheroidal form the basal radius of the laminae increases upward and the laminae are domed at the top (Figure 15C). A stromatolitic limestone from the Pittenweem Formation (Figure 15A-C) demonstrates the vertical variability in form. This limestone has laminated forms at the base, brecciated stromatolites in the middle, and well formed discrete hemispheroids at the top. The brecciated forms contain sparse ostracod single valves within the cracks.

Type 1b: Oncoidal forms vary in size from centimeters to pisoliths (2 mm) and oolites (1 mm or less). All are composed of concentric laminations of sediment, the laminae are a few microns in thickness. Most algal limestones are variable across the horizon and contain elements of types 1a and 1b.

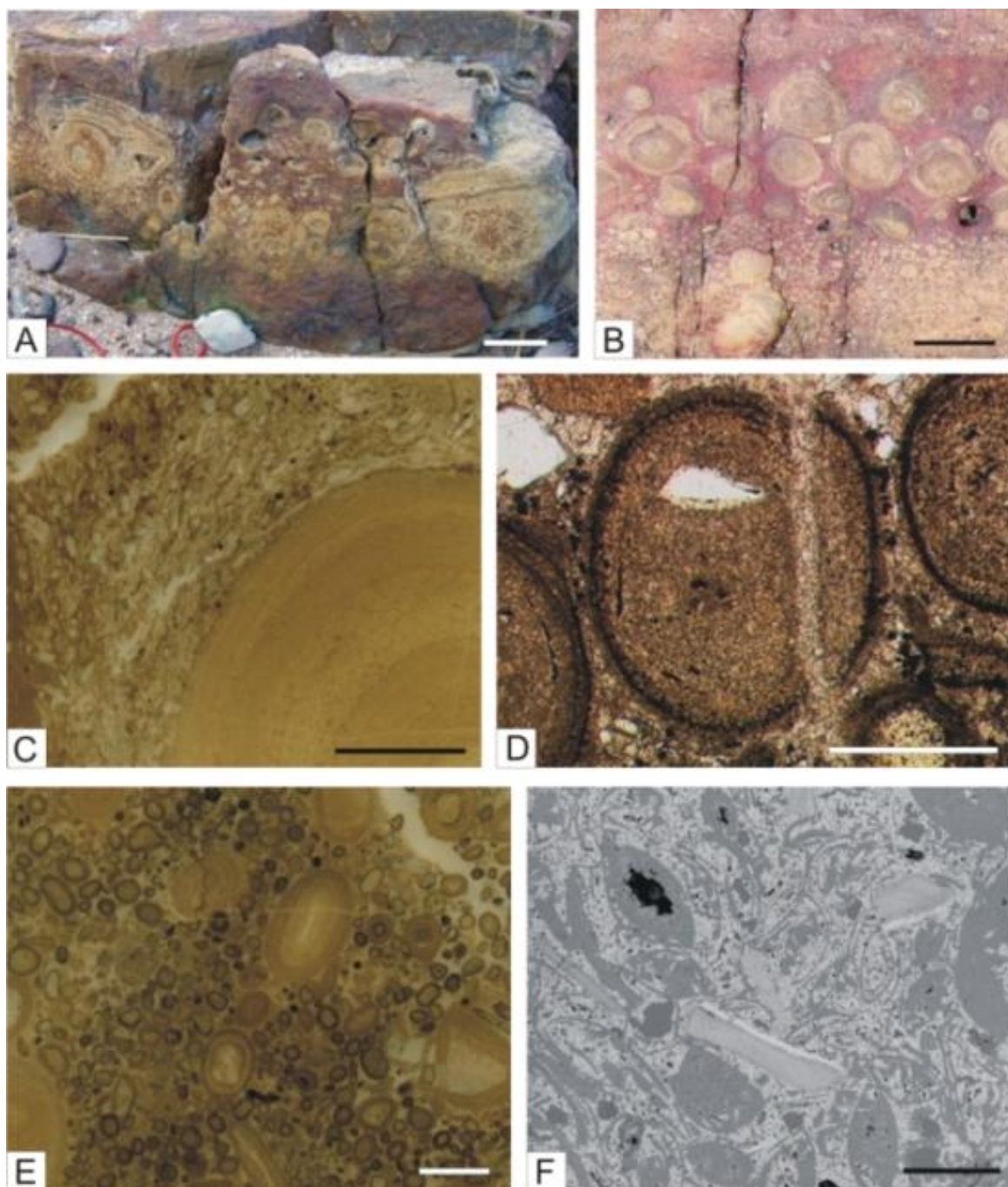


Figure 14. Randerston limestone 9, Anstruther Formation, a type 1b stromatolitic and oncooidal ostracod-bearing limestone. A: Vertically stacked hemispheroids, with oncooids in the space between them. B: Distinct layers of oncooids and pisoliths. C: Ostracod carapaces and single valves closely packed together around an oncooid, EL 5874C. D: a juvenile ostracod carapace in the centre of an oololith, EL 5872. E: Abundant oololiths in the sediment, EL 5874D. F: abundant ostracod carapaces, single valves and fish teeth, field sample 13. A, B: scale bar 2 cm, field photographs. C-F: scale bar 500 μm, polished thin sections.

The Randerston limestone 9 is stromatolitic and oncoidal, with a fauna of *Carbonita* sp. and fish teeth. Although stromatolites are abundant in some areas of the horizon (Figure 14A), the limestone is dominantly oolitic, pisolithic and oncoidal (Figure 14B-E). In some areas the different sized concentric coated grains are differentiated into layers (Figure 14B). Some of the oncoids incorporate pisoliths and ostracods in the centre (Figure 14D). This limestone contains the earliest *Carbonita* ostracods in the Strathclyde Group. In some areas of the horizon the ostracod assemblage consists of approximately 30% carapaces, whole single valves, and a range of adults and juveniles, thus representing a thanatocoenosis (Figure 14F). In other areas there are abundant single valves, densely packed together, representing a taphocoenosis (Figure 14C).

Type 2. Pisolithic plant-rich limestones

Pisolithic plant-rich limestones contain “*Spirorbis*”, fish (debris), ostracods and rare *Lingula* and *Myalina*. They occur only in the Anstruther Formation. An example from the Kingsbarns Section is composed of abundant, stacked log traces on the surface, some of which are up to 4 m long (Figure 15D). The sediment has a pisolithic carbonate layer on the bottom half (Figure 15E) and the top half is silt packed with organic layers rich in plant or wood debris (Figure 15F). The pisoliths are a variation in form of the type 1b oncoidal forms as they are irregular in shape. Ostracods are approximately 95% single valves, common throughout the limestone; some occur within pisoliths; all are poorly preserved.

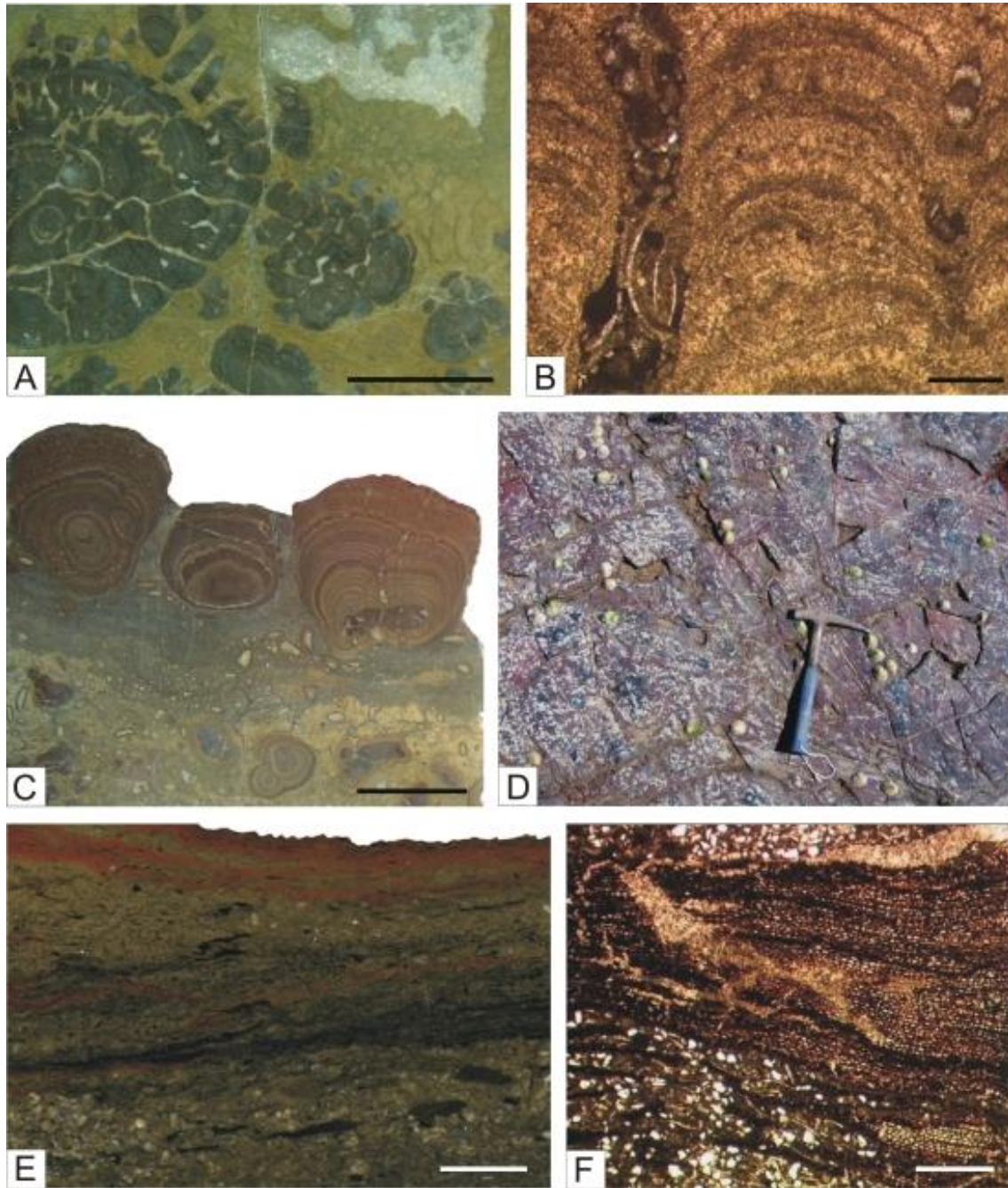


Figure 15. Type 1a and type 2 algal limestones containing ostracods. A to C: stromatolitic limestone from the Pittenweem Formation, SE 8699. A: brecciated discrete vertically stacked hemispheroids. B: ostracods filling the cracks of the stromatolite in A, SE 8699B. C: the top surface of well formed stromatolites. D to F: Kingsbarns pisolithic plant-rich limestone. D: The top surface of the limestone with numerous log traces. E: Rock section, the top layer is organic-rich, the bottom layer is pisolithic, field sample 19. F: thin section of a wood fragment preserving the cellular structure, field sample 19. A, C: scale bar 2 cm, rock scans. B, F: scale bar 500 μm , thin sections. D: field photograph. E: scale bar 10 mm, rock scan.

Freshwater – interpretation

Freshwater Swamps: The faunal content of the BBI lithology supports an interpretation of a freshwater environment. BBIs are common in the Pennsylvanian Coal Measures, with deposition in an environment between delta-top alluvial floodplains and coastal plain swamps with small lakes (Boardman 1989). The depositional setting of the sediments in this study is that of swampy conditions where plant debris had time to accumulate (and create the black laminae), alternating with shallow water deposition (iron-stained mudstone). The fine grain size and bioturbation suggests calm waters of deposition, possibly in a temporary pool or shallow lake. The change in sediment type on a laminae scale indicates fluctuating water levels and a periodic build-up of plant debris.

Mudstones or iron-rich mudstones containing Spinicaudata, *Naiadites*, fish, ostracods and an abundant plant content are interpreted as freshwater. Deposition of these sediments may have been in pools or shallow lakes, and this is a common habitat for Spinicaudata and fish in the Carboniferous.

The pisolithic plant-rich algal limestone is interpreted to have been deposited in a shallow carbonate-rich temporary pond, lake or swamp where pisoliths formed, and abundant plant debris and wood had time to accumulate. The environment of deposition is interpreted as freshwater, due to the lack of any brackish or marine fauna and the abundance of plant debris. The ostracods were subject to transport due to the high proportion of single valves, so their original ecology is uncertain.

Freshwater lacustrine: The Anstruther Formation consists of repeated units of non-marine limestones, mudstones and sandstones, which are interpreted as lake-deltaic cycles.

Occasional marine limestones are also present within this sequence, so there must have been a marine connection with the lake at certain times. From the fauna of the algal ostracod-bearing limestones a freshwater depositional environment is proposed.

The variation in the algal forms from stromatolitic to oncoidal (with different sizes) demonstrates a rapidly changing water line, agitated water and wave action (Logan *et al.* 1964). In areas of the Strathclyde Group where stromatolites are well formed, water conditions may have been less agitated, with possible lacustrine conditions. There were periods of exposure (brecciated stromatolites), but no pedogenic features are present, such as those seen in palustrine carbonates of the Late Devonian from Canada (MacNeil & Jones 2006). This implies that any sub-aerial exposure was of short duration.

Freshwater algal limestones (stromatolites, oncoids, laminates) from lacustrine and ephemeral ponds have been recorded in the Carboniferous from the Midland Valley of Scotland (Guirdham *et al.* 2003), the Pennsylvanian of France (Freyet *et al.* 2000) and the Pennsylvanian of Illinois (Scott 1944). Recent oncoids have been described from freshwater lakes (Davaud & Girardclos 2001, Wilkinson 1980), but oncoids can also occur in marine, brackish and hypersaline environments (see review in Peryt 1983).

Freshwater stromatolites are composed of a diverse community of algae and microinvertebrates, and it is necessary to recognize the diagenetic crystallisation fabrics of these associations in fossil specimens (Freytet & Verrecchia 1998). The limestones of the present study have been altered to ferroan dolomite and the stromatolites cannot be identified taxonomically. Therefore there is little direct algal evidence to support a hypothesis of freshwater conditions.

The evidence for freshwater conditions is the absence of a marine macrofauna and the presence of fish, plants and *Carbonita* ostracods. In some areas of the stromatolitic limestones, the high degree of single and broken valves shows the transport of ostracods, possibly by wave action. This is localised, in areas of a sample there is a high proportion of ostracod carapaces, suggesting an autochthonous assemblage.

Freshwater sediments do not contain the characteristic *Scoyenia* and *Mermia* ichnofacies of arthropod surface trails or fish grooves, which are common freshwater trace fossils in Carboniferous midcontinental lakes or upper estuary zones (Archer & Maples 1984, Buatois *et al.* 1998). The lack of these trace fossils could be due to preservation, as burrows are preferentially preserved over surface traces.

Ostracods and environment

Ostracod faunal associations of the key freshwater to brackish ostracods, *Cavellina*, *Shemonaella*, *Geisina* and *Carbonita*, are analysed (Figure 16). The macrofaunal associations show that *Cavellina* and *Shemonaella* have a wide salinity tolerance, while *Carbonita* and *Geisina* are mostly brackish to freshwater (Figure 16A). The ostracod associations show that *Cavellina* and *Shemonaella* most commonly occur with other eurytopic ostracods, while *Geisina* and *Carbonita* most commonly occur with each other (Figure 16B).

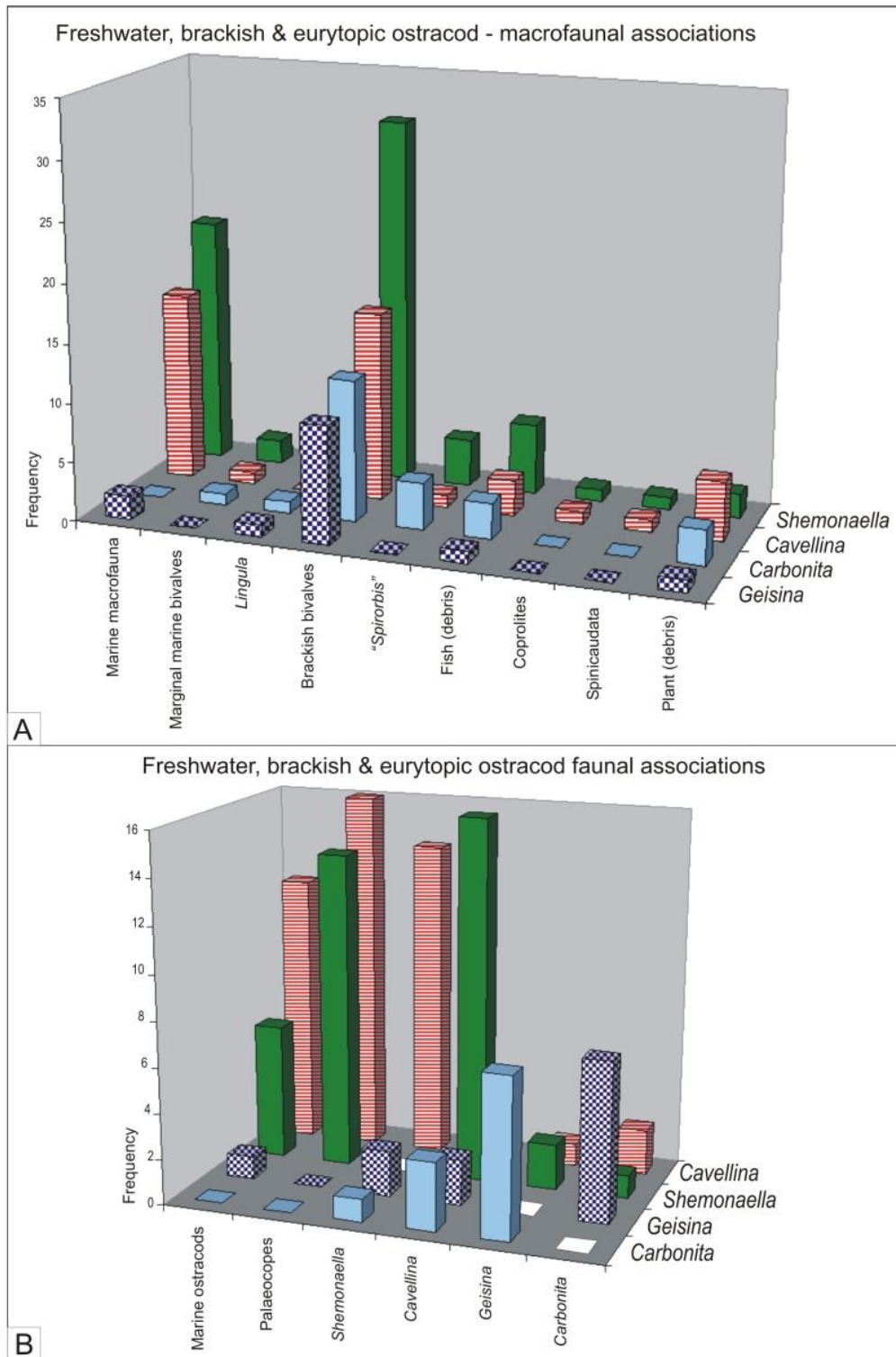


Figure 16. Faunal associations for the key non-marine ostracod genera of *Cavellina*, *Shemonaella*, *Geisina* and *Carbonita*. The faunal associations are plotted for occurrences with (A) macrofauna and (B) ostracods. On the x axis the faunal associations are: marine; marginal; brackish; and freshwater. The table of data used to construct the charts is in Appendix 3.

Marine: The marine ostracod fauna comprises 12 species (Figure 17), associated with marine macrofauna such as bryozoans, goniatites and brachiopods. The ostracods *Acutiangulata* sp. A, *Bairdia submucronata*, *Healdia* cf. *cuneata*, *Hollinella* (*Keslingella*) *radiata*, *palaeocope* sp. C and *Polycope elegans* n. sp. are stenohaline species, as they only occur in marine sediments. Apart from *Polycope elegans* n. sp., all the marine ostracods occur in mudstones of the Pathhead Lower Marine Band (Pathhead Formation), with stenotopic marine macrofossils. The fairly low diversity of stenohaline ostracods and lack of other typically marine Carboniferous genera such as *Kirkbya* and *Amphissites* (Coen *et al.* 1988, Olempska 1993) implies that fully marine conditions were restricted, or of short duration.

Bairdia is a typically stenohaline ostracod, and in open marine conditions it often constitutes up to 50% of the individuals in an assemblage (Lethiers 1981, Bless 1983, Bless *et al.* 1988). *Hollinella* typically occurs in marine bands of the Carboniferous (Athersuch *et al.* 2009, Přibyl 1960).

Acutiangulata is known for its possible brackish water tolerance, in carbonaceous facies assemblages (containing *Shemonaella*, *Cavellina* and “*Spirorbis*”) of the Mississippian of Britain (Robinson 1978). *Healdia* is a typically marine ostracod from the Mississippian (Olempska 1993). *Palaeocope* sp. C is associated with *Cavellina valida*, *Healdia* cf. *cuneata*, *Hollinella* (*Keslingella*) *radiata* and *Shemonaella siveteri* n. sp. The presence of only one specimen of both *Acutiangulata* sp. A and *Healdia* cf. *cuneata*, and only three specimens of *palaeocope* sp. C prevents a detailed environmental interpretation.

Polycope elegans n. sp. occurs in mudstones and silts associated with *Euphemites*, *Sanguinolites clavatus* and goniatites. The four assemblages of *Polycope elegans* n. sp. are mainly carapaces, one of which has butterfly preservation, suggesting a thanatocoenosis. Polycopids are considered to be nekton-benthonic marine ostracods (Horne 2003), and have been recorded from marine sediments in the Mississippian (Dewey & Fåhræus 1987).

Eurytopic: Seven eurytopic species range in occurrence from marine to non-marine sediments.

Cavellina benniei occurs in marine and brackish to freshwater mudstones of the Pathhead and Anstruther Formations (Figure 17). In marine sediments (one specimen) it is associated with *Cavellina valida*, *Hollinella* (*Keslingella*) *radiata*, *Shemonaella siveteri* n. sp., palaeocope sp. A and marine macrofauna. In brackish to freshwater sediments (three specimens) it is associated with *Cavellina valida* and *Naiadites*.

Cavellina valida occurs in marine sediments of the Pathhead and Sandy Craig Formation, and brackish to freshwater sediments of the Pathhead, Sandy Craig and Anstruther Formation (Figure 17). It is more abundant than *Cavellina benniei*, and occurs with a greater range of macrofauna and ostracods. It is commonly found in mudstones and the plant rich laminae of BBI sediments associated with *Carbonita* sp., *Shemonaella siveteri* n. sp. and “*Spirorbis*”.

Cavellina sp. occurs in marginal marine, brackish and freshwater sediments of the Pathhead, Sandy Craig and Anstruther Formations (Figure 17). It is associated with a wide range of macrofauna and ostracods (Figure 16A, B). *Cavellina* is known for its brackish water tolerance in the carbonaceous facies assemblage of the Mississippian of Britain

(Robinson 1978). *Cavellina* is also recognised as a marginal marine to brackish tolerant genus from the Ballagan Formation (Williams *et al.* 2005, 2006).

Palaeocope sp. A occurs in marine, marginal marine and brackish to freshwater sediments of the Pathhead Formation, and brackish to freshwater sediments of the Sandy Craig Formation (Figure 17). In the Sandy Craig Formation one single specimen occurs in a mudstone associated with *Shemonaella siveteri* n. sp., fish (debris) and coprolites.

Palaeocope sp. B occurs in brackish and freshwater sediments of the Pathhead Formation, and marginal marine sediments of the Anstruther Formation. The brackish to freshwater occurrences are in mudstones associated with *Cavellina* sp., palaeocope sp. A, *Shemonaella siveteri* n. sp. and *Naiadites*. Only five specimens of this species are recorded, so the palaeoenvironmental interpretation is uncertain.

Paraparchites armstrongianus occurs in marine and marginal marine mudstones of the Pathhead Formation, associated with *Shemonaella siveteri* n. sp., marine macrofauna, *Curvirmula*, *Lingula*, *Sanguinolites* and *Schizodus*. Species of *Paraparchites* with dorsal spines have been described in the Mississippian in association with marine ostracods such as *Amphissites* and *Bairdia* (Sohn 1969).

Shemonaella siveteri n. sp. is one of the most common species in the Strathclyde Group. It occurs in marine to freshwater sediments (Figure 17), often in high abundance, associated with a range of macrofauna and ostracods (Figure 16). Many records of *Shemonaella* in the Mississippian are from a marine environment (for example Crasquin 1985, Dewey 1993, Sohn 1971). However, the earliest record of a brackish water *Carbonita*

fauna from the early Carboniferous also contains species of *Shemonaella* (Tibert & Scott 1999).

Brackish to freshwater: Brackish ostracods are dominated by *Paraparchites circularis* n. sp. and *Shemonaella ornata* n. sp., with a few specimens of *Geisina arcuata* and *Silenites* sp. A.

Geisina arcuata occurs in association with marine, marginal marine and brackish to freshwater sediments (Figure 17). Brackish and freshwater sediments are most commonly mudstones with *Naiadites* and *Carbonita*. The species may have a wide environmental occurrence, but it is usually associated with brackish and freshwater macrofauna (Figure 16). It is recorded as a brackish to freshwater ostracod; in the Pennsylvanian Coal Measures of Belgium (Bless *et al.* 1987): In the Coal Measures of Britain it is associated with *Carbonita* (Pollard 1966, 1969, Anderson 1970, Bless & Pollard 1973), where it is considered as a freshwater indicator which may have also had a fairly wide salinity tolerance (Pollard 1966). Post-Palaeozoic ostracods of the Suborder Platycopina are exclusively marine (Horne 2003) and the relationship between the Carboniferous *Cavellina*, *Geisina* and *Glyptolichvinella* and Recent platycopes is poorly understood.

Paraparchites circularis n. sp. occurs solely in brackish to freshwater mudstones of the Sandy Craig Formation (Figure 17). *Paraparchites circularis* n. sp. occurs within a 20 cm thick interval of black-banded ironstone and also in brackish to freshwater mudstones. The great abundance of this species in the black-banded ironstone sediments may represent opportunistic reproductive strategies to quickly take advantage and colonise this temporary environment rich in plant foods. It is speculated that other Paraparchitoideans in the

Carboniferous may have used possible progenesis and parthenogenetic strategies (Dewey 1987). Species of *Paraparchites* have been recorded from environments interpreted as marine (Dewey 1988) and non-marine (Kummerow 1953, Williams *et al.* 2005c)

Shemonaella ornata n. sp. is recorded in brackish to freshwater mudstones of the Pathhead Formation, associated with *Acratia* sp. A, *Cavellina valida*, *Cavellina* sp. *Geisina arcuata*, palaeocope sp. A, *Shemonaella siveteri* n. sp., *Naiadites*, fish and plant (debris). Only six specimens of this species are recorded, so the palaeoenvironmental interpretation is uncertain.

Silenites sp. A. occurs in brackish to freshwater silts of the Pathhead Formation associated with *Cavellina* sp., palaeocope sp. A, *Shemonaella siveteri* n. sp. and *Curvirimula*. One specimen occurs in a black-banded ironstone of the Sandy Craig Formation, associated with *Paraparchites circularis* n. sp. Only three specimens of this species are recorded, so the palaeoenvironmental interpretation is uncertain. *Silenites* has been recorded in marine Mississippian sediments of Canada (Crasquin 1985).

Freshwater: Only species of *Carbonita* occur exclusively in freshwater sediments, from the Sandy Craig Formation (Figure 17): *Carbonita bairdioides* (Jones & Kirkby, 1879) and *Carbonita* cf. *inflata* (Jones & Kirkby, 1879) occur in BBIs associated with *Cavellina valida* and plant debris. *Carbonita* is not present in coals in this study, although it is common in coals from the Pennsylvanian (Scott & Summerson 1943, Scott 1944, Cooper 1946, Kummerow 1949, Buschmina 1959, Přibyl 1960, Pollard 1966, 1969, Anderson 1970, Bless & Pollard 1973, Sohn 1977, Schäfer 2007). *Carbonita* cf. *fabulina* (Jones &

Kirkby, 1879) occurs in an iron-rich silt associated with plant macrofossils. *Carbonita* cf. *humilis* (Jones & Kirkby, 1879) occurs in a mudstone associated with fish (debris).

Carbonita sp. occurs in brackish to freshwater argillaceous sediments and stromatolitic limestones of the Sandy Craig and Anstruther Formations. Associated fossils are rare marginal marine macrofaunas, brackish bivalves, “*Spirorbis*”, fish, plants, and *Geisina arcuata* is the most common ostracod (Figure 16).

Carbonita occurs in certain areas in the Mississippian, in what are interpreted as brackish water environments (Samoilova & Smirnova 1960, Buschmina 1965, Pollard 1985, Sohn 1985, Tibert & Scott 1999). The earliest record of *Carbonita* with detailed sedimentological and macrofaunal information is from Mississippian (Tournaisian) brackish sediments of Nova Scotia (Tibert & Scott 1999). It occurs with the ostracods *Bairdiacypris*, *Shemonaella* and *Copelandella* in a range of environments from near-shore marine to low salinity coastal ponds. *Carbonita* is widely reported in the Pennsylvanian Coal Measures of Britain (Anderson 1970, Pollard 1966), and across the globe, for example in Germany (Kummerow 1949) and Poland (Přibyl 1960). Most of the reports of *Carbonita* from the Pennsylvanian are from coals deposited near the coastline, which are interpreted as freshwater environments. The Pennsylvanian discovery by Vannier *et al.* (2003) is the first that documents *Carbonita* from an intramontain freshwater temporary pond, with no spatial or temporal marine connection. In the current study the first species of *Carbonita* are reported from freshwater environments of the early Mississippian.

Environment uncertain: A palaeoenvironmental interpretation is uncertain when only one specimen of a species occurs with few or no macrofauna.

Acratia sp. A. occurs in a mudstone below the Pathhead Upper Marine Band (Pathhead Formation), in association with *Curvirimula*, plant and fish (debris), *Shemonaella siveteri* n. sp., *Shemonaella ornata* n. sp., *Geisina arcuata* and *Cavellina valida*. *Acratia* is usually found in shallow marine settings (as in Olempska 1993), but this assemblage could be interpreted as brackish.

Glyptolichvinella spiralis occurs in an algal limestone of the Kingsbarns field section (Anstruther Formation). The limestone is pisolithic, with abundant plant fragments and bivalves (indet.). *Glyptolichvinella* is identified as a marginal marine to brackish tolerant genus from the Ballagan Formation (Williams *et al.* 2005, 2006).

Palaeocope sp. D occurs in mudstones of the Pathhead Formation, associated with palaeocope sp. A, *Shemonaella siveteri* n. sp. and *Cavellina* sp, all of which have a wide salinity tolerance.

Ostracod Biostratigraphy

The ostracod biostratigraphy and interpreted palaeoenvironments are shown in Figure 17. It is important to relate these factors, as certain ostracods only occur in one environment, for example the marine species of the Pathhead Formation.

In terms of biostratigraphy the ostracods of the Anstruther Formation and Pittenweem Formation are not useful. The only ostracod with a range restricted to the Anstruther Formation is *Glyptolichvinella spiralis*, of which there is only one specimen. The Pittenweem Formation only contains *Shemonaella siveteri* n. sp., which is a long-ranging species and indeterminate ostracods.

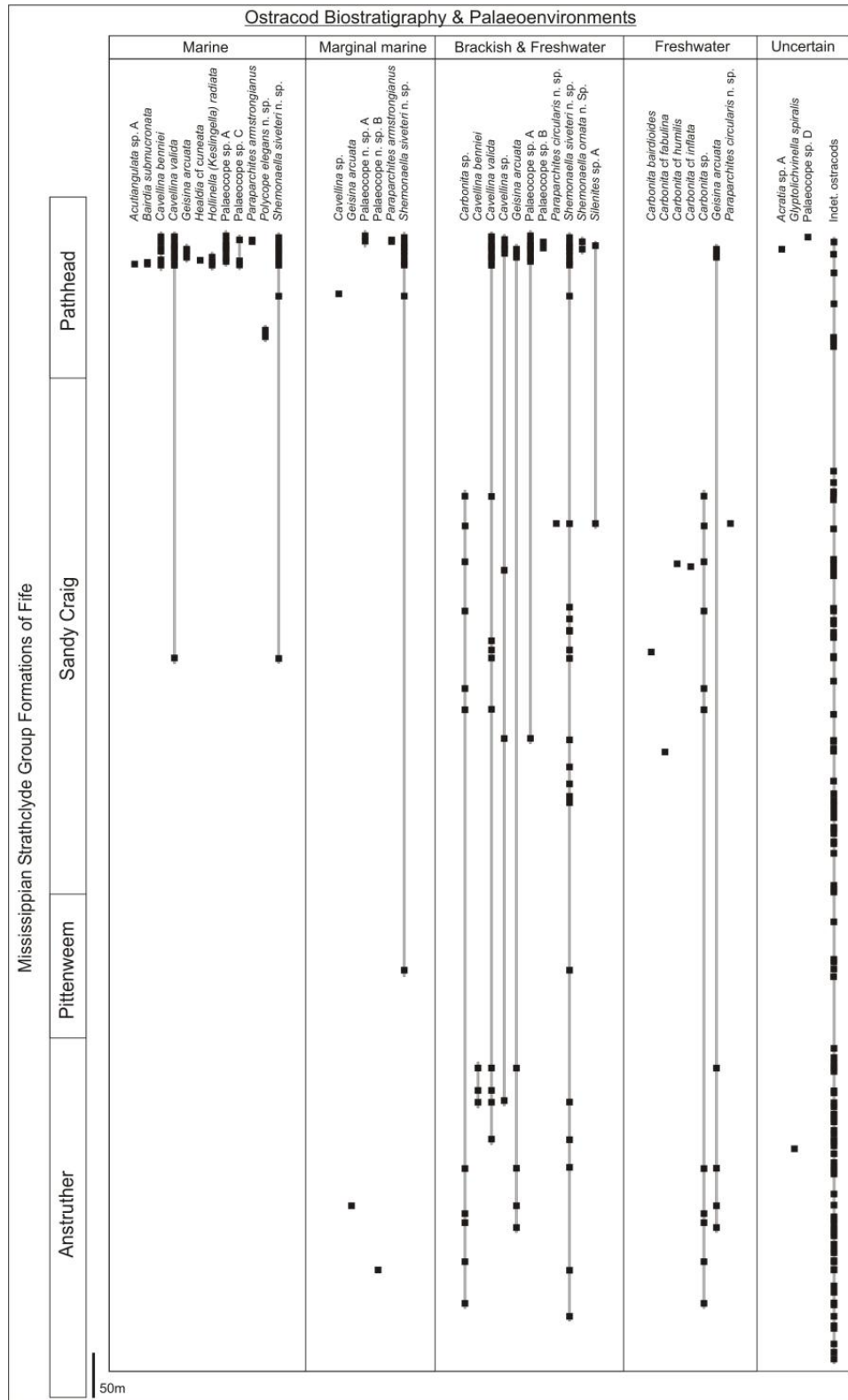


Figure 17. Ostracod biostratigraphy and palaeoenvironments of the Strathclyde Group. *Cavellina valida*, *Geisina arcuata*, *palaeocope* sp. A and *Shemonaella siveteri* n. sp. are long-ranging species.

The Sandy Craig Formation contains the range of species of *Carbonita* and *Paraparchites circularis* n. sp. The species of *Carbonita* are only present as a few specimens, so are not useful biostratigraphically. The unique biozone fossil is *Paraparchites circularis* n. sp., but its presence is biased towards brackish and freshwater sediments.

The Pathhead Formation contains the range of most of the marine ostracods (Figure 17). The potential biozone fossils are *Bairdia submucronata* and *Hollinella* (*Keslingella*) *radiata*, as they are fairly abundant. However, they only occur in stenotopic marine sediments, so their biostratigraphic potential is limited to marine sediments. Another problem is that these species have been recorded over the whole range of the Carboniferous (Robinson 1978). In summary, there are no key biostratigraphic ostracods that can be used for the Strathclyde Group, because of palaeoenvironmental factors.

Palaeoenvironmental model

The different palaeoenvironments in which ostracods are found are summarised in an environmental model (Figure 18). The model includes sedimentary, macrofossil and ostracod evidence from all the formations. The diagrams do not include ostracods that have an uncertain environmental position, or ostracods indet. The different environments are:

- Open marine, with stenohaline macrofossils and ostracods.
- Marginal marine, at the mouth of an estuary, a delta, embayments or lagoons in lower salinities than marine, marginal marine macrofauna and eurytopic ostracods.
- Freshwater to brackish, estuaries and lakes where there was a temporary marine connection, in which the salinity would have varied from brackish to freshwater.

- Freshwater, swamps with abundant plant debris and inland lakes with no marine connection. Deltaic, fluvial and floodplain sandstones are important environments, but usually do not contain ostracods.

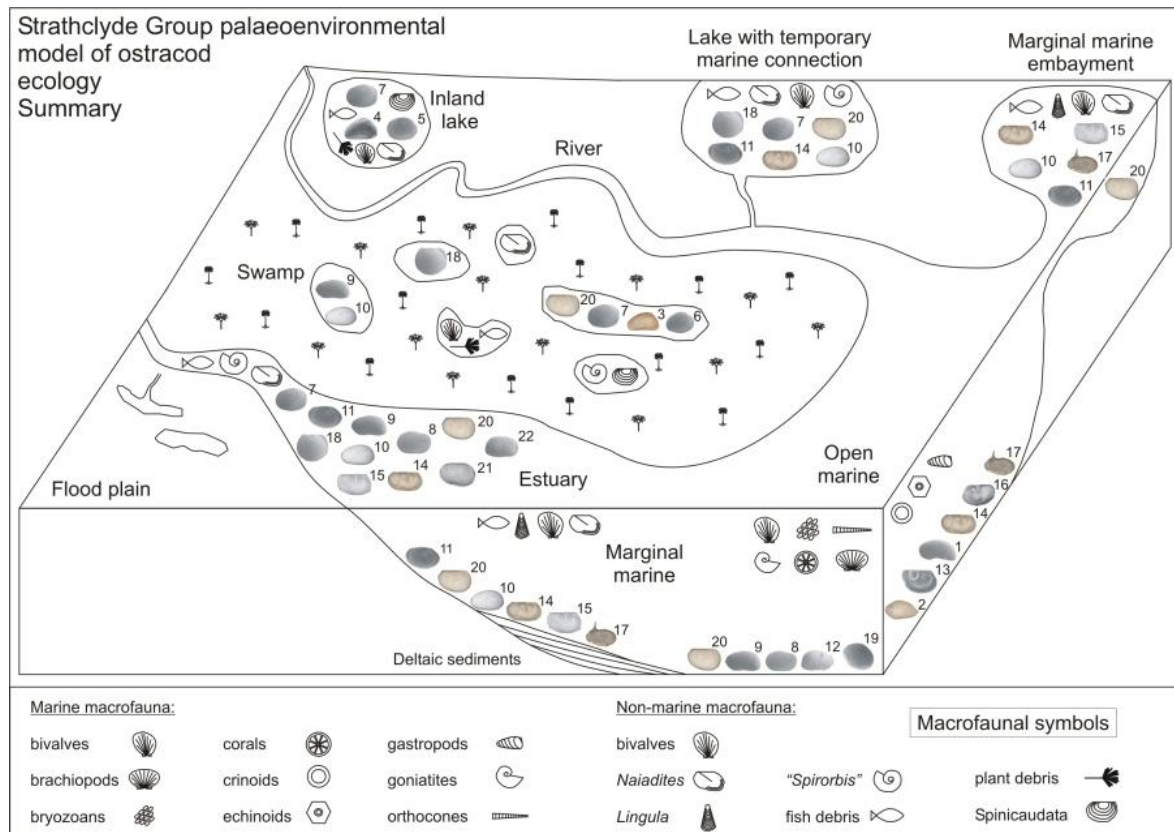


Figure 18. Palaeoenvironmental model for ostracods of the Strathclyde Group. The environmental range of each ostracod species is plotted using the data from Figure 17. Plants represented in the swamp area are representations of a Carboniferous lycopsid and of *Valmeyerodendron*. Ostracod numbering: 1; *Acutiangulata* sp. A, 2; *Bairdia submucronata*, 3; *Carbonita bairdioides*, 4; *Carbonita* cf. *fabulina*, 5; *Carbonita* cf. *humilis*, 6; *Carbonita* cf. *inflata*, 7; *Carbonita* sp., 8; *Cavellina benniei*, 9; *Cavellina valida*, 10; *Cavellina* sp., 11; *Geisina arcuata*, 12; *Healdia* cf. *cuneata*, 13; *Hollinella* (*Keslingella*) *radiata*, 14; palaeocope sp. A, 15; palaeocope sp. B, 16; palaeocope sp. C, 17; *Paraparchites armstrongianus*, 18; *Paraparchites circularis* n. sp., 19; *Polycopse elegans* n. sp., 20; *Shemonaella siveteri* n. sp., 21; *Shemonaella ornata* n. sp., 22; *Silenites* sp. A.

For each formation ostracods and macrofossils are represented in terms of the different palaeoenvironments. The environment is taken as the most common in that formation, for

example the Sandy Craig Formation is predominantly non-marine so only has a restricted marine connection.

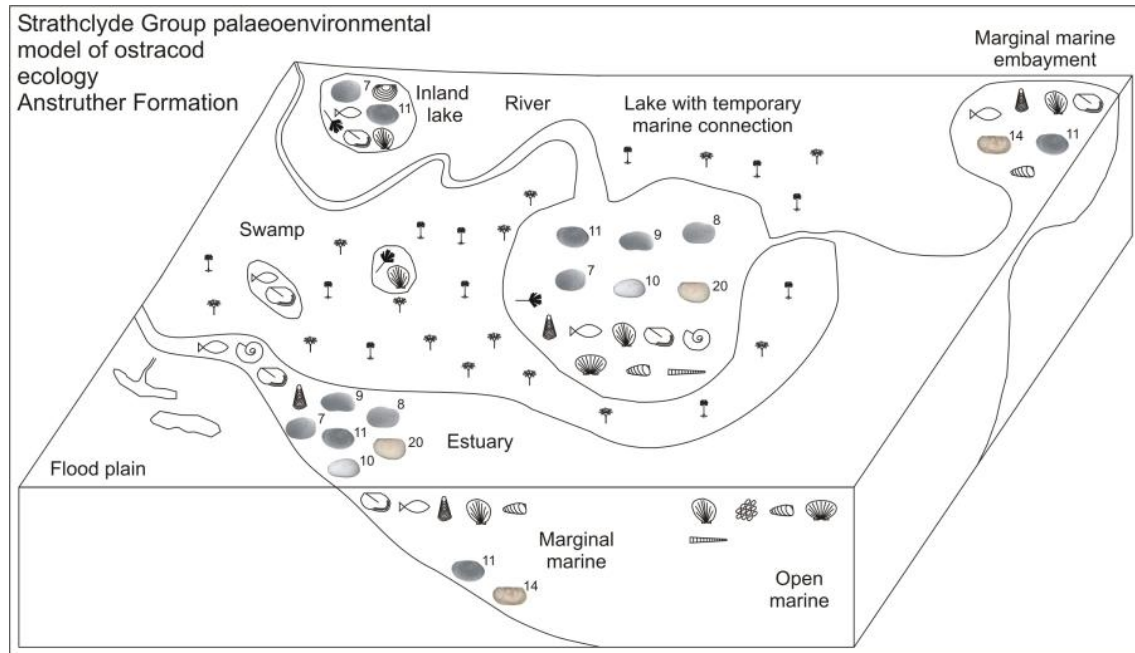


Figure 19. Palaeoenvironmental model of the ecological range of ostracods from the Anstruther Formation. Numbers for ostracod taxa are the same as for Figure 18.

Anstruther Formation: There are no marine and only two marginal marine ostracod species (Figure 19). The most important depositional environment of the formation is a lake with the temporary marine connection. Here lake-deltaic cycles of sandstones and non-marine limestones are deposited. Algal limestones contain abundant plant debris, hence the location near to a swamp. *Naiadites* “mussel bands” are common, and may have been deposited in the lake, or if they contain a more marginal marine fauna, in the embayment or estuary. Occasional marine limestones with a fairly low-diversity marine fauna were deposited in times of marine transgression over the lake. Spinicaudata and ostracods lived in what are interpreted as inland lakes, associated with plant and fish debris. Ostracods are

not found in swampy environments; BBI lithologies are not present and coals are fairly rare.

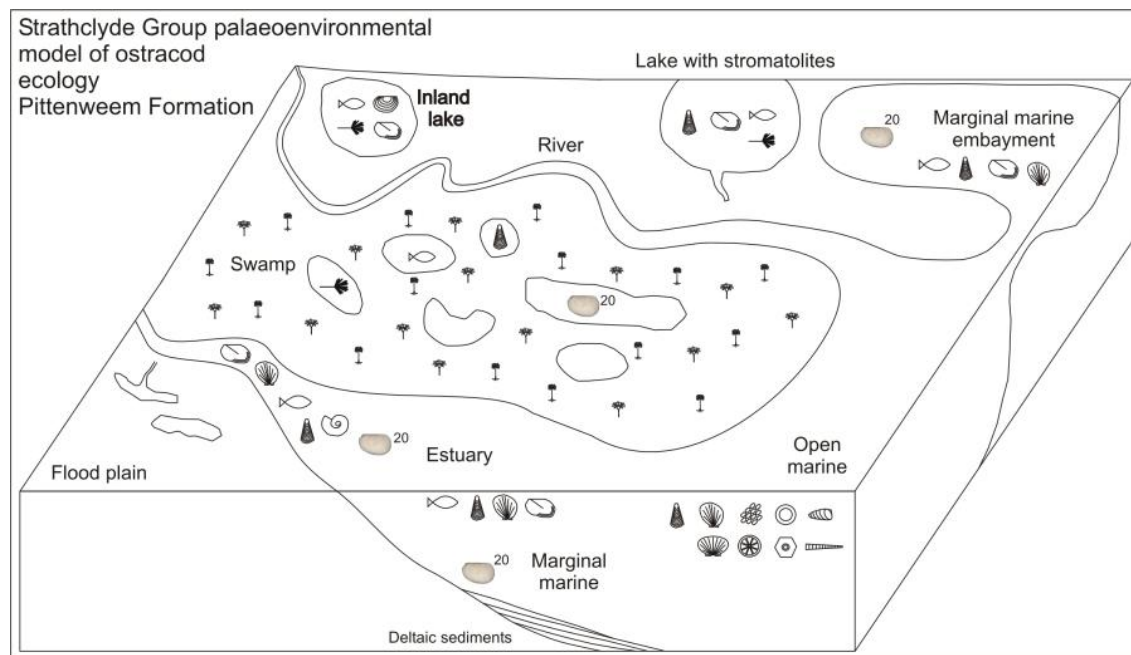


Figure 20. Palaeoenvironmental model of the ecological range of ostracods from the Pittenweem Formation. Numbers for ostracod taxa are the same as for Figure 18.

Pittenweem Formation: Ostracod preservation is very poor, and this is reflected in the presence of only one identifiable species (Figure 20). *Shemonaella siveteri* n. sp. occurs in marginal marine, brackish to freshwater (estuary) and freshwater (swamps). Marine conditions were open, with a high diversity of marine macrofauna. Marginal marine sediments are common, along with numerous brackish *Naiadites* “mussel bands”, some of which contain ostracods. These were deposited in estuary mouths and embayments. Freshwater coals and BBIs are fairly rare, and were deposited in swampy conditions including temporary pools, with Spinicaudata and ostracods. Stromatolitic limestones and mudstones with Spinicaudata that are interpreted as lacustrine are present in this formation, but do not contain ostracods.

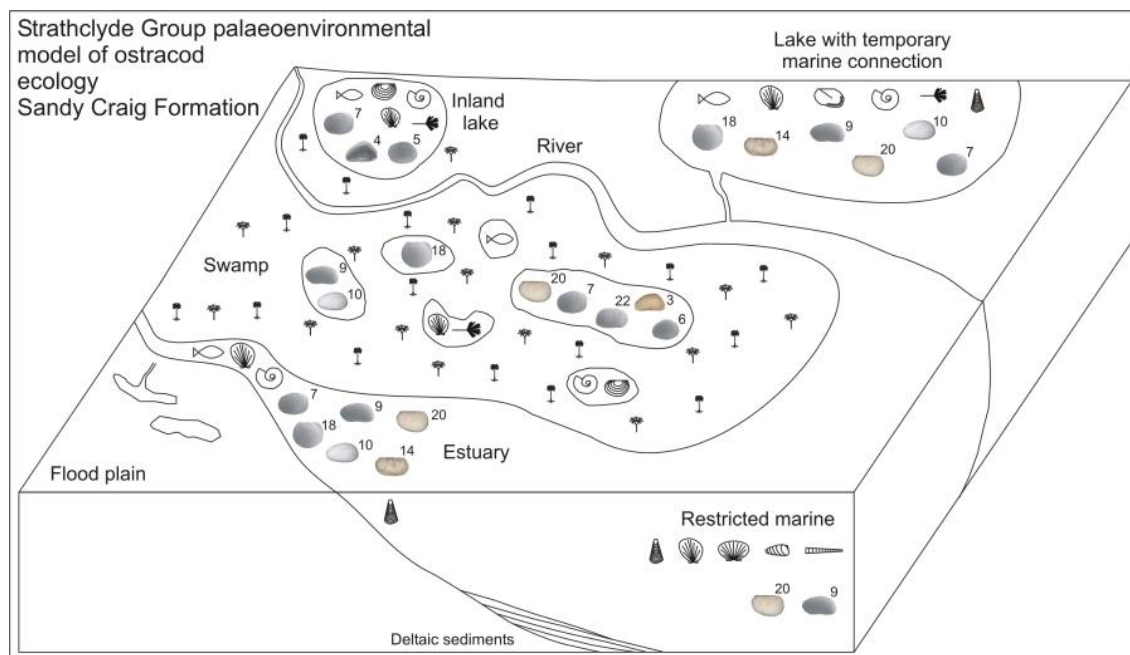


Figure 21. Palaeoenvironmental model of the ecological range of ostracods from the Sandy Craig Formation. Numbers for ostracod taxa are the same as for Figure 18.

Sandy Craig Formation: This formation is the most non-marine, with only a restricted marine connection (Figure 21). Rare restricted marine mudstones containing ostracods were deposited during transgressions over a dominantly fluvial and coal-swamp environment. There are no marginal marine ostracods. The predominantly lacustrine deposition of the Anstruther Formation is not seen here. Stromatolites and non-marine limestones such as *Naiadites* “mussel bands” are rare (and do not contain ostracods). This indicates that although brackish to freshwater lacustrine conditions were present, it was not the primary site of deposition. Instead, there are numerous coals and BBIs, which were deposited in swampy conditions. These contain freshwater Spinicaudata and numerous ostracods, including species of *Carbonita* and *Paraparchites circularis* n. sp. *Carbonita* is also present with Spinicaudata and *Curvirimula* in what are interpreted as inland lakes, in mudstones with a lower organic content.

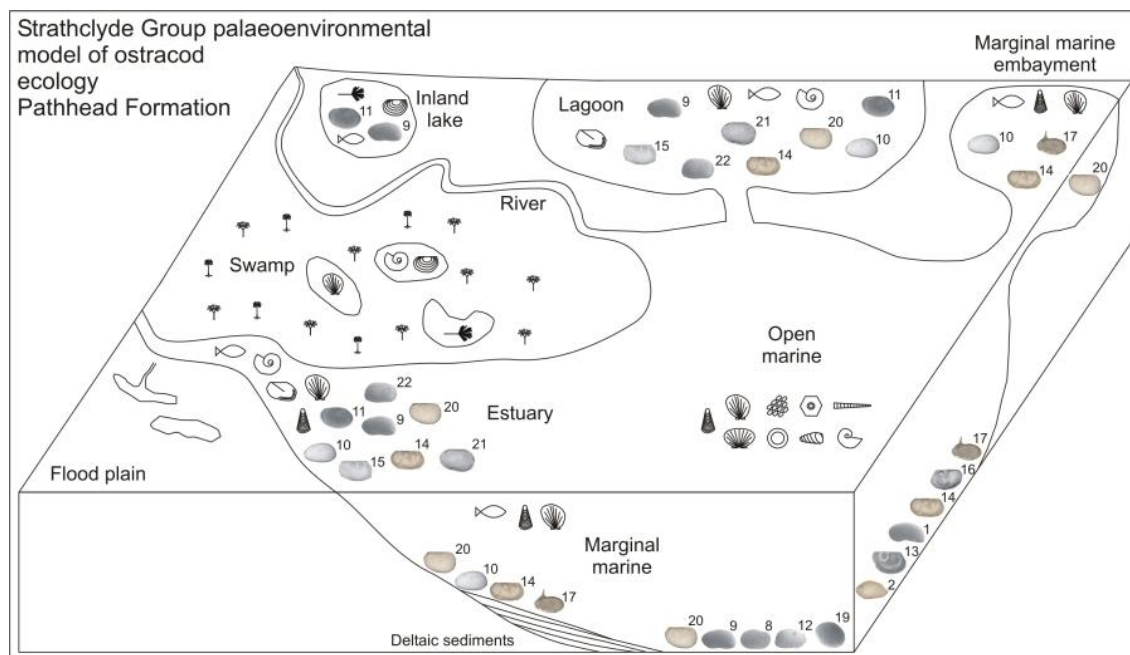


Figure 22. Palaeoenvironmental model of the ecological range of ostracods from the Pathhead Formation. Numbers for ostracod taxa are the same as for Figure 18.

Pathhead Formation: This formation was deposited at the time of the most open marine conditions, and contains the highest proportion of marine sediments. Cephalopods and crinoids represent more open marine waters, as does the higher diversity of stenotopic ostracods (Figure 22). There is a fairly high diversity of brackish to freshwater and eurytopic ostracods, indicating that lagoonal or estuarine conditions were dominant. Spinicaudata, fish and ostracods are deposited in mudstones in inland lakes, which contain only a freshwater fauna. BBIs, coals, fluvial and floodplain sandstones are present but do not contain ostracods. Stromatolitic limestones are absent, so a near-shore lake is excluded from the model.

Discussion

The algal limestones were the first sediments to be colonised by *Carbonita* sp. in the Midland Valley of Scotland. If the stromatolites are truly freshwater in origin then they contain the earliest global record of freshwater ostracods. Where the ostracod taphonomy represents a thanatocoenosis it is likely that the ostracods were feeding off the algae. This has been interpreted from ostracods recorded in stromatolitic limestones in the Palaeozoic: the Pennsylvanian of Illinois contains thin limestones, abundant in ostracods indet. and “*Spirorbis*”, but lacking other fossils. They are interpreted to have formed in a shallow water lake, with ostracods feeding off the algae (Scott 1944). The Leperditicopida, a putative ostracod group, are also found in association with stromatolites as a possible food source (see Siveter 1984, Vannier *et al.* 2001, Warshauer & Smosna 1977). In some brackish to freshwater records the relationship between the ostracods and the algae is unclear (Crawford 1995, Hmich *et al.* 2006).

Early records of freshwater or brackish ostracods from the Mississippian are in coastal environments. *Carbonita* is present in the early Mississippian in what are interpreted as brackish water sediments; in a range of environments from near-shore marine to low salinity coastal ponds (Tibert & Scott 1999). This is also the case for most of the Pennsylvanian record, for example the Joggins Formation, where *Carbonita* is present in brackish seas and poorly drained coastal plain sediments (Falcon-Lang *et al.* 2006, Tibert & Dewey 2006). Brackish and freshwater environments were colonised through the migration of animals from the marine realm, via estuaries (Gray 1988, Park & Gierlowski-Kordesch 2007). These findings indicate the colonisation pathways of non-marine ostracods, which had a marine origin.

The freshwater macrofauna and sediments of the Midland Valley of Scotland are characteristic of a wetland coal-measures type environment. There are no terrestrial fauna present, such as in the land snail-*Archandon* bivalve-tetrapod assemblage of the Pennsylvanian Joggins section, Nova Scotia (Hebert & Calder 2004). All the formations have frequent coal bands, and the BBIs of the Anstruther, Pittenweem and Sandy Craig formations are also interpreted as a wetland swamp deposit. The occurrence of *Carbonita* and other ostracod species in sediments of the Pennsylvanian Coal Measures (for example Sohn 1985), and in organic rich sediments here (such as the black-banded ironstone lithology) gives rise to the question of possible semi-terrestrial ostracods. Genetic studies estimate that terrestrial ostracods may have been present as far back as the Ordovician (Newman 2005). The ostracods in organic rich sediments in this study are assumed to be fully aquatic, but as has been discussed by Horne (2003), it is possible that the absence of a fossil record of terrestrial ostracods may be a preservational rather than ecological issue, as carapaces are unlikely to be preserved in the acid peat-bog environment of coal deposits. Further studies on coals are needed to confirm an ostracod presence in coal deposits and a possible semi-terrestrial lifestyle for Mississippian ostracods.

In the Midland Valley of Scotland some of the freshwater macrofaunas and ostracods also have a brackish water tolerance, as is seen by their faunal associations. The deposits are not truly continental, but were probably deposited near to the coastline in waters that had a spatial or temporal marine connection. The pattern of marine bands shows that there were fairly frequent (but mostly shortlived) marine transgressions. The estuary effect of non-marine colonisation (Park & Gierlowski-Kordesch 2007) is important in the Carboniferous. It allowed invertebrates and other groups to exploit marine transgressions and varying

salinity to inhabit otherwise insupportable non-marine environments, and some groups eventually adapted to freshwater.

Conclusions

- The Mississippian of the Midland Valley of Scotland contains some of the earliest freshwater and brackish ostracods. The Strathclyde Group from Fife represents a range of different depositional settings, from fully marine conditions to deltaic sediments, marginal marine estuaries and lagoons, and brackish to freshwater lakes, swamps and fluvial systems. Freshwater *Carbonita* is described from the Arundian, Anstruther Formation. Important brackish ostracods are *Geisina arcuata*, and *Paraparchites circularis* n. sp.
- Using assemblage occurrence data and a review of the literature macrofossils are assigned to marine, marginal marine, brackish and freshwater environments, and this is used to interpret the environmental tolerance of the ostracods.
- Macrofossil indicators of freshwater are the bivalves *Anthraconaia*, *Carbonicola* and *Cardiopteridium*, spinicaudant conchostracans, fish and plant debris. Freshwater ostracods are species of *Carbonita*, which are found in organic-rich mudstones and stromatolitic limestones.
- Brackish to freshwater macrofauna includes *Naiadites*, *Curvirimula* and “*Spirorbis*”. Brackish water ostracods are *Geisina arcuata*, *Paraparchites circularis* n. sp., *Shemonaella ornata* n. sp. and *Silenites* sp. A.

- Typical macrofossil indicators of marginal marine conditions are *Schizodus*, *Sanguinolites* and *Lingula*. Ostracods that are eurytopic (with a wide salinity tolerance) are *Cavellina benniei*, *Cavellina valida*, palaeocene sp. A and B, *Paraparchites armstrongianus* and *Shemonaella siveteri* n. sp.
- Marine ostracods are *Acutiangulata* sp. A, *Bairdia submucronata*, *Healdia* cf. *cuneata*, *Hollinella* (*Keslingella*) *radiata*, palaeocene sp. C and *Polycope elegans* n. sp. They occur with a high diversity of marine macrofauna. There are six ostracod species whose environmental conditions are not known.
- The biostratigraphy is assessed in terms of the palaeoenvironmental setting. *Cavellina valida*, *Geisina arcuata*, palaeocene sp. A and *Shemonaella circularis* n. sp. are the longest ranging and mostly eurytopic. Due to environmental biases the ostracods are not a useful biostratigraphic tool.
- The environmental setting and depositional character of each of the formations is different. The Anstruther Formation is non-marine dominated, with brackish to freshwater ostracods in lacustrine settings associated with algal limestones. The Pittenweem Formation is mostly marine to marginal, with few ostracods preserved. The Sandy Craig Formation is mostly non-marine, with ostracods in swampy environments. The Pathhead Formation is the most open marine, with a high diversity of marine and eurytopic ostracods.
- This study places the first freshwater ostracods in the early Mississippian (Arundian), while previous studies have recorded freshwater ostracods from the late Mississippian (Namurian).

Chapter 5: Algal palynomorphs, palynofacies and arthropod fragments from the Mississippian of Scotland: insights into brackish and freshwater palaeoenvironments

Abstract

Botryococcus sp. and three new types of algal palynomorph are described from the Mississippian of the Midland Valley of Scotland. Sediments bearing algal palynomorphs are non-marine mudstones, silts, carbonaceous mudstones and coals. The palynomorphs are associated with brackish to freshwater macrofossils and ostracods; *Carbonita* sp. and *Geisina arcuata* ostracods, *Estheria conchostracans*, the vermiform microchonchid “*Spirorbis*”, fish (debris), the brachiopod *Lingula* and the bivalves *Carbonicola*, *Curvirimula* and *Naiadites*. The algal palynomorphs are associated with some of the earliest *Carbonita* specimens, a noted freshwater ostracod in the Carboniferous. The algal palynomorphs are interpreted as freshwater based on their morphology and affinities to living species. Associated with the coals are appendages that belong to aquatic arthropods and an arachnid cuticle fragment. The palynofacies percentages of high dark woody and sheet cellular concentrations can be useful in determining a non-marine environment.

Introduction

The Mississippian of the Midland Valley of Scotland contains sediments from marine to non-marine depositional environments. Some of the earliest freshwater and brackish ostracods are present in non-marine sediments of the Tournaisian and Viséan (Williams *et al.* 2006, Bennett 2008). The oldest occurrence of *Carbonita* Strand, 1928 is from mudstones and limestones of the Anstruther Formation. Palynological samples were taken

from non-marine ostracod-bearing sediments throughout the Mississippian of the Strathclyde Group of Fife, Scotland, to provide further details of the palaeoenvironment. The samples range were taken from the Anstruther to Pathhead Formation (Table 1), and cover the palynological biozones TC (Arundian, Anstruther Formation), NM (Asbian, Pittenweem and Sandy Craig Formation) and VF (Brigantian, Pathhead and the top of the Sandy Craig Formation) (Owens *et al.* 2005).

System	Series	Paly. Zones	Midland Valley of Scotland Lithostratigraphy				Group	
			Central Coalfield & Ayrshire	Fife	West Lothian	East Lothian		
Mississippian	Viséan	VF	Lawmuir Fm	Pathhead Fm	West Lothian Oil Shale Fm	Aberlady Fm	Strathclyde Group	
		NM	Kirkwood Fm	Sandy Craig Fm				
				Pittenweem Fm				
		TC	Clyde Plateau Volcanic Fm	Anstruther Fm	Gullane Fm			
		TS						
		Pu		Fife Ness Fm				
	Tournaisian		Clyde Sandstone Fm					Inverclyde Group
		CM	Ballagan Fm					
		PC	Kinneswood Fm					

Table 1. Stratigraphy of the Midland Valley of Scotland, showing the Strathclyde Group formations of Fife. Adapted from Browne *et al.* (1999).

Algal palynomorphs from this study are undescribed species of probable zygnematacean spores of filamentous green algae, and other chlorophytes such as *Botryococcus*.

Zygnematacean algae are an extant group that occur in freshwaters such as stagnant or oxygenated pools, streams, ditches, swamps, moist soils and peats and bogs (see references within Grenfell 1995). Palaeozoic zygnematacean algae are classified according to their morphology, and are only found in non-marine sediments. Fossil occurrences of freshwater algae are common in Permian sediments (for example Stephenson *et al.* 2008), and there

are also several Carboniferous examples (see references within Grenfell 1995). The types of sediment hosting the algae are coals, carbonaceous shales, silts and sandstones, many of which are associated with a general coal-swamp depositional environment.

The Ballagan Formation from the Inverclyde Group of the Midland Valley of Scotland (Table 1) contains algal palynomorphs from fresh to brackish conditions (Stephenson *et al.* 2004). The types of palynomorphs are *Brazilea* sp. B, ?*Carbaneuletes* sp. A, ?*Reduviasporites* sp. and algal palynomorph spp. 1 to 4. They occur with ostracods that are associated with brackish conditions such as *Beyrichiopsis*, *Cavellina*, *Knoxiella*, *Shemonaella* and *Sulcella*. A Cretaceous study of the Upper Weald Clay sediments also found freshwater ostracods in association with green algae palynomorphs (Nye *et al.* 2008).

This study examines the algal palynomorph component of marine and non-marine palynological samples from the Strathclyde Group of the Midland Valley of Scotland. The sedimentology, macrofauna and ostracods of non-marine sediments are described. These samples are of special interest as they contain some of the earliest freshwater to brackish ostracods. The palynofacies of the sediments is discussed in terms of the component of spores, dark woody material, sheet cellular material, amorphous organic matter and algae, to elucidate the palaeoenvironment. In addition enigmatic sheet cellular and arthropod fragments are also illustrated. The algae *Botyrococcus* sp. and three new types of non haptotypic algal palynomorph are described and illustrated. The algal palynomorphs are discussed in terms of their possible environment of deposition.

Geological Setting

In the Mississippian the Midland Valley of Scotland was situated on the southern edge of Laurussia at the equator, and within a restricted marine seaway. Deposition was in a shallow marine basin, with restricted marine estuaries and lagoons, and episodes of non-marine deposition in lakes and swamps. The sediments of the Strathclyde Group of Fife consist mainly of marine and non-marine mudstones, siltstones, sandstones, marine and non-marine limestones and coals. The formations are correlated by using key marine horizons or non-marine limestone beds. The deposits usually form in a pattern of upward coarsening deltaic cycles (Browne *et al.* 1999), and deltaic to fluvial sandstones are the most common lithology in the successions.

Methods and Materials

Palynological slides were made from mudstone and siltstone sediments of 53 samples, 50 of which are non-marine, and three are from marine mudstones. Non-marine versus marine samples were determined by their macrofaunal and ostracod content. These samples range in age throughout the Mississippian, and were taken from boreholes and field sections of the Strathclyde Group (Figure 1, 2). The formations of the Strathclyde Group each have a different character in terms of sediments, macrofossils and ostracods (Figure 2).

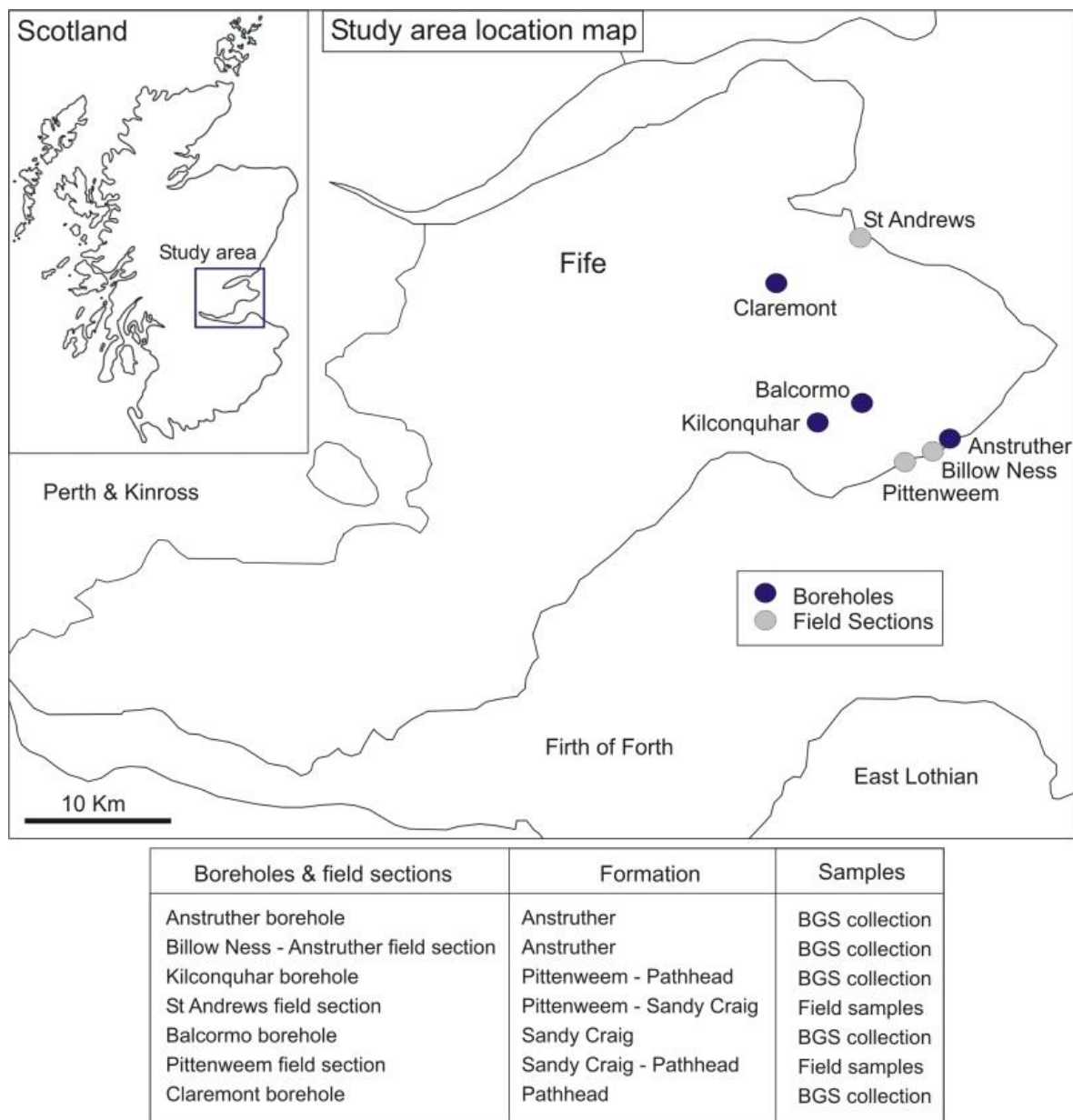


Figure 1. Location map and table of boreholes and field sections from which palynological samples were taken. Boreholes were loaned from the British Geological Survey, field samples were collected in 2008 from coastal sections.

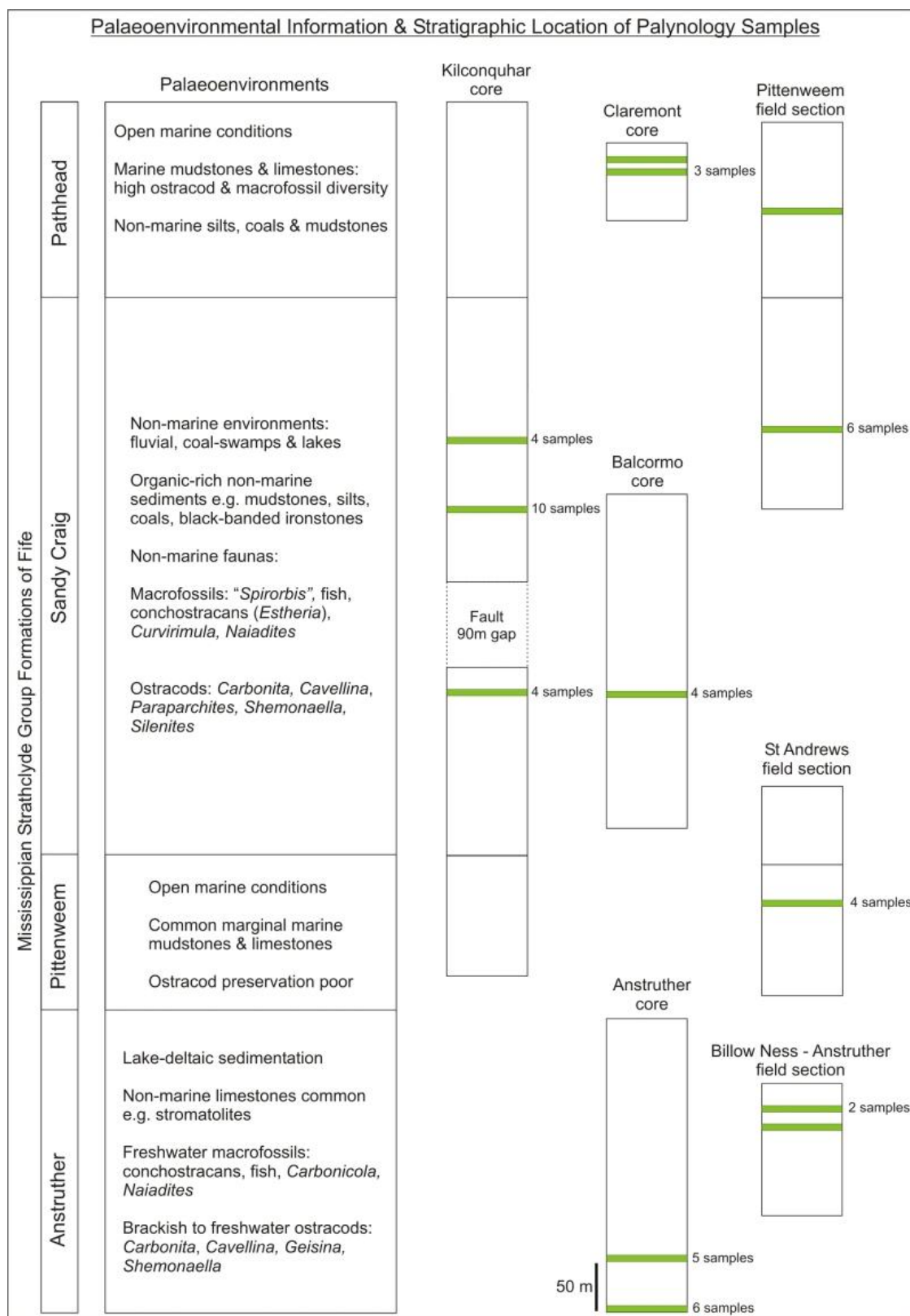


Figure 2. Stratigraphic location of palynological samples from the Strathclyde Group and the palaeoenvironmental character of the formations.

Sediment samples were processed using standard palynological techniques at the Palynological Laboratory at the British Geological Survey, Keyworth. The preparation of strew mounts for palynological analysis involved well-established procedures of crushing followed by hydrochloric and hydrofluoric acid treatments (Wood *et al.* 1996). Post-hydrofluoric acid organic residues were oxidized with Schulze's Solution and dilute nitric acid. MPA numbers relate to the BGS palynological sample numbers; between two to four slides were studied for each sample. Palynological slides were examined on a standard palynological microscope, and specimen locations are recorded using an England Finder.

A large number of the assemblages (21 samples out of 53) are classified as degraded, with a 90% or greater component of amorphous organic matter (AOM). The AOM in the samples obscures spores and algal palynomorphs. There is no lithological pattern as to which samples are degraded, half are sediments containing iron-oxide, others are mudstones (Table 2). It is possible that the sheet cellular, dark woody material and spores were eroded out of the sediments at the time of deposition, or that elements of these palynofacies broke down due to diagenetic processes and formed the AOM. The poor preservation of algal palynomorphs and rarity of components other than AOM in these assemblages biases palaeoenvironmental analysis.

Sediments and palaeontology

The sediments and fauna of each sample are detailed in Table 2. The sedimentary and palaeontological context is important in understanding the palaeoenvironment in terms of palynofacies and palynomorphs. The marine samples were selected from a marine band of

the Pathhead Formation (Table 2). This marine band contains a diverse marine macrofauna of bivalves, bryozoans, brachiopods, cephalopods, crinoids and gastropods.

The non-marine samples selected for palynological analysis contain the ostracods *Geisina arcuata* (Bean), 1836 and *Carbonita*, which are known freshwater to brackish genera in the Carboniferous (Bennett 2008). Other samples that do not contain ostracods were sampled near to ostracod-bearing samples, or contain what are considered as a non-marine macrofauna. Macrofossils interpreted as non-marine do not occur with marine macrofossils, and usually form lower-diversity assemblages. The bivalve *Schizodus*, and the brachiopod *Lingula*, are found with marine macrofossils in about half of the samples in which they are present, so they are interpreted as marginal marine faunas. The faunal association of non-marine macrofossils indicates the following environmental tolerances: Brackish to freshwater: the bivalves *Curvimula* and *Naiadites*, vermiform microconchids (*"Spirorbis"*) and fish. Freshwater: the bivalve *Carbonicola* and conchostracan Spinicaudata (*Estheria*).

Carbonicola, *Curvimula* and *Naiadites* are frequently recorded from Pennsylvanian freshwater coal-measure settings (for example Pollard 1966, Eagar & Belt 2003, Falcon-Lang *et al.* 2006). *"Spirorbis"* is found in a range of non-marine environments in the Palaeozoic (see a review by Taylor & Vinn 2006). Freshwater lacustrine fish have been described from the Mississippian Midland Valley of Scotland (Dineley & Metcalf 1999), although the fish from this study have not been identified. Conchostracans are an extant freshwater crustacean, and they are known from freshwater environments from the Pennsylvanian (Orr & Briggs 1999, Vannier *et al.* 2003).

Non-marine sediments are coals, shaley coals, carbonaceous mudstones, iron-rich mudstones and black-banded ironstones (BBI), all of which have a high plant matter content (Table 2). Silts and mudstones containing non-marine macrofossils are also considered as non-marine, and some of these occur above a non-marine stromatolitic limestone. The palaeoenvironmental interpretation of the non-marine sediments is a swampy palaudal environment for the coals, black-banded ironstones, iron-rich mudstones and carbonaceous mudstones. In the Pennsylvanian black-banded ironstones have been recorded from a freshwater marsh environment (Boardman 1989). Silts may have been deposited in floodplains or estuaries, and mudstones with a non-marine fauna are interpreted as lacustrine.

D?	Sample	Fm	Depth (m)	Sediments and associated fossils	Percentage components in slide					Form of SC	Algal Paly.				
					spore	DW	SC	AOM	algal		Art.	Bot.	A	B	C
	56512	P	x	laminated silts, fish (debris)	1	36	60	3	0	tubes, spines					
	56511	P	x	coal, top part, no fossils	3	50	37	10	0	tubes, spines	*				
	56510	P	x	coal, bottom part, above a rooted SST	0	90	10	0	0		*				
	56464	P	19.00	silts, <i>Geisina</i> , <i>Curvirimula</i>	20	20	20	40	0			*		*	
	56462	P	27.69	marine mudstone band, <i>Strebloteria</i>	70	15	10	5	0			*			
	56463	P	28.09	marine mudstone band, goniatite (frag.)	60	20	15	5	0	tubes		*			
	56465	P	28.73	marine mudstone band, <i>Shizodus</i>	70	10	10	10	0					*	
	56509	P	94.00	shaley coal, no fossils	1	95	2	2	0						
D	56499	SC	362.70	BBI, <i>Carbonita</i> , plant (debris)	0.2	0	0	99.8	0						
D	56498	SC	362.81	black-banded ironstone, fish (debris)	0.5	0.5	0	99	0						
D	56497	SC	362.84	black-banded ironstone, plant (debris)	0.5	0	2	97.5	0						
D	56496	SC	363.00	black-banded ironstone, plant (debris)	0.5	0.5	0	99	0						
	56485	SC	420.61	Iron-rich mudstone, <i>Estheria</i>	12	1	50	35	2	spines			*		
	56484	SC	420.79	Iron-rich mudstone, <i>Estheria</i>	50	4	12	33	1				*	*	
	56486	SC	420.86	Iron-rich mudstone, <i>Estheria</i>	88	3	3	5	1				*	*	
	56488	SC	420.90	Iron-rich mudstone, <i>Estheria</i>	6	2	8	83	1	sheets, spines				*	
	56487	SC	422.00	Iron-rich mudstone, no fossils	10	5	30	54	1			*	*	*	
D	56489	SC	422.64	Iron-rich mudstone, " <i>Spirorbis</i> ", ostracods	2.8	0.2	1	95	1	spines					
D	56490	SC	422.92	Iron-rich mudstone, fish (debris), ostracods	1	0	1	98	0	tubes, spines					
D	56491	SC	423.20	Iron-rich mudstone, " <i>Spirorbis</i> ", ostracods	1	0	2	97	0	tubes, spines					
D	56500	SC	424.45	Iron-rich mudstone, fish (debris), ostracods	1	0	0	99	0						
D	56501	SC	424.90	Iron-rich mudstone, fish (debris)	1	0	0	99	0	sheets, tubes					
	56508	SC	326.00	silts above a coal, no fossils	40	25	33	2	0	tubes		*		*	
	56507	SC	326.00	3cm thick coal seam, no fossils	5	63	30	2	0						
	56506	SC	326.00	shaley coal, no fossils	25	60	14	1	0	tubes, spines					
	56505	SC	326.00	shaley coal, no fossils	40	50	8	2	0	tubes, spines, fill.					
	56504	SC	326.00	shaley coal, no fossils	8	50	37	5	0	tubes, spines					
	56503	SC	326.00	coal seam, above <i>Monocraterium</i> SST	10	40	45	5	0	sheets, filaments				*	
	56495	SC	536.40	mudstone, ostracods, fish, plant, <i>Curvirimula</i>	30	15	24	30	1	tubes, spines, fill.		*			
	56493	SC	537.30	mudstone, ostracods, fish, plant, <i>Curvirimula</i>	30	1	1	68	0	tubes, spines		*			
D	56492	SC	537.60	mudstone, ostracods, fish, plant, <i>Curvirimula</i>	4	0	2	94	0						
D	56494	SC	537.75	mudstone, ostracods, fish, plant, <i>Curvirimula</i>	0	5	1	94	0			*			
D	56472	SC	254.17	mudstone, <i>Lingula</i> , bivalves, fish (debris)	3	5	2	90	0						
	56471	SC	254.18	mudstone above a coal, <i>Lingula</i>	14	5	12	69	0					*	
D	56470	SC	254.30	mudstone above a coal, no fossils	5	1	2	92	0						
D	56469	SC	254.90	mudstone above a coal, no fossils	2	0	0	98	0						
	56516	Pit	135.00	coal, top part, no fossils	0	98	2	0	0						
	56515	Pit	135.00	coal, bottom part, no fossils	2	55	40	3	0	tubes, spines		*			
	56514	Pit	135.00	shaley coal, no fossils	4	60	36	0	0			*			
	56513	Pit	135.00	silts with plant roots (<i>Monocraterium</i>)	8	66	25	1	0	tubes		*			
D	56466	A	27.00	mudstone, fish, plant (debris)	2	0	0	98	0						
D	56467	A	27.00	mudstone, <i>Geisina</i> , fish, plant (debris)	1	0	1	98	0						
D	56468	A	50.00	mudstone, fish, plant (debris)	3	0	1	96	0						
D	56473	A	247.93	mudstone, <i>Carbonicola</i> , <i>Geisina</i>	0	0	0.2	99.8	0						
D	56481	A	247.95	mudstone, <i>Carbonicola</i> (abundant)	0	0	0	100	0						
D	56474	A	247.98	mudstone, <i>Carbonicola</i> (abundant)	0	0.2	0	99.8	0						
	56482	A	248.01	mudstone, <i>Carbonicola</i> (abundant)	0	0	80	20	0						
D	56475	A	248.69	mudstone, <i>Naiadites</i> , fish (debris)	2	0	1	95	2	filaments				*	
	56476	A	302.62	mudstone above an algal LST, <i>Naiadites</i>	10	80	5	1	4	sheets, spines			*	*	*
	56477	A	302.69	mudstone, <i>Naiadites</i>	20	10	60	6	4	sheets				*	*
	56478	A	302.87	mudstone, <i>Naiadites</i>	13	50	30	5	2				*	*	
	56479	A	303.00	mudstone, ostracods	8	2	66	18	6	sheets, filaments			*	*	
	56480	A	303.12	mudstone, ostracods, fish (debris)	9	2	70	18	1	filaments					
	56483	A	303.33	carbonate rich mudstone, no fossils	9	70	15	5	1					*	

Table 2. Table with details of all the palynological samples. Samples highlighted in grey contain greater than 1% of algal palynomorphs, but algal palynomorphs are also present in other samples. Sample numbers relate to BGS palynological MPA samples. Depth is measured from the sample location in boreholes, or depth down the field section. Samples are in stratigraphic order from youngest to oldest down the table. Abbreviations used: D; degraded sample, Fm; formation; P; Pathhead, SC; Sandy Craig, Pit; Pittenweem, A; Anstruther. DW; dark woody material, SC; sheet cellular, AOM; amorphous organic matter. SC forms; the morphological forms of sheet cellular in the sample, fill.; filaments, art.; arthropod fragments in the sample, Bot.; *Botryococcus*, A-C; algal palynomorph types A-C, described in the text.

Palynofacies

The following palynofacies components are present in the slides:

Spores: The marine samples have a high abundance of spores, and no acritarchs (phytoplanktonic cysts) are present in marine or non-marine samples. Some samples from mudstones with *Naiadites*, shaley coals, silts with *Curvirimula* and *Geisina*, and iron-rich mudstones with *Estheria* have a fairly high spore percentage of 20% or greater. Iron-rich mudstones samples containing *Estheria*, algal palynomorph types A, B and a high spore content are shown in Figure 3, from the Sandy Craig Formation, at 420.79 and 420.86 meters.

Dark woody material: Dark woody material is a common component in all slides. It is most abundant in coal samples, where there is a wide variety of types of phytoclast, from fragments with a cellular structure to irregular flat black fragments. The percentage of dark woody material is a direct correlation to the amount of plant material in that sample, so coals for example have a higher content than shaley coals. Examples of these sediments from the Pittenweem Formation are shown in Figure 3. Samples with a high dark woody content are from silts, mudstones, carbonaceous mudstones and coals. The fauna from sediments with an abundant (greater than 50%) dark woody content are *Naiadites*, plant roots, arthropod fragments, sheet cellular forms, and algal palynomorphs type A, B and C.

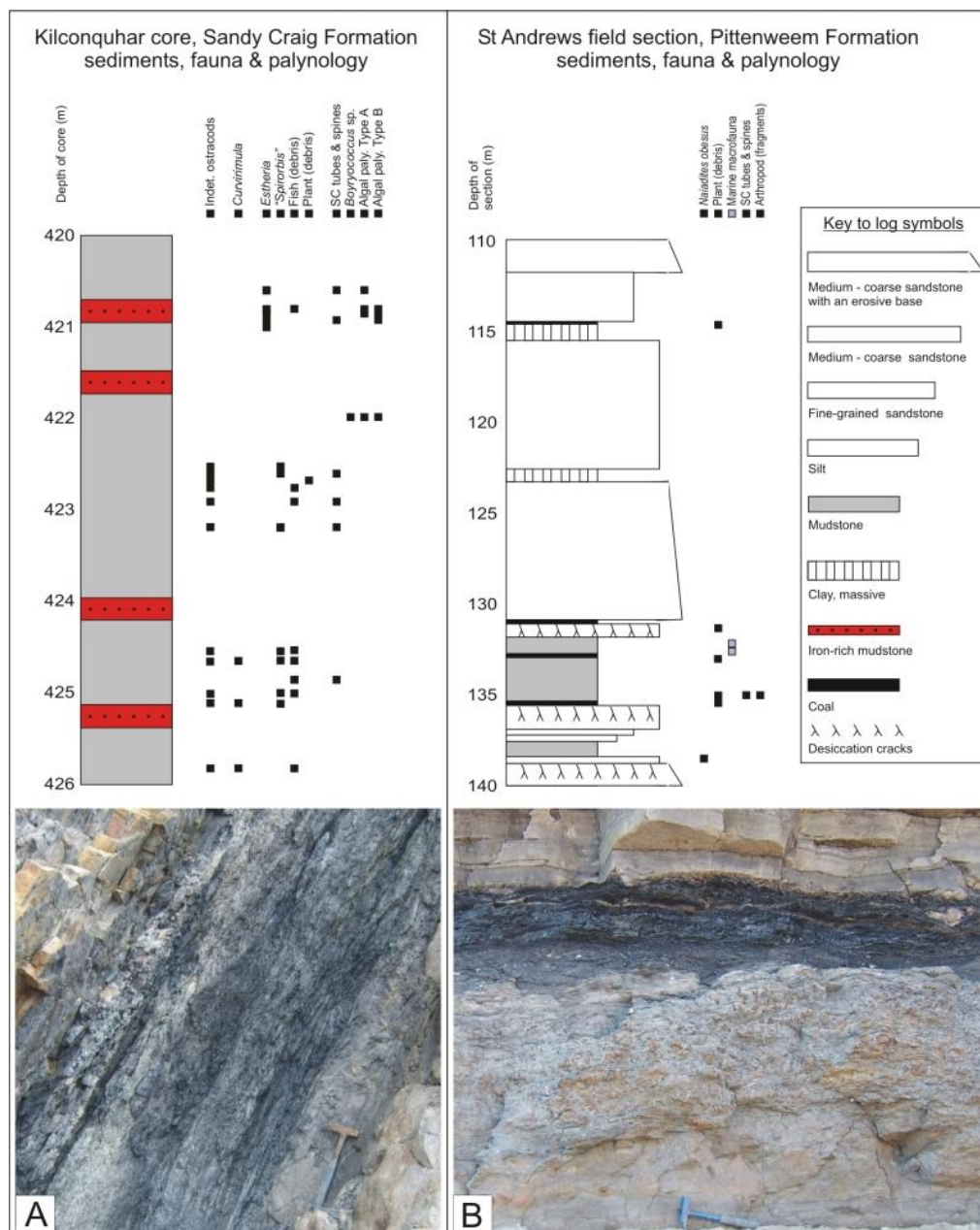


Figure 3. Sedimentary logs and field photographs of certain palynological sampling locations. The occurrence of ostracods, macrofossils and palynomorphs is noted, with details in Table 1. In the Kilconquhar core algal palynomorphs from mudstone sediments are associated with the conchostracan *Estheria* and fish (debris). In the St Andrews field section algal palynomorphs are absent and arthropod fragments are associated with carbonaceous mudstones and coals. Palynology sample location photos: A: organic rich shale and thin coal seams, containing ostracods, Sandy Craig Formation, field section at Pittenweem. The section represents the nature of carbonaceous mudstone and coaly shale seen in the core from this formation. B: rooted sandstone and coals, Pittenweem Formation, field section at St Andrews, at 136 m section depth.

Sheet cellular: Samples with a high sheet cellular content (50% or greater) are from carbonaceous silts containing fish, iron-rich mudstones with *Estheria*, mudstones with *Carbonicola*, *Naiadites*, ostracods and fish (Table 2). 70% of samples that are not degraded contain significant amount of sheet cellular material in the form of tubes, spines and filaments. Sheet cellular material in less abundance (20% or greater) is common in carbonaceous mudstones and coals with a high dark woody content.

The forms of sheet cellular material present are diverse and include tracheed fragments; large thin sheets; sheets with filaments; isolated filaments; masses of branching filaments or tubes; sheets with spines; single tubes; single spines; multiple spines (Figure 4). Filaments and masses of branching tubes have many different forms (Figure 4, images 1-3). Tubes, spines and spines attached to cellular sheets are the most common in the shaley coals and shales of the Sandy Craig and Pathhead formations (Figure 4, images 3-7). Spines attached to sheets are distinctive in occurring in large fragments, the sheet is thick, the spines appear soft and gelatinous and have rounded tips (Figure 4, images 4, 5). Individual or multiple spines also have many different forms (Figure 4, images 6, 7).

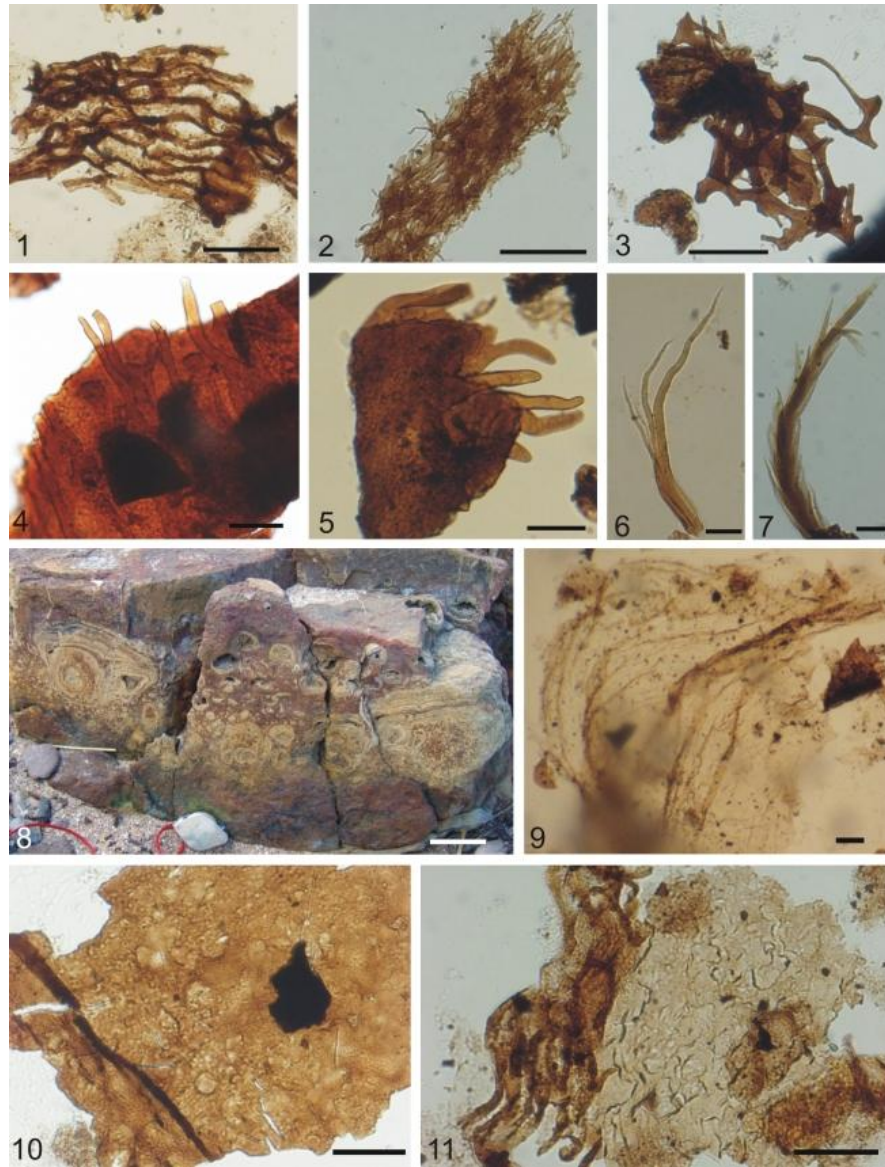


Figure 4. Sheet cellular palynofacies elements. Numbers and letters refer to position of specimen on the England Finder, MPA numbers refer to BGS sample numbers. 1: fragment with possible filaments, from a non-marine mudstone, J65/3, MPA 56495. 2: branching mass of tubes, from a marine sample, O48/1, MPA 56465. 3: branching mass of tubes, from a shaley coal, G66/2, MPA 56508. 4 and 5: fragments with spines attached, from silts above a coal, MPA 56512. 4: L59/2. 5: L59/1, side view. 6 and 7: fragments from a shaley coal and silts. 6: multiple spines joined at the base, N58, MPA 56505. 7: branching spine, K56/1, MPA 56506. 8: A stromatolitic limestone with the ostracod *Carbonita* sp., Anstruther Formation, field photograph. 9 to 11: large sheet fragments, from a mudstone with ostracods and high algal palynomorph content, located 20 cm above the stromatolitic limestone in the Anstruther core, MPA 56479. 9: F69. 10: T69/2. 11: fragment with filamentous shapes on the left side, N68/4. 1-5 and 9-11: scale bar 30 µm. 6 and 7: scale bar 10 µm. 8: scale bar 2 cm.

Filamentous debris and most commonly large cellular sheets occur in mudstone samples a few tens of centimetres above a stromatolitic limestone containing *Carbonita* sp. ostracods (Figure 4, images 8-11). They are also present in mudstones, shaley coals and coals (Table 2).

AOM: A high component of AOM is taken to indicate a degraded sample (Table 1), especially where the AOM contains degraded or broken spores. The organic material is light green coloured, often in large clumps, and there are pyrite crystals present in the organic matter and spores. The most common spores in these samples are *Lycospora*, many of which are split open or otherwise poorly preserved. Excluding degraded samples, amorphous organic matter is still a common component in some slides.

Algal: The different types of algal palynomorphs consist of *Botryococcus* sp., and three other types that are previously undescribed. Out of the 33 non-degraded samples 19 samples contain *Botryococcus* or algal palynomorph types A-C. The greatest amount of algal palynomorphs in a slide is 6%, but most samples contain less than 1%. Sediments with the highest abundance of algal palynomorphs are mudstones located above a stromatolitic limestone, the best example of which is those from the Anstruther Formation (Anstruther core) between 302.62 and 303 meters (see Table 1). Samples that do not contain any algal palynomorphs are degraded samples, or those with a high dark woody or sheet cellular content.

Botryococcus sp. occurs in eight samples, associated with ostracods indet., *Geisina*, *Curvirimula*, marine macrofauna, fish and plant macrofossils, in mudstones, iron-rich mudstones and silts (Table 1). *Botryococcus* sp. is subcircular in outline, and composed of

cells that radiate from a central point to form a colony. Often two or more colonies are joined together to give an uneven outline shape. The cells are usually elongate to cylindrical in shape, of a micron scale, and most clearly seen at the edges of the colony (Plate 1, fig. 2). The specimens resemble *Botryococcus type I* from the Holocene of Rio Grande do Sul, Brazil (Medeanic 2006).

Algal palynomorph types A to C occur in sixteen samples, from a range of sediments; silts, mudstones, iron-rich mudstones, carbonate-rich mudstones, coals and one marine mudstone sample. The fauna associated with these palynomorphs are fish, ostracods indet., *Geisina arcuata*, *Curvirimula*, *Naiadites*, *Estheria*, *Schizodus* and *Lingula*. The sediments frequently contain high proportions of dark woody material or sheet cellular material. Algal palynomorph type B is the most common, while type C is only present in two samples (Table 2).

Arthropod fragments: These fragments are not common within the palynological slides and are not traditionally considered as a part of a palynofacies analysis. However, they are an interesting component that may shed light on the palaeoenvironment. The arthropod fragments are well preserved, ranging from black opaque, to brown and translucent. Most of the specimens consist of appendages (podomeres). Arthropod fragments are present in five samples from coal lithologies, from the Pathhead and Pittenweem formations (Brigantian and Holkerian in age respectively). The sediments range from coals to organic-rich mudstones, to siltstones with less organic matter and rooting (*Monocraterium*). The coals overly rooted sandstones and siltstones, in typical cyclotherm-type depositional sequences.

The appendage fragments are generally two or three podomeres in length, and in some specimens attached to a base. The arthropod fragments can be categorised into several types based on the morphology:

- Appendages in which the basal podomere has a serrated edge: Out of 26 the articulated fragments (of two podomeres or more), nine have serrated basal podomeres (for example Plate 1, figs. 3, 4, 6, 9). Some are only serrated on one side, while the other side is undulose.
- Long and thin appendages, composed of at least three podomeres: Plate 4, fig. 6 is a well preserved example, with four thin podomeres that taper towards the distal point. The basal appendage is serrated. The largest appendage found has a serrated basal podomere and is 235 μm in length (Plate 1, fig. 9). The second and third podomeres are not as elongate as the specimen in fig. 6. Two more specimens that are less well preserved also have a three-podomere thin appendage with possible serrated bases (Plate 1, figs. 15, 16).
- Distal parts of appendages: with a fairly wide base and fine branching podomeres at the end composed of three segments (Plate 1 figs. 5, 18).
- Distal parts of appendages: composed of three podomeres, sometimes with a curved shape that tapers towards the distal point (Plate 1, figs. 1, 2, 3, 4, 7). Of these figs. 1 and 2 have a wide basal segment.

- Appendages with unusual basal segments: The basal segment has an acuminate end (Plate 1, figs. 8, 12). Another unusual feature is podomeres that are roughly equal in size that seem to split off symmetrically from the base (Plate 1, figs. 8, 10).
- Broken segments of appendages: Composed of two or more podomeres with evidence of breakage (Plate 1, figs. 11, 13, 14, 17).
- Cuticle fragment: One large cuticle fragment has two size orders of pores, large dark spines, and a whole range of smaller spines down to setae-like filaments (Plate 1, figs. 19, 20).

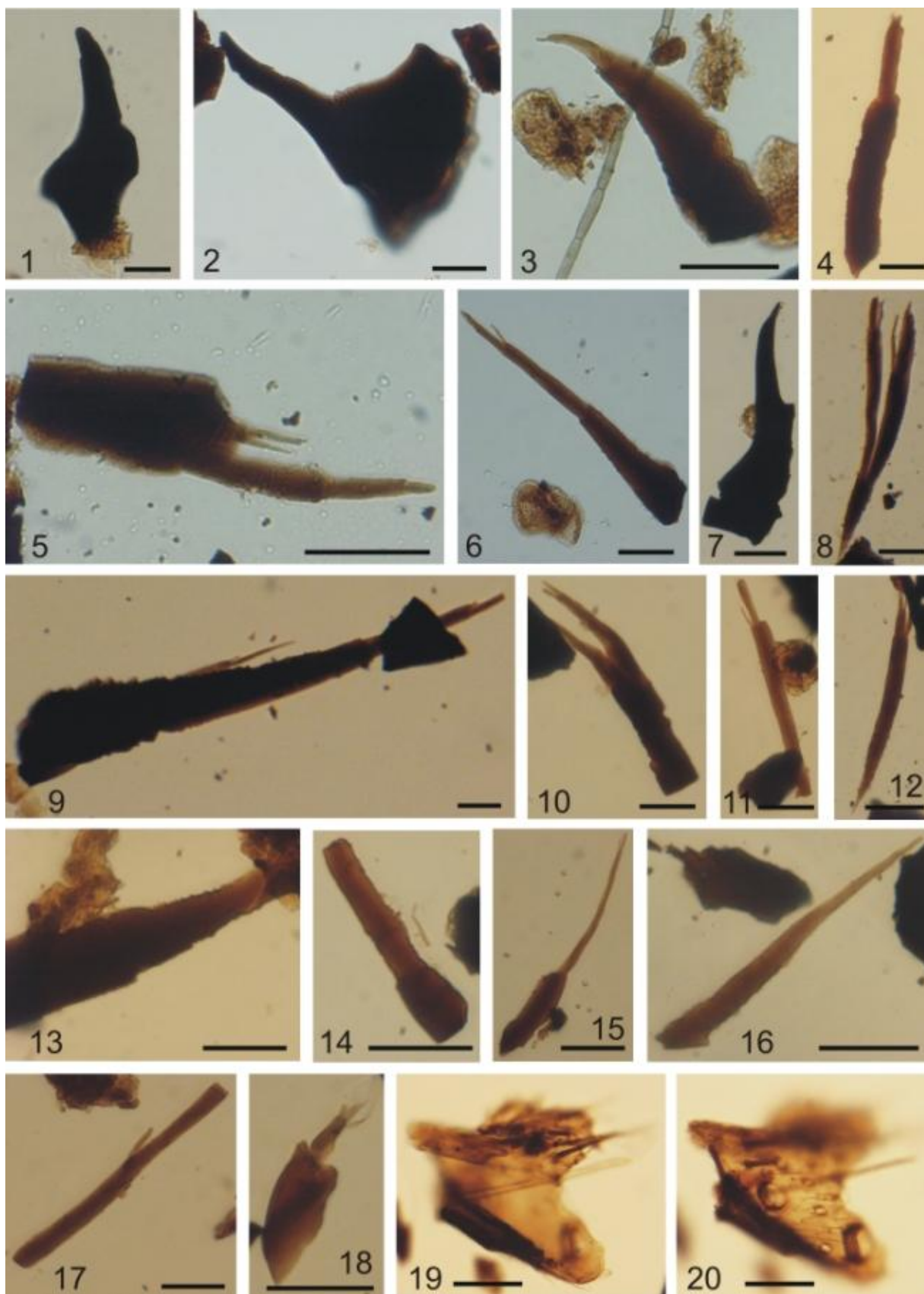


Plate 1: Arthropod fragments. 1: opaque segmented arthropod fragment, V70, MPA 56513. 2: possible scelerodont fragment, L45/2, MPA 56511. 3: arthropod limb with a serrated edge, O48/2, MPA 56511. 4: two podomere limb with a hooked end and serrated edges to both segments, O20/2, MPA 56516. 5: arthropod limb with two podomeres, L46/3, MPA 56510. 6: arthropod limb with three segments, the basal of which has a serrated edge, L43, MPA 56511. 7: arthropod fragment with a serrated edge, D63, MPA 56515. 8: joined segments of three to four podomeres, O31/3, MPA 56510. 9: large arthropod limb fragment, O27/1, MPA 56510. 10: jointed segments, G34/3, MPA 56507. 11: thin fragment with two podomeres, F22/3, MPA 56511. 12: fragment with four podomeres, and a tapered base with serrated edges, M28/4, MPA 56510. 13: close up of the basal part of a segment, with tooth-like serrated edges, P14/3, MPA 56511. 14: basal segments of an appendage, M14/4, MPA 56511. 15: three podomere long appendage fragment, C16/2, MPA 56511. 16: Two podomere long fragment, H21, MPA 56510. 17: smooth edged fragment, with a broken off podomere at the top and a small appendage attached at the middle, G73, MPA 56511. 18: distal appendage fragment, with small segments, G27, MPA 56510. 19 and 20: arthropod cuticle with pores and spines of various sizes, Q13/2, MPA 56514. 1 – 18: scale bars 25 μm . 19 and 20: scale bar 50 μm .

Palynofacies and palaeoenvironment

A summary of the relationship between sediment type, palynofacies, arthropod fragments and algal content is shown in Figure 5. The data combines samples of the same sediment type (Table 2) across the Strathclyde Group. The sediment types contain the following fauna: Non-marine silts; fish, *Geisina arcuata* ostracods, *Curvirimula* and *Monocraterium* roots. Non-marine mudstone; *Carbonicola*, *Curvirimula*, *Naiadites*, ostracods indet., fish and plants. Iron-rich non-marine mudstone; *Estheria*. Shaley coal; fossils are sparse, one sample contains *Lingula*. Coal; no ostracods or macrofossils. Marine mudstone; goniatite, *Schizodus* and *Streblopteria*. The graphs show these common palynofacies trends

- Spore content is highest in the marine samples.
- Coal samples have a high dark woody and arthropod content.
- Sheet cellular content is high in all non-marine samples.

- AOM does not show a clear trend.
- Algal content is highest in non-marine mudstones.

These trends can be interpreted in terms of the palaeoenvironment of deposition.

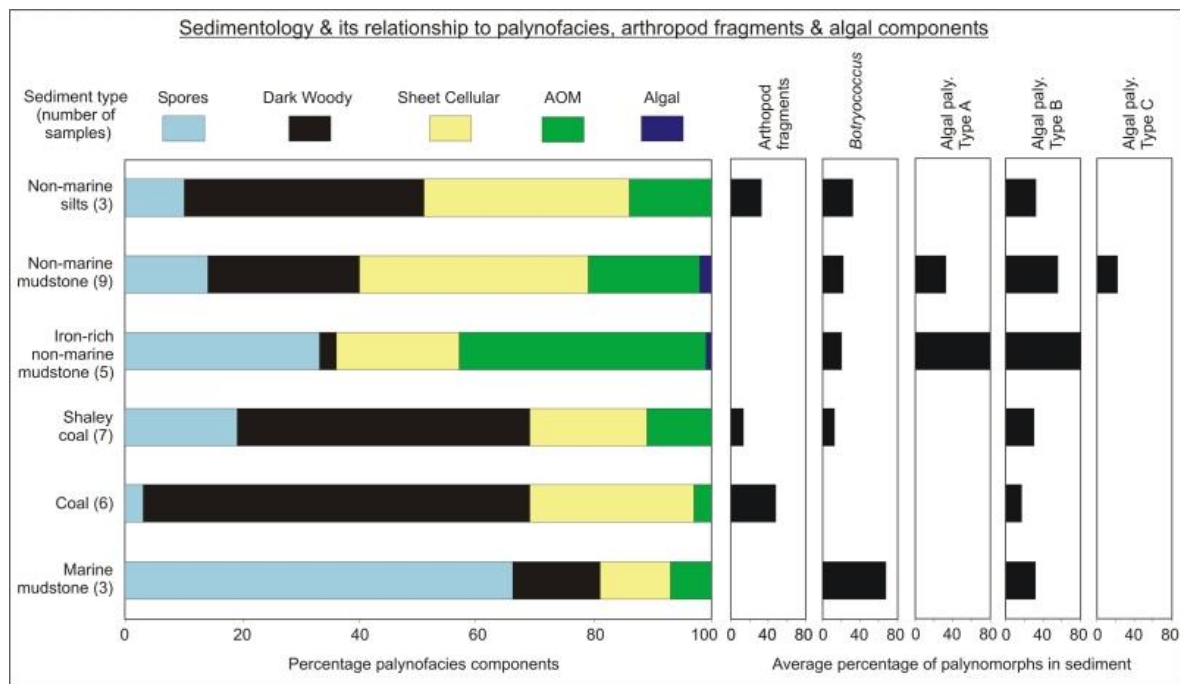


Figure 5. Percentage graphs of the average palynofacies components, arthropod fragments and algal palynomorphs for each sediment type. The percentage palynofacies components is a cumulative bar chart plot of the percentage of components on a slide (as is represented in Table 2). The mean of this data is taken, including all the samples for a certain sediment type, for example seven shaley coal samples. The average percentage of palynomorphs in the sediment is an average percentage of the occurrence of that palynomorph (see Table 2) in the slides from that sediment type.

Spores: A high spore content in non-marine samples may indicate a proximity to terrestrial plant sources, such as might be found in floodplain sediments, ephemeral lakes and swampy conditions. However, this is dependent on the preservation of the sample. Some iron-rich mudstones from the same section as those with a high spore content (containing “*Spirorbis*”, ostracods and fish) have a very low spore content. This is interpreted as a

preservational rather than palaeoenvironmental signal, as the samples have an unusually high AOM content and some are degraded. The significance of a high spore content in marine samples is uncertain, it may have resulted from a far-reaching marine transgression that resulted in a large amount of plant matter deposition in the sea.

Dark woody material: Sediments with a high dark woody content are interpreted to have formed in shallow water to exposure level floodplain deposits (with plant roots) and in coal-swamps. The associated fauna and palynofauna of *Naiadites*, arthropod fragments and algal palynomorphs type A, B and C is consistent with this type of environment, which is interpreted as freshwater.

Sheet cellular: The original plant source of the sheet cellular material is unknown, but its large variety may represent a high diversity of plant types as the source. The palaeoenvironmental significance of sheet cellular material is that in high abundances it represents a near-continental environment. There is no evidence to suggest that the sheets and filaments associated with the stromatolitic limestone have a microbial mat origin, their presence represents a near-terrestrial plant-rich environment. The fauna that are found with large abundances of this material (fish, *Estheria*, *Carbonicola* and *Naiadites*) are representative of freshwater conditions. The environment of deposition based on the macrofauna and palynofacies is interpreted as palaudal (marshy) environments (where there is a high dark woody component) or temporary ponds and lakes.

AOM: The palaeoenvironmental significance of AOM is unclear. There is more present in non-marine samples, but it does not correlate with the proportions of other palynofacies, the

sediment, macrofauna, microfauna or palynology. It may be that degraded sheet cellular material and spores appears as AOM.

Algal: Algal palynomorphs are most common in non-marine mudstones, and they are least common in shaley coals and coals (Figure 5). This does not exclusively represent an environmental factor, as they are not absent from all coal samples. Where there is a large amount of plant debris present (in the form of dark woody or sheet cellular), the abundances of algal palynomorphs are reduced, purely because of the large amount of plant material at that site of deposition. Therefore it is possibly a taphonomic signature rather than an environmental one. The palaeoenvironmental significance of the algal palynomorphs will be further discussed in a later section.

Arthropod fragments: The arthropod fragments are most common in shaley coals and coal sediments (Figure 5). Chitinous fragments in coals are known for their good preservation (Goodarzi 1984), so small fragments of animals that would otherwise be missed as macrofossils may be useful in terms of understanding the ecology. Fossilised soft-parts including arthropod cuticle have been recorded in coals from the Upper Carboniferous of Lancashire (Anderson *et al.* 1999) and Yorkshire (Bartram *et al.* 1987).

The single cuticle fragment is likely to be of terrestrial origin. The appendages of spiders and centipedes are distinctive because they have hairs attached down the length of the appendage, and claws at the end of the appendage, for example those of the Devonian of Gilboa, New York (Shear *et al.* 1987, 1998). The cuticle fragment is similar to arachnid cuticle from the Devonian of Gilboa (Shear *et al.* 1987), apart from the specimen in Plate 1, figs 19 and 20 also has fine setae that are not present in the Gilboa specimens.

The majority of the fragments are arthropod appendages, and these are interpreted as not of a terrestrial origin. The appendage fragments are likely to belong to small aquatic arthropods on the basis of the smooth nature of the podomere cuticle and lack of hairs, spines or claws. The affinity of the appendages is unknown, they appear to be leg or antennae-like limbs. The appendages with serrated edges could belong to a different group than those with smooth edges to the podomeres.

The specimen in Plate 1, fig. 6 is similar in size (150 μm in length) and approximate form to an ostracod appendage, such as the seventh limb of, for example *Pattersonocypris micropapillosa* Bate, from the Lower Cretaceous (Smith 2000). However, the basal appendage is wide to be of ostracod origin, and ostracods do not have serrated podomeres.

Certain specimens have an affinity with the limbs of copepods, especially that of Plate 1, fig. 18 (Boxshall pers. comm.). The oldest previously recorded fossil specimen of this group is a parasitic copepod from ichthyodectid fish of the Lower Cretaceous Santana Formation of Brazil (Cressey & Boxshall 1989, Cressey & Patterson 1973). The appendages of parasitic copepods are commonly coated in fine hairs (for example see specimens within Dojiri & Cressey 1987), unlike the ones from this study. The appendages are more like those of marine calanoid copepods, from a variety of distal podomeres of appendages (Mauchline 1998).

Future studies with a larger sieving size may reveal more complete arthropod fragments and elucidate their origin. Their future identification may help to provide information to the diversity of fauna present in these palaeal settings, where macrofossils are not preserved.

Systematic Palynology

UNKNOWN AFFINITIES

Algal Palynomorph type A, Plate 2, 4-12.

Description: Circular in outline, single walled, with no dehiscence, mostly dark coloured (brown, some are orange). The wall outer surface has a denticulate sculpture; it is densely covered in small spines of a micron scale (1-2µm length). The shape of the spines varies from thin and pointed (Plate 2, figs. 4, 5, 9), to thicker or shorter spines with rounded ends (Plate 2, figs. 6, 7, 10), to triangulate small stubby spines (Plate 2, fig. 12).

Dimensions: Range in diameter from 45–90 µm, average diameter 58 µm (20 specimens).

Material: This palynomorph occurs in seven samples, and is quite common.

Remarks: Some specimens have a folded interior, and are similar to specimens of algal palynomorph type B (Plate 1, figs. 7, 8, 10, 12). However, the presence of spines in type A and the thinner single wall of type B specimens distinguish the different groups. These specimens are similar to Carboniferous specimens of ?algal palynomorph sp. 1 and 2 of Stephenson *et al.* (2004).

Algal Palynomorph type B, Plate 3, 1-10.

Description: Circular in outline, thin single wall with no dehiscence, light yellow to dark coloured (most are brown). The surface of the wall is smooth, with some specimens exhibiting a granulose texture that is due to the presence of submicron size spherical bacteria (Plate 3, fig. 6). Some specimens contain what appear to be ridges (Plate 3, figs. 4,

5, 10), but this may just be wrinkling of the wall. In all specimens the wall is folded in preservation (Plate 3).

Dimensions: Range in diameter from 57-140 μm , average diameter 83 μm (20 specimens)

Material: Common occurrence in fifteen samples.

Remarks: These specimens are similar to the Carboniferous ?algal palynomorph sp. 1 and 2 of Stephenson *et al.* (2004). Some of the type B specimens from this study are similar to leiospheres/sphaeromorphs from Triassic sediments (Zavattieri & Prámparo 2006); they are described as inaperturate, subspherical bodies, with a smooth or faintly ornamented wall, usually folded, and putatively placed as algal in origin.

Algal Palynomorph type C, Plate 3, 11, 12.

Description: Spherical in outline, orange in colour, single walled, with no dehiscence. A vermiculate pattern of very fine branching tubes is present across the wall surface, the tubes are randomly orientated. Some specimens are folded.

Dimensions: Range in diameter from 60-80 μm , average diameter 69 μm (4 specimens).

Material: Rare occurrence, only present in two samples, which are associated with the stromatolitic limestone.

Remarks: Vermiculate spores are present, but the vermiculate palynomorphs do not have a dehiscence, the vermiculae are much finer and have a more random pattern.

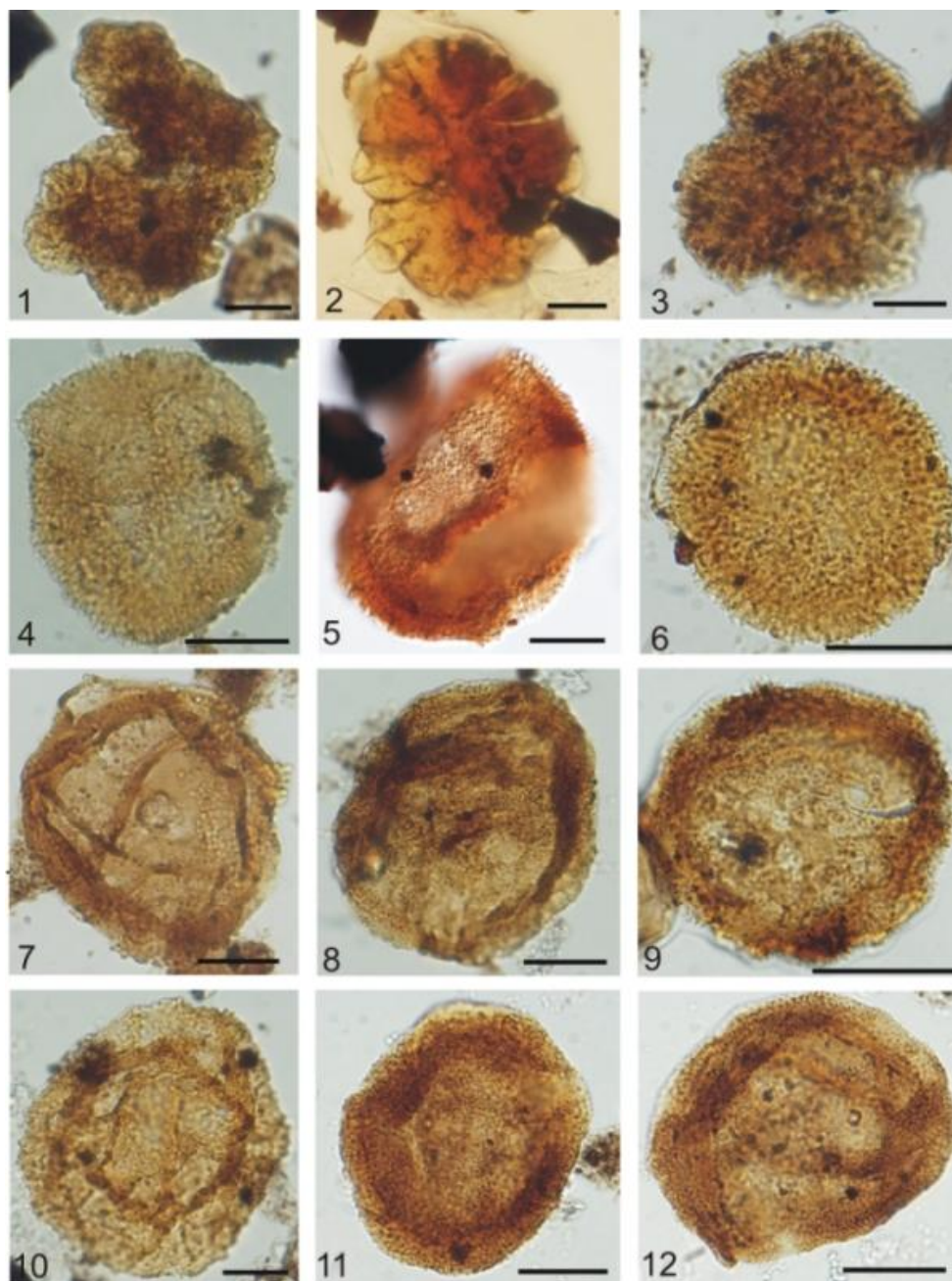


Plate 2. *Botryococcus* sp. and algal palynomorph type A. 1-3: *Botryococcus* sp. 1: two joined colonies, O47/4, MPA 56508. 2: specimen with distinct cone shaped cells, U15, MPA 56513. 3: A typical sub-spherical form composed of three subcolonies, R59/2, MPA 56495. 4 to 12: algal palynomorph type A. 4: specimen with thin pointed spines, E60/3, MPA 56487. 5: folded specimen with thin pointed spines, M64/4, MPA 56476. 6: specimen with rounded-end spines, O69/1, MPA 56579. 7: folded specimen with rounded-end spines, G60, MPA 56488. 8: O61/3, MPA 56478. 9: specimen with thin pointed spines, Q71/4, MPA 56484. 10: folded specimen with rounded-end spines, K64/4, MPA 56478. 11: V64, MPA 56578. 12: specimen with small triangulate spines, H63, MPA 56478. Scale bars 20 μ m.

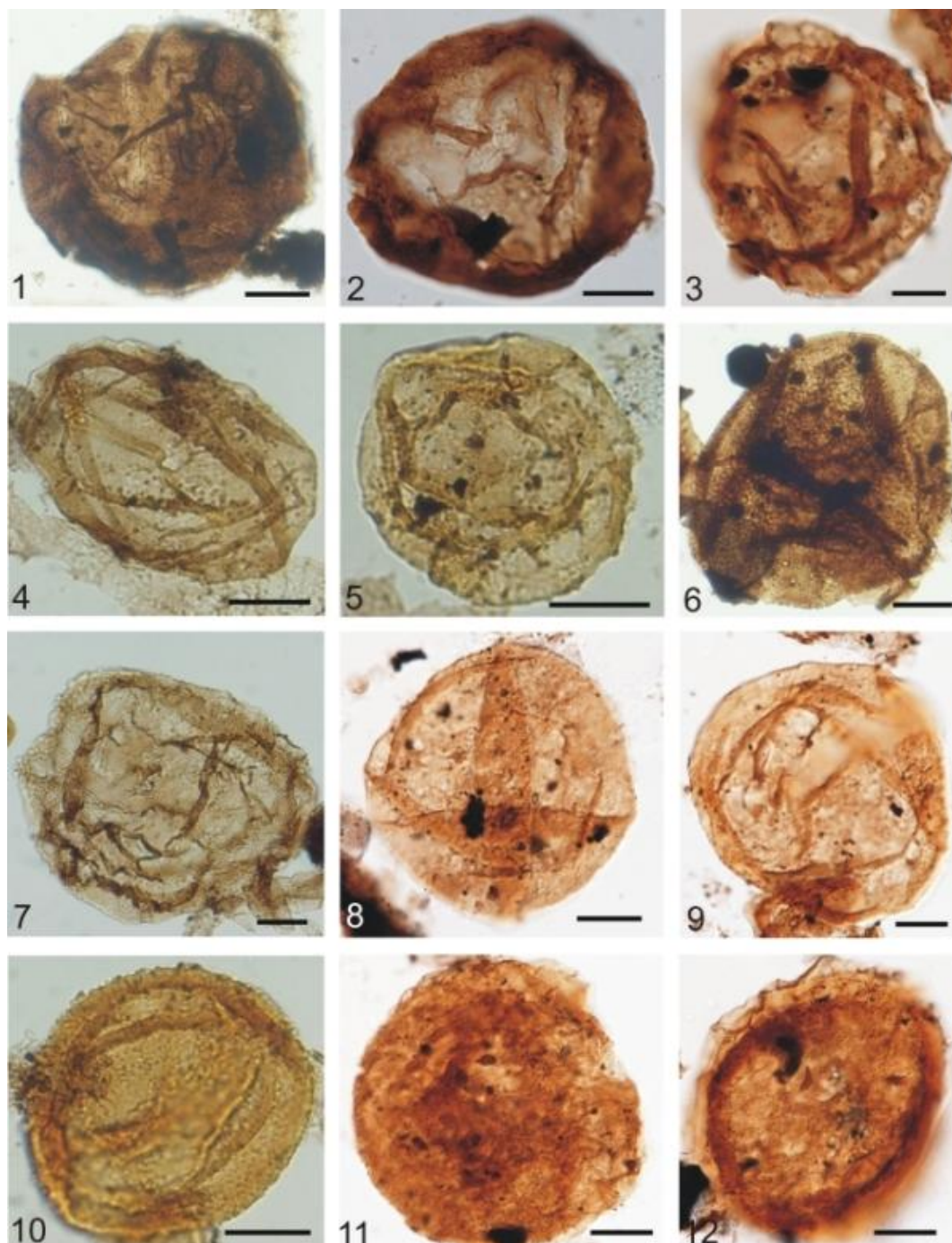


Plate 3. Algal palynomorph types B and C. 1 to 10: algal palynomorph type B. 1: W52, MPA 56487. 2: B43/1, MPA 56476. 3: D46/2, MPA 56476. 4: specimen with putative ridges, F65, MPA 56484. 5: another specimen with putative ridges, R67/3, MPA 56479. 6: specimen with bacterial growth on the surface, T52/3, MPA 56465. 7: a large specimen, D of England, MPA 56484. 8: N66/1, MPA 56477. 9: K61/3, MPA 56477. 10: another specimen with putative ridges, G54, MPA 56479. 11 and 12: algal palynomorph type C. 11: a well preserved specimen, G66/3, MPA 56477. 12: a folded specimen, N66, MPA 56477. Scale bars 20 μ m.

Palaeoenvironmental interpretation of algal palynomorphs

Botryococcus sp. occurs with ostracods indet., *Geisina*, *Curvirimula*, marine macrofauna, fish and plant macrofossils. Excluding the marine samples, the ostracods and macrofauna represent a freshwater environment. The marine samples are interpreted as possibly marginal marine based on the abundant spore content and restricted macrofauna. It is possible that *Botryococcus* sp. in the marine sediments represents a taphocenosis, and that it was transported from freshwaters.

Botryococcus has been recorded as a dominant flora in Triassic lacustrine sediments, in what are interpreted as fairly deep-water lakes (Cole & Crittenden 1997, Zavattieri & Prámparo 2006). In more recent sediments from the Holocene, *Botryococcus* is an indicator of freshwater conditions; from the environments of freshwater marsh, salt marsh, fluvial and peat bog (Medeanic 2006). *Botryococcus* is also described as abundant in palynofacies dominated by amorphous organic matter, from what is interpreted as a lacustrine environment with high productivity (Batten & Grenfell 1996).

Algal palynomorph types 1-3 are most common in non-marine mudstones associated with ostracods indet., *Geisina*, *Curvirimula*, *Naiadites*, *Estheria*, *Schizodus*, fish and *Lingula*. This range of ostracods and macrofauna represents a brackish to freshwater environment. The palaeoenvironmental interpretation of the non-marine sediments the palynomorphs occur in ranges from a swampy coal-measures environment with ephemeral pools to estuaries, floodplains and lacustrine conditions. Spores of zygnematacean algae may have been able to survive periods of desiccation, as is the case with the modern pondweed *Spirogyra* (van Greel & Grenfell 1996). In this way the algal palynomorphs could

successfully colonise temporary freshwater environments such as pools, floodplains and marshes.

Algal palynomorph types A and B from this study are similar to the Carboniferous ?algal palynomorph sp. 1 and 2 of Stephenson *et al.* (2004), which are considered as spores of zygnematacean algae from a freshwater environment. Some type B palynomorphs resemble leiospheres/sphaeromorphs from Triassic sediments (Zavattieri & Prámparo 2006), which are interpreted as freshwater forms.

The Ballagan Formation (Inverclyde Group of the Midland Valley of Scotland) contains algal palynomorphs from what are interpreted fresh to brackish conditions (Stephenson *et al.* 2004). The diversity of palynomorphs is greater than that from the Strathclyde Group (this study), and the palynomorphs reflect freshwater conditions. The macrofauna (“*Spirorbis*”, fish, the bivalve *Modiolus*, rare brachiopods and orthocones) and ostracods (*Beyrichiopsis*, *Cavellina*, *Knoxiella*, *Shemonaella* and *Sulcella*) associated with the palynomorphs of the Ballagan Formation are different from this study. They are more indicative of marginal marine to brackish conditions, while the macrofauna and ostracods from this study that are associated with palynomorphs are more indicative of brackish to freshwater.

Conclusions

- The Mississippian of the Midland Valley of Scotland contains marine to non-marine sediments which contain some of the earliest non-marine ostracods. Non-marine sediments that contain a range of macrofauna and ostracods are interpreted as

brackish to freshwater. Recorded from these samples are the algal palynomorphs *Botryococcus* sp. and algal palynomorph types A to C.

- A palynofacies analysis identifies that the most important components in non-marine samples are a high degree of dark woody material and sheet cellular material, both of which are derived from plant macrofossils. These components in abundance are indicative of near-land depositional settings such as swamps and temporary pools, where there was time for large amounts of organic material to accumulate. The quantities of spores and amorphous organic matter were less important due to the poor preservation (degradation) of some of the samples.
- One cuticle specimen from a possible terrestrial arachnid, and the appendages of small aquatic arthropods are present in shaley coals, coals and non-marine silts. Although the arthropod appendages found are of unknown origin, their future identification may help to provide information on the diversity of fauna present in these palaeodal settings, where macrofossils are not preserved.
- The algal palynomorphs are taxonomically described, with algal palynomorph types A to C left in open nomenclature. They are compared to other modern and fossil taxa, and are similar to living and Palaeozoic freshwater algae.
- The discovery of freshwater algal palynomorphs in the non-marine sediments of the Strathclyde Group adds more evidence to an interpretation of freshwater environments in the Mississippian. This is of significance for ostracods, which were first colonising non-marine environments at this time.

Chapter 6: The carapace ultrastructure of Carboniferous ostracods

Abstract

Assessing the preservation of fossil shells is essential prior to any isotopic analysis for palaeoenvironmental insights. Ostracods from the Carboniferous (Mississippian) of the Midland Valley of Scotland are all diagenetically altered. Ostracods composed of diagenetic calcite may be mistaken for pristine specimens without a study of the carapace ultrastructure. The fidelity of ultrastructural preservation in Carboniferous specimens was compared to Recent ostracods caught *in vivo*. Twentytwo Carboniferous species were studied, from the Myodocopida, Palaeocopida and Podocopida, compared with nine species of extant podocope ostracods. Recent ostracods have a smooth epicuticle a few microns thick and a procuticle composed of equant to elongate calcite crystals ($<0.5\ \mu\text{m}$ size). The crystals are aligned with their long axis parallel to the carapace margins, to produce a foliated to multi-laminate fabric, which is more pronounced at the areas of curvature such as the valve margins. In Carboniferous specimens, the epicuticle is not preserved and the procuticle is recrystallised by neomorphic calcite, resulting in equant calcite crystals. The calcite crystals are $1\text{--}3\ \mu\text{m}$ long at the valve margins, and $1\text{--}2\ \mu\text{m}$ size in the interior of the procuticle. The recrystallisation texture is similar to that seen in fossil planktonic foraminifera that have undergone early diagenesis. Some Carboniferous specimens have a multi-laminate procuticle, and this is a remnant of the original carapace structure. The procuticle layer of Recent and Carboniferous specimens is homogeneous, and is not differentiated into exocuticle and endocuticle layers, as is seen in some arthropods.

Introduction

Crustaceans have an exoskeleton consisting of a multi-laminate chitin-protein complex which is commonly calcified (Dennell 1960, Neville 1975, Stevenson 1985). Ostracod carapaces consist of an interlocking lattice of calcite crystals surrounded by chitinous membranes (Bate & East 1972). The carapace is secreted after each moult stage, with typically eight moults before the adult carapace. At the pre-moult stage of the penultimate instar, the new outer lamella (calcified carapace) is formed beneath the old outer lamella before moulting (Yamada *et al.* 2005), and calcium is not reabsorbed from the old carapace prior to moulting (Turpen & Angell 1971). The process of carapace formation has been and is currently an ongoing area of research for ostracodologists (for example, see Rosenfeld 1979, Yamada *et al.* 2005). Preliminary studies by Okada (1981, 1982), Keyser (1995) and Yamada *et al.* (2005) have shown that the external carapace morphology represents the arrangement and function of the epidermal cellular tissue. For example, each reticulate polygon of the external surface of *Bicornucythere bisanensis* is formed by the calcification of one epidermal cell (Okada 1982).

A carapace composed of pristine calcite is critical to preserve geochemical information from the time of deposition. Diagenetically altered specimens will have a surface that is pitted, dissolved, or recrystallised. Several techniques have been used to assess diagenesis in Recent ostracods; a visual preservation index (Dwyer *et al.* 2002, Keatings *et al.* 2002), and image analysis techniques using scanning electron microscopy, to assess surface recrystallisation (Mischke *et al.* 2007). This study assesses the carapace ultrastructure to examine the preservation.

There have been few studies of the carapace ultrastructure of the outer lamella in living ostracods (Kornicker 1969, Sylvester-Bradley & Benson 1971, Bate & East 1972, Okada 1982, Sohn & Kornicker 1988, Keyser 1995, Yamada *et al.* 2005). Only one study has compared the outer lamella carapace ultrastructure of living specimens with fossil ostracods (Dépêche 1982).

The calcified part of the ostracod carapace is the outer lamella cuticle, which is approximately 30 μm thick and consists of the procuticle layer (Bate & East 1972, Sylvester-Bradley & Benson 1971). The carapace is covered by a continuous cuticular integument, composed of chitin and organic material. The outer layer of this integument is the epicuticle. The epicuticle is a thin, smooth, chitinous membrane that covers the external surface of the carapace (Figure 1). The epicuticle is of sub-micron thickness and decays when the carapace is fossilised (Dépêche 1982). The procuticle layer is composed of sub-micron size calcite crystals which can be foliated or laminated, thus the procuticle has also been called the foliated layer (Sylvester-Bradley & Benson 1971). Okada (1982) describes the individual procuticle crystals as about 0.3 μm in thickness and 2 μm in width, with the long axis parallel to the valve margins. The epidermis is an organic membranous layer that protects the internal soft parts of the ostracod, and is located next to the inner edge of the procuticle. It is not calcified, and rarely fossilised. Approximately 10 μm thick, the epidermis includes outer epidermal cells, subdermal cells, glands, nerves, and the base of the pore canals through which the sensilla pass. The key area of interest for this study is the calcified procuticle layer.

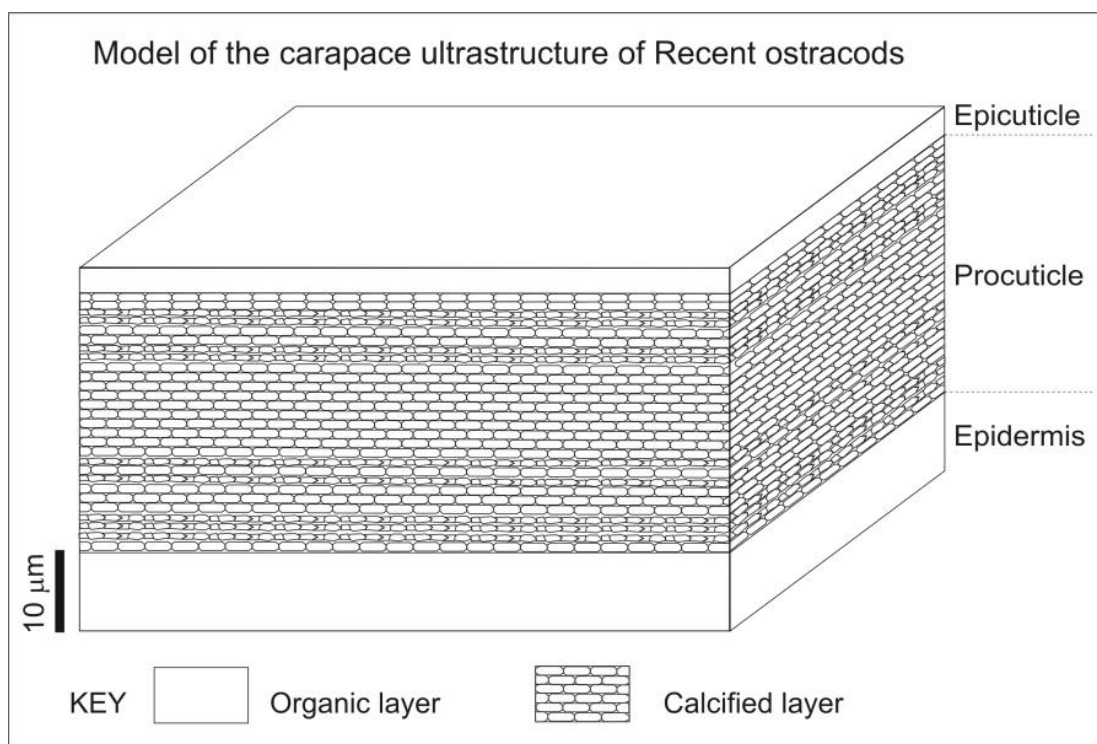


Figure 1. Model of the carapace ultrastructure of Recent ostracods, adapted from Sylvester-Bradley & Benson 1971. The procuticle is also called the calcified outer lamella, and is the main area of interest in this study.

This study compares the ultrastructure of a range of living and Carboniferous specimens. Carboniferous ostracods are recrystallised, and the diagenetic product is described. The calcified procuticle layer of living and Carboniferous ostracods is documented in terms of crystal textures, multi-laminate structure and mineralogy. Despite diagenetic alteration, some Carboniferous specimens retain a multi-laminate carapace structure. This structure is discussed in terms of the ultrastructure of Recent specimens.

Materials and Methods

Recent ostracods: Living ostracods were collected *in vivo* from a range of locations in England and Japan, such as temporary ponds, estuaries and rock pools (Table 1). The

Recent ostracods are podocopes and include representatives from the Superfamilies Cypridoidea (Families Candonidae and Cyprididae) and Cytherocopina (Families Cytherideidae and Hemicytheridae). The specimens were preserved in ethanol, then picked and stored dry in microfossil slides, or in ethanol in test tubes. Specimen information is recorded in appendix 5.

Recent Ostracods			
Ostracod species	Locality Information		
<i>Aurila woutersi</i> Horne, 1986	Porlock, Severn Estuary, donated by Dr D J Horne (Queen Mary Uni. of London)		
<i>Bradleystrandesia fuscata</i> (Jurine, 1820)	A shallow temporary pond, Flatford Mill, Suffolk (TM 077 332)		
<i>Candona candida</i> (Müller, 1776)	The river Stour, Flatford Mill, Suffolk (TM 081 327)		
<i>Candonopsis tenuis</i> (Brady, 1886)	Lake Biwa, Japan, specimens donated by Dr Robin J Smith (Lake Biwa Museum)		
<i>Cyprideis torosa</i> (Jones, 1850)	A salt marsh at Pegwell Bay, Isle of Thanet, Kent, from a salt marsh (TR 344 635)		
<i>Cythere lutea</i> Müller, 1875	A saltwater rock pool, Foreness Point, Isle of Thanet, Kent (TR 384 716)		
<i>Eucypris virens</i> (Jurine, 1820)	A shallow temporary pond, Flatford Mill, Suffolk (TM 077 332)		
<i>Fabaeformiscandona japonica</i> (Okubo, 1990)	Lake Biwa, Japan, donated by Dr Robin J Smith		
<i>Hemicythere villosa</i> (Sars, 1866)	Blue Anchor, Severn Estuary, donated by Dr David J Horne		
<i>Pseudocandona sucki</i> (Hartwig, 1901)	The river Stour, Flatford Mill, Suffolk (TM 081 327)		
Carboniferous Ostracods			
Boreholes & field sections	Formation	National Grid Reference	Samples
Inverclyde Group: Heads of Ayr field section	Ballagan	NS 2933 1870	BGS collection
Inverclyde Group ostracod species: <i>Acratia</i> sp., <i>Cavellina</i> sp., <i>Cavellina benniei</i> (Jones, Kirkby & Brady, 1874) <i>Cavellina</i> aff. <i>coela</i> Rome, 1973, <i>Cavellina incurvscens</i> (Jones & Kirkby, 1896), <i>Shemonaella</i> sp. A.			
Strathclyde Group: Randerston field section Anstruther borehole Billow Ness - Anstruther field section Kilconquhar borehole Balcormo borehole Claremont borehole Denork borehole	Anstruther Anstruther Anstruther Pittenweem - Pathhead Sandy Craig Pathhead Pathhead	NO 6150 1125 NO 5650 0355 NO 5590 0271 NO 4844 0304 NO 5084 0408 NO 4518 1419 NO 4540 1409	Field samples BGS collection BGS collection BGS collection BGS collection BGS collection BGS collection
Strathclyde Group ostracod species: <i>Acutiangulata</i> sp. A, <i>Bairdia submucronata</i> Jones & Kirkby, 1879, <i>Carbonita</i> sp. <i>Cavellina benniei</i> (Jones, Kirkby & Brady, 1884), <i>Cavellina valida</i> (Jones, Kirkby & Brady, 1884), <i>Geisina arcuata</i> (Bean, 1836) <i>Healdia</i> cf. <i>cuneata</i> Robinson, 1978, <i>Hollinella</i> (<i>Keslingella</i>) <i>radiata</i> (Jones & Kirkby, 1886), <i>palaeocope</i> sp. A <i>palaeocope</i> sp. B, <i>palaeocope</i> sp. C, <i>Paraparchites circularis</i> n. sp., <i>Paraparchites armstrongianus</i> (Jones & Kirkby, 1886) <i>Polyclope elegans</i> n. sp., <i>Shemonaella ornata</i> n. sp., <i>Shemonaella siveteri</i> n. sp., <i>Silenites</i> sp. A			

Table 1. List of the Recent and Carboniferous ostracod species used in this study, with their collection locations. Carboniferous borehole and some field section samples are stored at the BGS in Edinburgh. The Inverclyde Group specimens are from the early Mississippian (Tournaisian) of Ayrshire, the Strathclyde Group specimens are from the middle Mississippian (Viséan) of Fife. The formations become younger in age from Ballagan; Anstruther; Pittenweem; Sandy Craig; Pathhead.

Ostracod carapace ultrastructure was analysed from whole carapaces or valves and broken ostracod shell fragments, mounted onto Scanning Electron Microscope (SEM) stubs using PVA glue mixed with water, and then gold coated using an Emitech Sputter Coater K500X. Individual ostracod carapaces were embedded in an araldite thin section. This thin section was cut to a thickness of 160 μm and polished to a 0.25 μm size grade (polished thin section standard). The section was subsequently re-ground to a thickness of 100 μm to reveal different areas of the ostracod carapaces. The thin section, carapace fragments and whole ostracods were analysed at high and partial vacuum on a Hitachi S-3600N Scanning Electron Microscope. The secondary electron (SE) detector was used for imaging the surface structure of specimens. The back-scattered electron (BSE) detector was used for identifying changes in composition, and can produce semi-quantitative element data derived from a cobalt standard.

Carboniferous ostracods: Sediments containing ostracod fossils are studied from the Mississippian successions of the Midland Valley of Scotland (Table 1). Carboniferous ostracods include representatives of the Podocope Families Bairdiidae, Bairdiocyprididae, Carbonitidae, Cavellinidae, Geisinidae, Healdiidae and Paraparchitidae, the Palaeocope Family Holliniellidae, and the Myodocope Family Polycopidae.

Fossil ostracods were picked off the surface of rock samples with a needle, and no sediment processing techniques were used. Whole carapaces, valves and broken shell fragments were mounted on SEM stubs. Polished thin sections were made from ostracod-rich sediments, and cut to a standard thickness of 30 μm . These samples were analysed under the SEM using the same techniques as for recent specimens, and the BSE detector was used for the elemental mapping of carapace structures. The thin sections were analysed under

cathodoluminescence (CL) at the University of Liverpool, to highlight diagenetic cements and multi-laminar structures. The CL setup consists of an optical microscope cold cathode vacuum setup, with argon gas as an inert vacuum component. Concentrations of manganese result in a bright orange luminescence, while iron acts to inhibit the luminescence (Marshall 1988).

Carbon coated polished thin sections were analysed using a JEOL JXA-8600S electron microprobe, to produce quantitative results of ostracod shell chemistry. The settings for analysis are an accelerating voltage 15 kV, and a probe current of 30 nA. The smallest beam diameter of 15 μm was used, and testing was focused on specimens with a thick carapace, or areas of the carapace such as the hinge or ventral commissure. 20 second count times were used for measurement of characteristic peak intensities, with 10 seconds at each of the background positions selected on either side of the peak. The quantitative results were calibrated to standards used for carbonate analysis, with an analytical error of 0.1wt%.

Assessing the preservation of fossil ostracods

To assess the fidelity of preservation in Carboniferous ostracods, a study of the carapace ultrastructure is necessary, with reference to pristine Recent ostracods. Some of the Carboniferous specimens are superficially well preserved, composed of low-magnesium calcite with detailed original surface ornamentation. It is only when the ultrastructure is examined that neomorphic calcite is seen to be pervasive throughout the carapace. The following sections detail the ultrastructure of the epicuticle and procuticle layers in Recent and Carboniferous specimens.

1. Ultrastructure of the external carapace surface

a. Recent specimens

The external layer of the cuticle of Recent ostracods is the epicuticle, which contains the exterior ornament of the carapace. Pores and sensory setae emerge from the epicuticle, allowing fluid and gas exchange and sensory connections with the ostracod animal inside the carapace (Figure 2). The epicuticle is a smooth layer a few microns in thickness, no crystal structures are evident as it is composed of chitin and organic material.

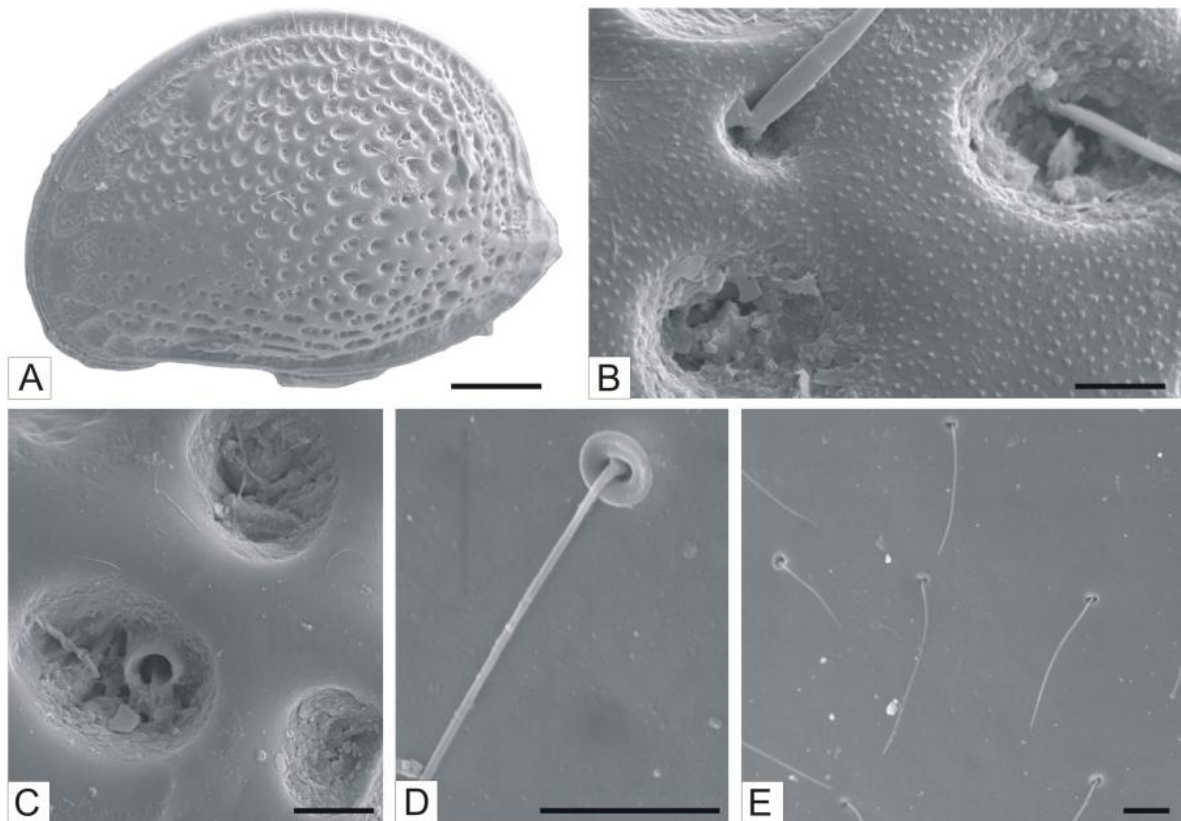


Figure 2. The epicuticle ultrastructure of Recent ostracods. A, B: *Aurila woutersi*, female, carapace, CEB8: A: left lateral view. B: the external surface of the epicuticle, with pores, setae, and a granulate ornament. C: *Hemicythere villosa*, male, carapace, a smooth epicuticle with pores, CEB49. D: *Candonopsis tenuis*, male, carapace, a disk-shaped pore and setae on the epicuticle surface, CEB14. E: *Fabaeformiscandona japonica*, female, carapace, a smooth epicuticle with multiple pores and setae, CEB45. A: scale bar 100 µm. B-E: scale bar 10 µm.

b. Carboniferous specimens

Twenty two Carboniferous ostracod species, from ten families were analysed for the ultrastructure of the carapace. The specimens are composed of calcite, from the Inverclyde and Strathclyde Groups (Table 2). In contrast to the smooth epicuticle of living ostracods, the external carapace of Carboniferous specimens have a crystalline ultrastructure in the form of interlocking euhedral calcite crystals which are of 1-3 μm in size. Surface features such as pores, spines, tubercles and reticulation are present, and are also composed of euhedral calcite crystals (Figure 3A, E). No overgrowth textures are seen. In some specimens clear facets are seen on the individual crystals; in the form of crystal faces, growth lines and ridges (Figure 3C, D). In other specimens the crystal edges are smooth, and there are gaps between the crystals (Figure 3F, G).

Ostracods from the Inverclyde Group have an epicuticle ultrastructure of 2 – 6 μm size calcite crystals, of two size populations (Table 2). The crystals are columnar shaped, with their long axis arranged perpendicular to the carapace surface (Figure 3B). The crystals have a more euhedral form and larger size than those from the Strathclyde Group specimens.

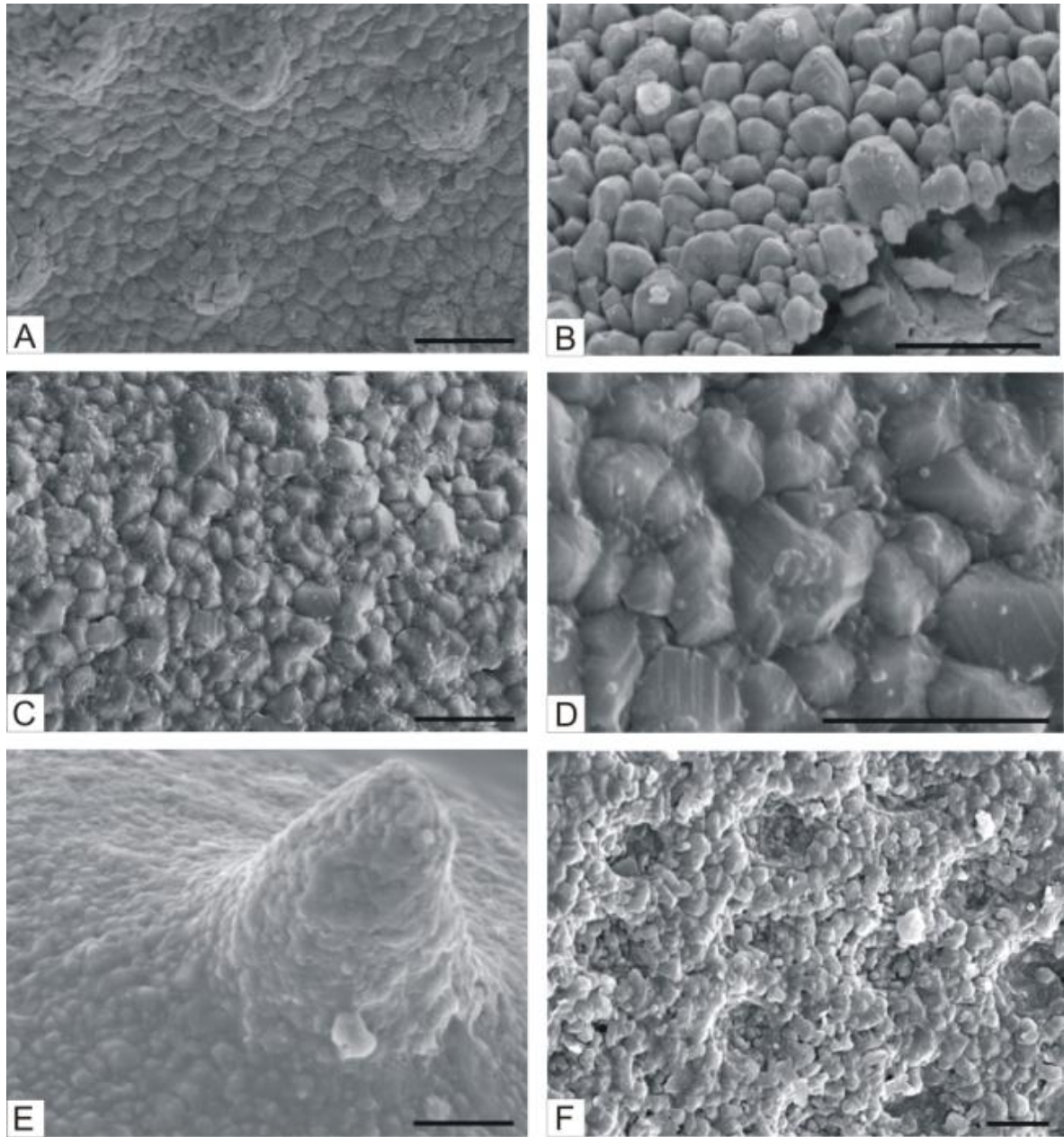


Figure 3. The external carapace surface ultrastructure of Carboniferous ostracods. Sample numbers refer to BGS rock samples that the ostracods are picked from. A: *Hollinella (Keslingella) radiata*, male, carapace, epicuticle surface near to the ventral margin, with a tuberculate ornament, EN 4885. B: *Shemonaella* sp., carapace, with a hole in the epicuticle layer to the bottom right, MPA 49788. C, D: *Geisina arcuata*, carapace, with faceted calcite crystals, EN 4827. E: palaeocope sp. C, juvenile, carapace, posterodorsal spine, EN 4848. F: *Shemonaella ornata* n. sp., carapace, with a circular pitted reticulate ornament, some of the calcite crystals have some gaps between them, EN 4804. Scale bars 10 μ m.

Some species have smaller crystal sizes, between 0.5 – 1 μm in (Table 2). In general these small crystals occur in genera from the Strathclyde Group that have a smaller carapace size, such as *Acutiangulata*, *Cavellina* and *Healdia*, while larger ostracods have on average a 1-3 μm size crystals (Table 2). Some specimens do not fit with this trend, such as the palaeocopes and *Silenites* sp. A. All of the Inverclyde Group ostracods have two size orders of crystals, with no correlation between the size of the crystals and carapace size. There is no relationship between age of the sample, species, host lithology (they are all from mudstone sediments) and the crystal size.

Ostracod Species	Carapace length	Sample	Crystal size	External Surface of Carapace Texture
<u>Inverclyde Group</u>				
<i>Acratia</i> sp. A	820 μm	MPA 49788	5-6 & 2-3 μm	faceted crystals, two size orders
<i>Cavellina</i> sp.	700 μm	MPA 49788	4-5 & 2 μm	crystals perpendicular to carapace surface
<i>Cavellina benniei</i>	630 μm	MPA 49788	5-6 & 2 μm	equant, faceted crystals
<i>Cavellina</i> aff. <i>coela</i>	750 μm	MPA 49788	6 & 2 μm	equant crystals, two size orders
<i>Cavellina incurvescens</i>	680 μm	MPA 49788	5 & 2 μm	equant crystals, two size orders
<i>Shemonaella</i> sp. A	650 μm	MPA 49788	5-6 & 2-3 μm	large crystals of epicuticle
<u>Strathclyde Group</u>				
<i>Acutiangulata</i> sp. A	450 μm	EN 4885	0.5 μm	fine equant crystals
<i>Bairdia submucronata</i>	830 μm	EN 4885	1 - 3 μm	some surface dissolution and pitting
<i>Cavellina benniei</i>	730 μm	EN 4801	1 - 2 μm	granulose texture, iron oxide on surface
<i>Cavellina valida</i>	570 μm	EN 4859	0.5 μm	fine equant crystals
<i>Geisina arcuata</i>	1000 μm	EN 4827	1 - 3 μm	multi-faceted crystals
<i>Healdia</i> cf. <i>cuneata</i>	420 μm	EN 4849	0.5 - 1 μm	crystals angular, irregularly shaped
<i>Hollinella</i> (<i>Keslingella</i>) <i>radiata</i>	1050 μm	EN 4840	1 - 3 μm	ornament well preserved
palaeocope sp. B	600 μm	EN 4805	5 μm	porus, extensive surface dissolution
palaeocope sp. C	600 μm	EN 4856	1 - 3 μm	some surface dissolution
<i>Paraparchites armstrongianus</i>	1800 μm	EN 5188	1 - 3 μm	equant crystals
<i>Shemonaella ornata</i> n. sp.	1600 μm	EN 4808	1 - 3 μm	surface dissolution, rounded crystal edges
<i>Shemonaella siveteri</i> n. sp.	1200 μm	EN 4787	1 - 3 μm	some local surface dissolution
<i>Silenites</i> sp. A	690 μm	EN 5249	0.5 - 1 μm	fine crystals, surface dissolution

Table 2. External carapace surface ultrastructure information for Carboniferous ostracods. The crystals are measured from the outer surface of the epicuticle. The Strathclyde Group samples are from the Pathhead Formation. Species were analysed from multiple samples, with the most representative information for that species listed here.

Interpretation of the external carapace ultrastructure of Carboniferous specimens: The ultrastructure of interlocking euhedral calcite crystals is diagenetic calcite. The crystalline calcite replaces of forms just underneath the epicuticle layer, as the surface features such as

pores and tubercles are still present. This preservation of the ornament indicates that the calcite is neomorphic (using the terminology as applied to diagenetically altered foraminifera in Sexton *et al.* 2006), produced by recrystallisation. Sub-micron size biogenic calcite has been replaced by inorganic calcite crystals of a larger size, but preserving the original crystal configuration.

The neomorphic calcite extends throughout the procuticle and entire thickness of the carapace. Where there are two size orders of crystals within the epicuticle or procuticle, this represents the crystal growth history, with larger calcite crystals growing first. The difference in crystal size in different species may show evidence for the presence of an epidermal cellular template.

The recrystallisation of the procuticle may have occurred during different periods, or during the same event. The process of original calcite dissolution and recrystallisation into larger neomorphic crystals is poorly understood. All that can be assumed is that the recrystallisation happened relatively soon after the burial of the ostracods, as the original external carapace features are retained, including small pores.

Studies on diagenetically altered planktonic foraminifera from the Cenozoic reveal a similar shell ultrastructure of neomorphic calcite crystals (Pearson *et al.* 2001, Sexton *et al.* 2006, Williams *et al.* 2005a, b, 2007, Pearson & Burgess 2008). The foraminifera have a sub-micron low magnesium calcite crystal ultrastructure when well preserved, that is replaced by neomorphic calcite of 1-2 μm size crystals that is present throughout the thickness of the test. These specimens appear opaque or “frosty” when compared to living or fossilised pristine planktonic foraminifera, which appear transparent or “glassy”. The

neomorphic calcite is interpreted to have grown by dissolution of the test and recrystallisation at shallow burial depths, of less than 300 m (Pearson *et al.* 2001).

Diagenetic alteration was more common in open ocean pelagic oozes and chalks, with more pristine specimens preserved in impermeable clays (Pearson & Burgess 2008). In this study all the specimens are from the same sediment type.

2. Ultrastructure of the procuticle

a. Recent specimens

The procuticle and epicuticle carapace layers of Recent ostracods are permeated by pore canals containing the sensilla (Figure 4A, B). In broken carapace fragments the epicuticle can clearly be distinguished from the procuticle, as it forms a thin, smooth outer layer (Figure 4E). The procuticle is homogeneous, with a crystalline to granular texture, composed of sub-micron size tabulate to elongate crystals, less than 0.5 μm in length.

The crystals are aligned parallel to the carapace margins to produce a spectrum of aligned crystal textures (Table 3), for example foliated (Figure 4C), strongly foliated (Figure 4F), or a multi-laminate texture (Figure 4D, E). Folded or curved areas of the carapace, such as at the ventral margin, have the most strongly aligned crystals (Figure 4E, F). In many thin sectioned specimens, numerous cracks occurred in the carapace parallel to the carapace margins (Table 3).

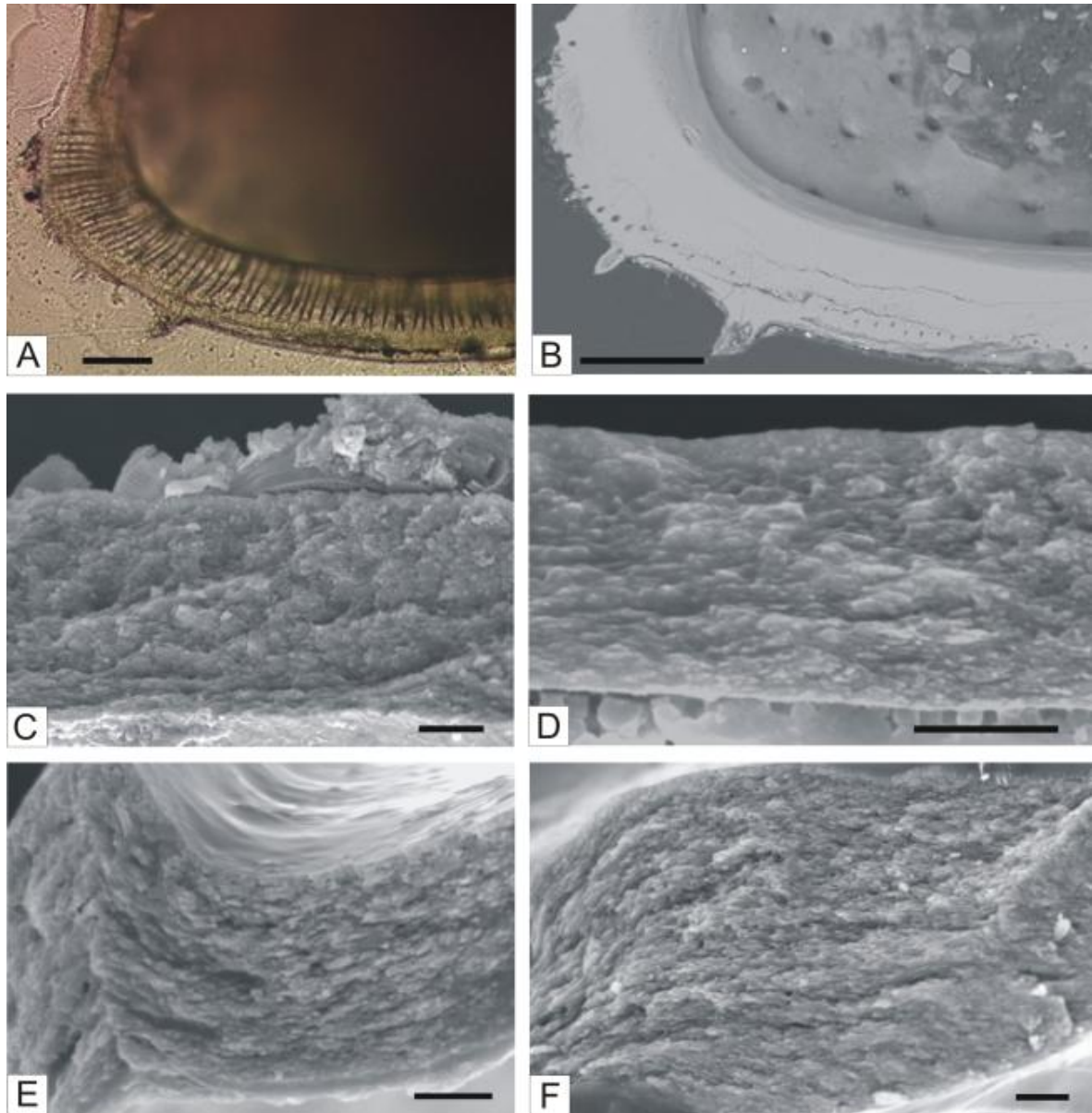


Figure 4. The procuticle ultrastructure of Recent ostracods. A, B: *Aurila woutersi*, female, carapace, araldite polished thin section, CEB9. A: the posteroventral area with setae along the carapace margin, light microscope image viewed in plane polarised light (so the thickness of the carapace is transparent). B: the same area of the carapace, showing a cut through the pore canals, SEM image of the surface of the thin section. A few cracks are present parallel to the carapace margins. C to F: broken carapace fragments, the epicuticle layer is at the top of the images. C: *Cyprideis torosa*, male, carapace, with a foliated texture, the epicuticle is coated in a diatom-rich carbonate cement, CEB17. D: *Bradleystrandesia fuscata*, female, single valve, with a multi-laminate texture, CEB11. E: *Eucypris virens*, female, single valve, the ventral end of valve with a multi-laminate texture, CEB43. F: *Cythere lutea*, male, carapace, a curved area of the valve, a strongly foliated texture, CEB31. A, B: scale bar 50 μ m. C-F: scale bar 5 μ m.

Recent ostracod species	Procuticle texture in broken fragments	Procuticle texture in thin section
<i>Aurila woutersi</i>	x	cracks parallel to valve margins
<i>Bradleystrandesia fuscata</i>	multi-laminate, strongly where valve curves	x
<i>Candona candida</i>	foliated, multi-laminate where valve curved	x
<i>Candonopsis tenuis</i>	very fine crystal size, no textures seen	thin carapace, no textures seen
<i>Cyprideis torosa</i>	foliated, multi-laminate where valve curved	foliated, cracks parallel to valve margins
<i>Cythere lutea</i>	strongly foliated where valve curves	multi-laminate, cracks parallel to valve margins
<i>Eucypris virens</i>	foliated, multi-laminate where valve curved	x
<i>Fabaeformiscandona japonica</i>	strongly foliated	thin carapace, no textures seen
<i>Hemicythere villosa</i>	x	multi-laminate, cracks parallel to valve margins
<i>Pseudocandona sucki</i>	foliated	x

Table 3. Procuticle textures of Recent ostracods, from broken carapace fragments and polished thin sections. Each specimen had a procuticle crystal size less than 0.5 μm . Crosses indicate where no useful information was recovered, due to poor preparation of the specimens in an araldite thin section, or where a small number of broken fragments provided insufficient data.

Interpretation of the procuticle ultrastructure of Recent specimens: There is no distinction between the exocuticle and endocuticle layers of the procuticle. The crystals of the procuticle are visible under the SEM, but are of sub-micron size. This is smaller than recorded from other Recent specimens, for example in the procuticle of *Herpetocypris chevreuxi*, composed of prismatic calcite crystals of 1-2 μm size (Dépêche 1982).

The texture of the procuticle is more commonly foliated than multi-laminate. A similar foliated texture is seen in the carapace of a specimen of *Henryhowella asperima* near the dorsal margin (Sylvester-Bradley & Benson 1971). The specimens exhibit a more laminate structure at the carapace margins or at folded areas of the carapace. This is interpreted as a function of aligned crystal growth in a restricted area. This has been recorded in previous studies, for example in *Heterocypris incongruens* and *Cypridopsis vidua*, where the procuticle is only laminated near the hinge and in the selvage (Bate & East 1972). The cracks in the carapace parallel to the valve margins, seen in thin section, indicate planes of weakness along the laminae.

b. Carboniferous specimens

The crystalline ultrastructure seen on the surface layer of Carboniferous specimens is present throughout the entire thickness of the carapace, as seen, for example, in *Shemonaella* and *Cavellina* (Figure 5A-C). The procuticle consists of finer crystals, of average 1-2 μm size, with a fairly random crystal alignment (Figure 5E). The outer and inner margins of the procuticle have larger crystals (Figure 5A-D). For example, in a palaeocope specimen (Figure 5D), the inner procuticle margin of the valve has crystals of 1-2 μm size, with a smaller crystal size of 0.5 μm present throughout the thickness of the procuticle. In a specimen of *Cavellina valida* the procuticle is mostly composed of 1-2 μm size crystals, but there are also a few sparse 4-5 μm size crystals (Figure 5F).

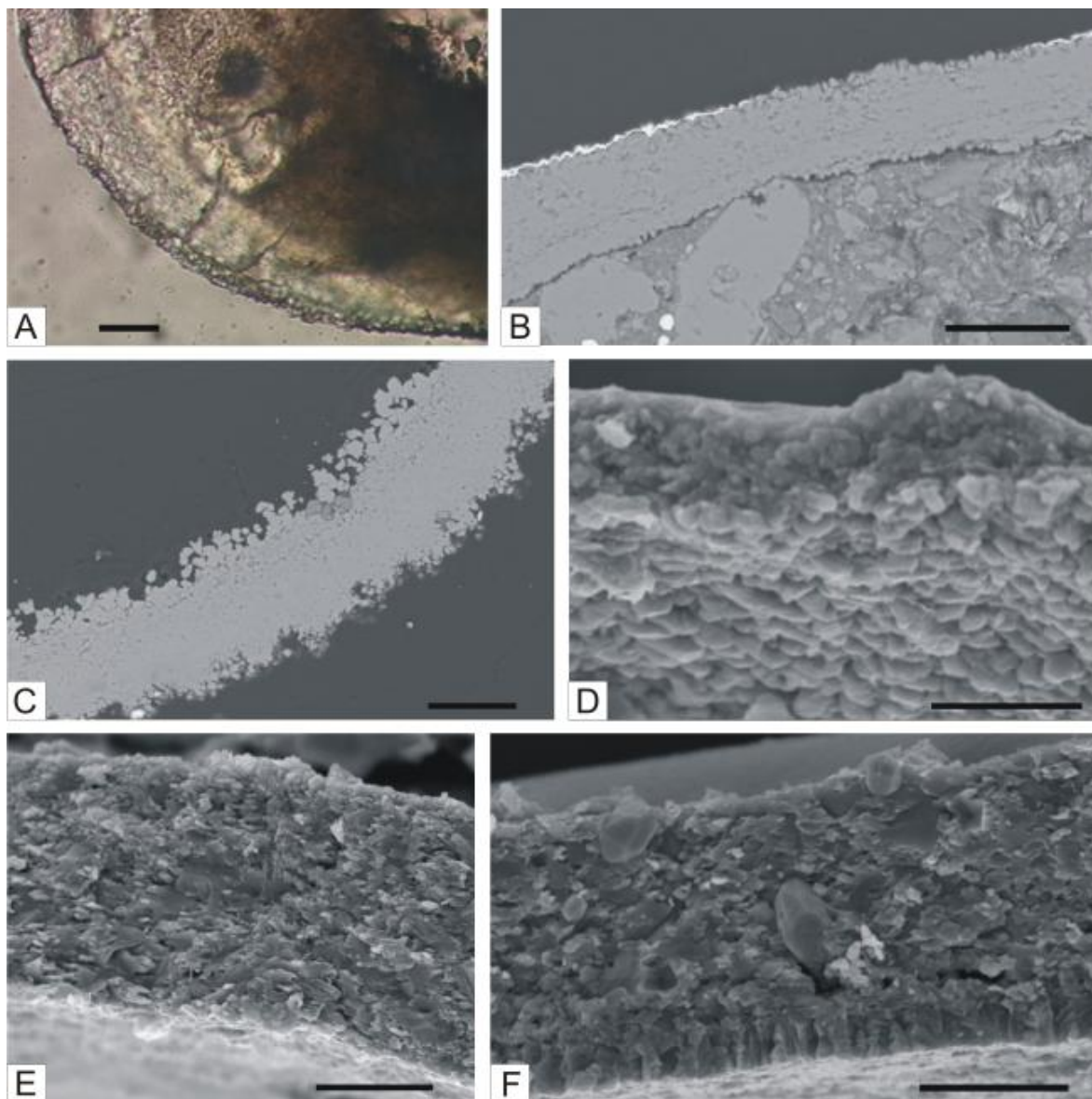


Figure 5. The procuticle ultrastructure of Carboniferous ostracods. A, B: *Cavellina* sp., carapace, MPA 49788. A: the anterior end of the carapace with a crystalline ultrastructure. B: the dorsal margin of the carapace with a multi-laminate ultrastructure. C: *Shemonaella siveteri* n. sp., left valve, the posteroventral region of the valve, EN 4801. D to F: broken shell fragments, the outer carapace margin is towards the top of the images. D: *palaeocope* sp. A, juvenile, single valve, with larger crystals on the carapace inner margin than the procuticle, EN 4793. E: *Hollinella* (*Keslingella*) *radiata*, male, carapace, with a fine crystalline ultrastructure, EN 4841. F: *Cavellina valida*, carapace, EN 4885. A-C: scale bar 30 μ m. D-F: scale bar 10 μ m

A multi-laminate procuticle structure is more often seen in polished thin sections than in broken carapace fragments. For example, a faint multi-laminate texture can be seen in a

specimen of *Cavellina* sp. (Figure 5B). The procuticle structure of Carboniferous specimens that were thin sectioned is displayed in Table 4. The composition of these ostracods varies from calcite to ferroan calcite to ferroan dolomite and some of the carapaces have iron oxide mineralisations. Despite extensive diagenetic alteration structural details of the carapace are visible.

Form.	Sample	Ostracod Genera	Carapace structure	Lumines.?	Composition
A	EK 9601	<i>Cavellina</i>	highly degraded, no structure	no	FD, iron oxide
A	field s 13	<i>Carbonita</i>	highly degraded, no structure	no	FD
Pit	SE 8751	<i>Shemonaella</i>	ML, iron oxide on laminae	no	FD, iron oxide
SC	SE 8526	<i>Shemonaella</i>	ML, iron oxide on laminae	yes, ML	FD, iron oxide
SC	SE 8474	<i>Cavellina</i> , <i>Shemonaella</i>	ML throughout procuticle	yes, ML	calcite
SC	SE 8412	<i>Paraparchites</i>	highly degraded, no structure	faint	FD, iron oxide
SC	SE 8411	<i>Paraparchites</i>	ML, iron oxide on laminae	no	FD, iron oxide
SC	SE 8373	<i>Paraparchites</i>	highly degraded, no structure	yes, ML	FC, some FD
SC	6E 6669	ostracods indet.	thin shells, no structure seen	yes, ML	calcite
P	EN 5329	<i>Polycope</i>	highly degraded, no structure	no	FD
P	EN 5250	<i>Cavellina</i> , <i>Shemonaella</i> , palaeocopes	thin shells, no structure seen	yes, ML	calcite
P	EN 5188	<i>Paraparchites</i>	thin shells, no structure seen	yes, ML	calcite
P	EN 4885	<i>Shemonaella</i> , <i>Cavellina</i> , <i>Bairdia</i>	ML throughout procuticle	yes, ML	calcite
P	EN 4849	<i>Hollinella</i> , palaeocopes, <i>Cavellina</i>	no structure seen	yes, ML	calcite
P	EN 4818	<i>Shemonaella</i> , <i>Cavellina</i> , <i>Geisina</i>	thin shells, no structure seen	yes, ML	calcite
P	EN 4786	<i>Shemonaella</i> , palaeocopes	some specimens ML	yes, ML	calcite

Table 4. Procuticle textures and composition of Carboniferous ostracods from polished thin sections. Abbreviations: Form.; Formation, A; Anstruther, Pit; Pittenweem, SC; Sandy Craig, P; Pathhead, ML; multi-laminated procuticle, FD; ferroan dolomite, FC; ferroan calcite. Lumines.? refers to if the specimens luminesce under cathodoluminescence, and if they show a multi-laminate structure.

A multi-laminate procuticle structure is seen in over one third of the thin sections. The laminae consist of densely packed fine bands (Figure 6). The density of the laminae ranges from approximately five to nine laminae per 10 μm carapace thickness (Figures 6, 7). In two-thirds of the sections a multi-laminate procuticle is visible under CL, whereas it may have been undetectable under SEM or PPL (see Table 4). Figure 7 shows ostracods from the same thin section under CL, PPL and SEM, to highlight this. The laminae are closely spaced and extend all the way around the carapace. They are approximately 1 μm in thickness, and they are close to the limits of detection under CL.

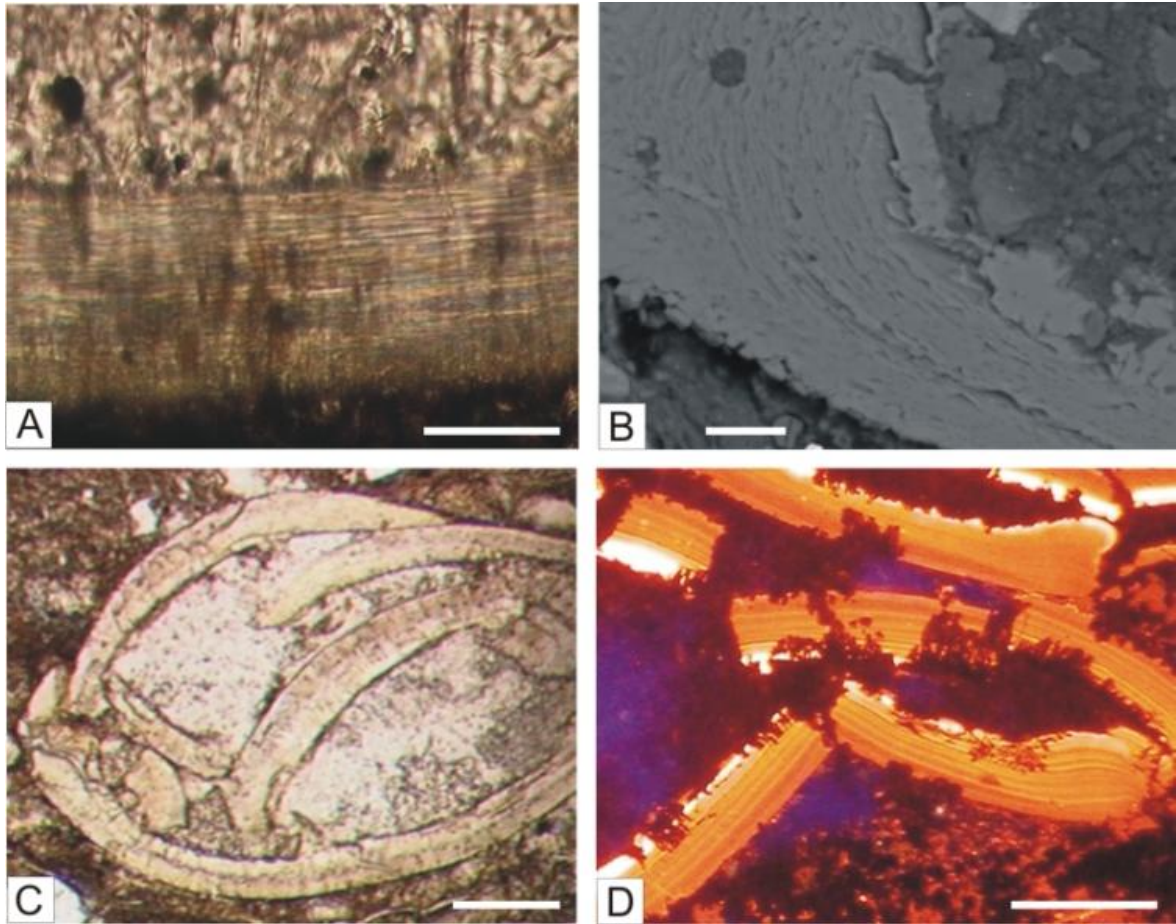


Figure 6. The procuticle ultrastructure of Carboniferous ostracods. The specimens have a multi-laminate structure in polished thin sections, under PPL, SEM and CL analysis, with no observable chemical differences between the laminae. A, B: Ostracod indet. carapaces, EN 4885 ts1. A: PPL image. B: SEM image of a different specimen. C, D: a crushed ostracod carapace, aff. *Shemonaella siveteri* n. sp., SE 8474 ts2. C: PPL image. D: CL image of part of the same carapace. A: scale bar 50 µm. B: scale bar 10 µm, C-D: scale bar 100 µm.

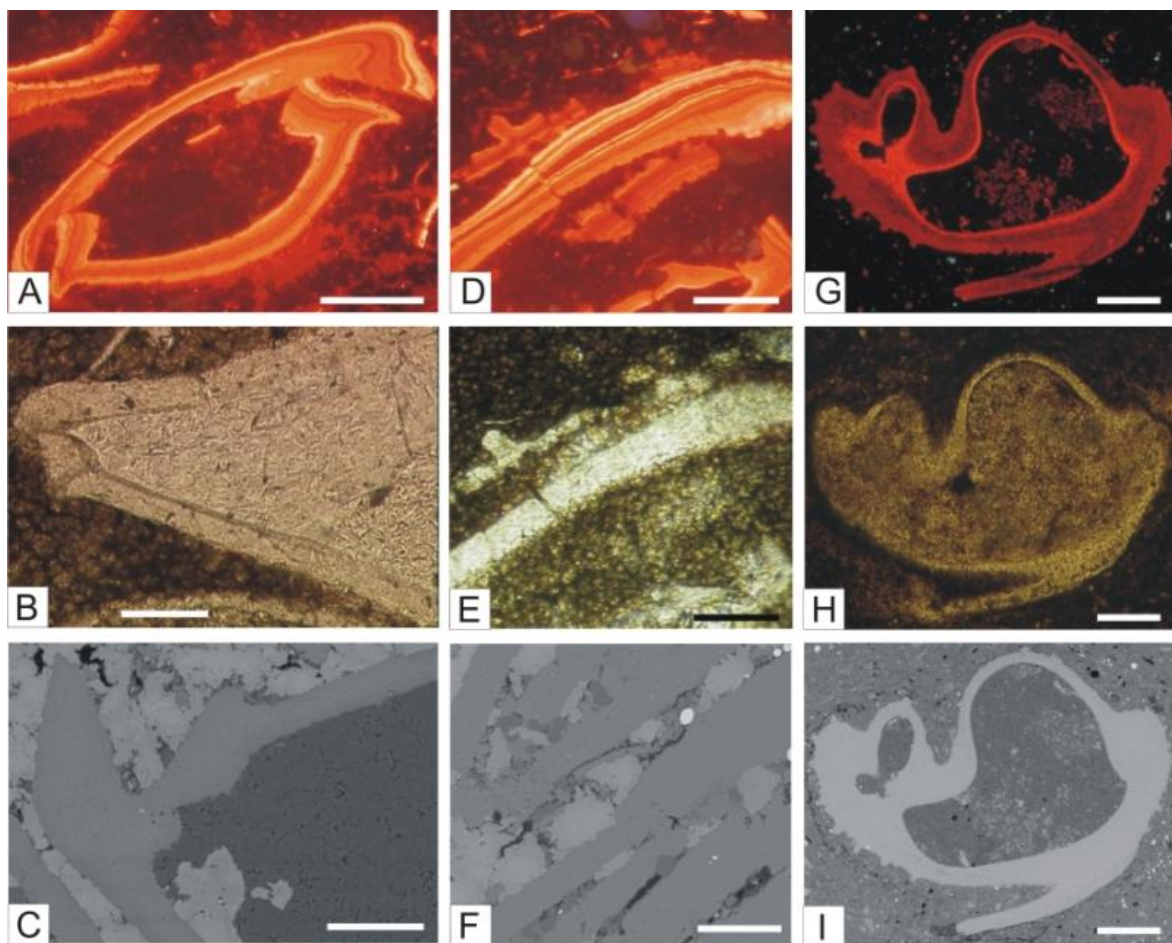


Figure 7. The procuticle ultrastructure of Carboniferous ostracods. The specimens have a multi-laminate structure under CL in polished thin section (images A, D, G), but this is not visible under PPL (images B, E, H) or SEM (images C, F, I). A-F: *Paraparchites circularis* n. sp. carapaces and single valves, SE 8373. A: carapace. B: part of a carapace. C: hinge of a carapace. D, E: a single valve fragment. The specimen in D has approximately 5 laminae 10 µm carapace thickness. F: single valves. G-I: *Hollinella (Keslingella) radiata*, carapace, EN 4849. A, D-E, G-I: scale bar 100 µm. B-C, F: scale bar 30 µm.

To test the composition of the carapace laminae, ostracods that displayed this structure were analysed under the electron microprobe. A comparison was made with the specimen in Figure 6B (multi-laminate under PPL, SEM and CL) and Figure 7G–I (only multi-laminate under CL). The specimen with a multi-laminate procuticle under all types of analysis (Figure 6B) did not have any chemical variation across the laminae (Figure 8A, Table 5). Trace amounts of magnesium, iron and manganese that were present in the

calcitic carapace cannot be linked across the carapace laminae. Elemental mapping of the same area under the SEM, from this specimen and others, also did not show chemical differences between the laminae. The specimen of *Hollinella* (*Keslingella*) *radiata* has an innermost procuticle layer that luminesces brightly under CL (Figure 7G). Electron microprobe analysis of these different carapace regions shows that the inner layer contained the highest concentrations of iron and magnesium, with a maximum of 0.8wt% MgO and 1.2wt% FeO (Figure 8B, Table 5).

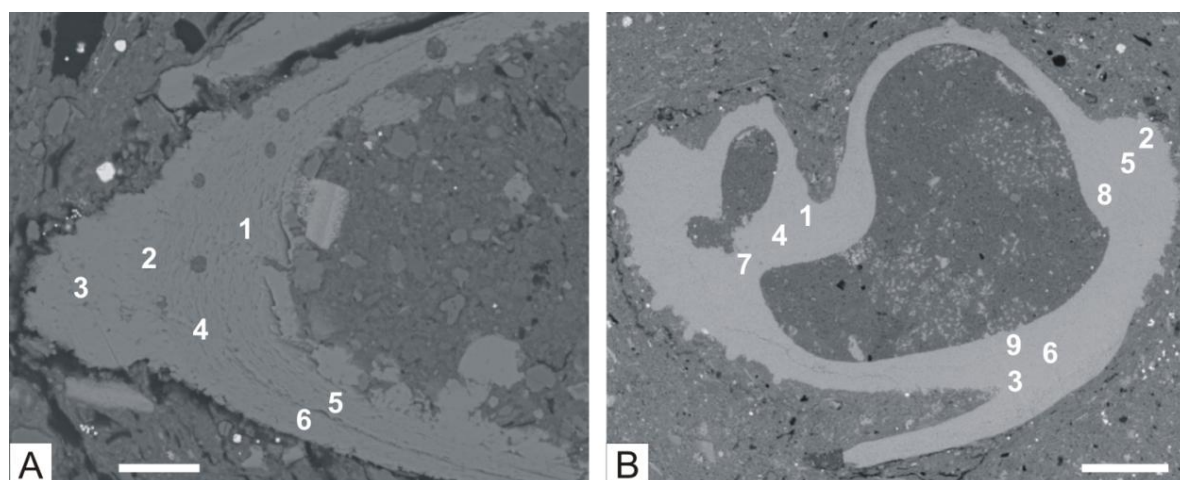


Figure 8. The procuticle ultrastructure of Carboniferous ostracods; electron microprobe analysis of polished thin sections. Numbers relate to analysis points, the results of which are shown in Table 5. A: Ostracod indet. carapace with a multi-laminate structure (shown in Figure 6B), EN 4885 ts1. The carapace has no significant chemical variation across the procuticle laminae. B: *Hollinella* (*Keslingella*) *radiata*, carapace, with no visible lamination (shown in Figure 8G – I), EN 4849. Test analyses 1-3 are from the outer carapace layer (light coloured in CL), tests 4-6 are from the middle carapace layer (dark coloured in CL), and tests 7-9 are from the inner carapace layer (light coloured in CL and strongly luminescent). A: scale bar 20 μ m. B: scale bar 100 μ m.

			Thin section EN 4849 <i>Hollinella (Keslingella) radiata</i>						
	1	2	3	4	5	6	7	8	9
	outer shell layer (tests 1 - 3)			middle shell layer (tests 4 - 6)			inner shell layer (tests 7 - 9)		
CaO	54.5	54.3	54.4	54.9	54.8	54.6	47.3	46.3	54.1
MgO	0.6	0.6	0.5	0.7	0.5	0.5	0.8	0.8	0.8
FeO	0.3	0.2	0.2	0.1	0.3	0.1	1.1	1.2	0.4
MnO	0.1	0.1	0.1	0.1	0.1	0.0	0.5	0.4	0.2
SrO	0.3	0.3	0.3	0.3	0.3	0.3	0.1	0.1	0.2
BaO	0.1	0.0	0.1	0.1	0.1	0.0	0.1	0.0	0.0
CO ₂	44.2	44.4	44.4	43.8	43.9	44.5	50.2	51.2	44.2
Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
			Thin section EN 4885 ostracod indet.						
			1	2	3	4	5	6	
		CaO	53.9	54.1	55.7	49.3	54.8	44.0	
		MgO	0.3	0.4	0.1	0.3	0.2	0.4	
		FeO	0.6	0.9	0.7	0.5	0.2	1.4	
		MnO	0.1	0.3	0.5	0.3	0.1	0.2	
		SrO	0.1	0.0	0.0	0.1	0.2	0.1	
		BaO	0.0	0.0	0.1	0.0	0.0	0.1	
		CO ₂	45.0	44.2	42.9	49.6	44.5	53.8	
		Total	100.0	100.0	100.0	100.0	100.0	100.0	

Table 5. Table of Carboniferous ostracod procuticle electron microprobe data for the two specimens shown in Figure 8A, B. Values are reported in weight percent, and numbers refer to where the spot analysis was taken on the specimen.

Ostracod carapaces composed of ferroan dolomite commonly have a multi-laminate procuticle structure that is distinguished by the growth of iron oxide along the laminae (Figure 9). Dolomitic ostracods have a submicron crystal size to the procuticle and epicuticle, they do not have the same neomorphic texture as the calcitic specimens. The laminae with iron oxide mineralisations are more widely spaced than those seen in the calcitic carapaces, for example the specimen in Figure 9B has approximately eight visible laminae per 50 μm carapace thickness.

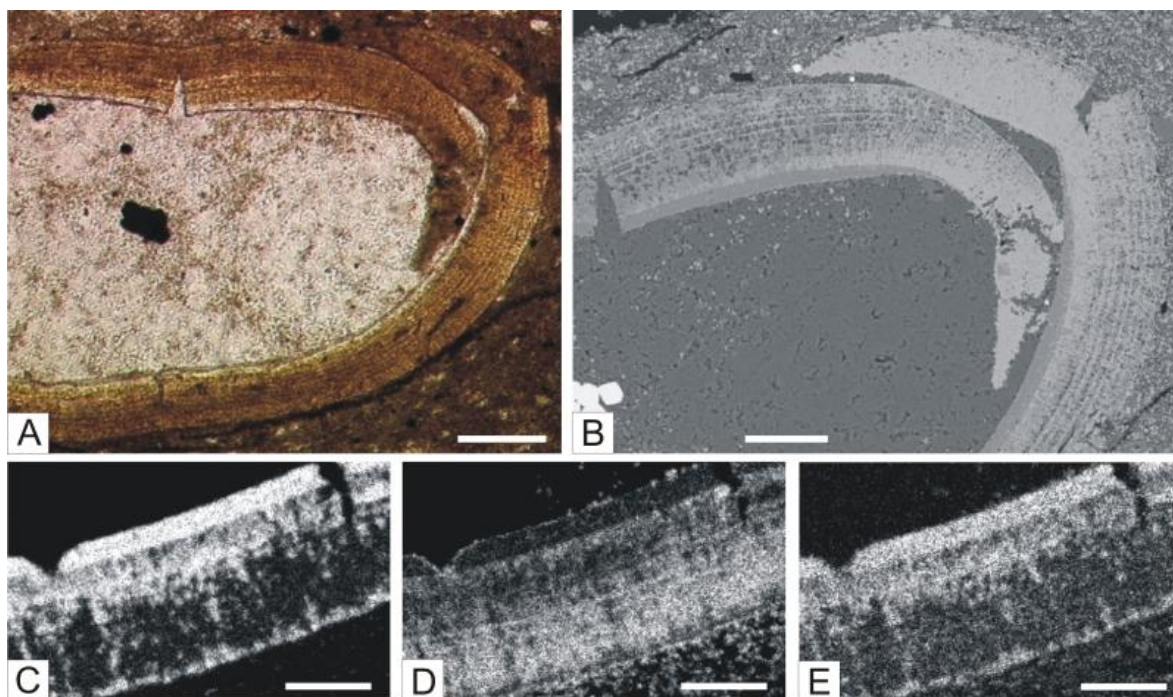


Figure 9. The procuticle ultrastructure of Carboniferous ostracods; polished thin sections of specimens with iron oxide mineralisation. All of the specimens have iron oxide growth behind a diagenetic inner carapace-lining cement of ferroan dolomite. A to E: *Paraparchites circularis* n. sp., carapace, SE 8411. A: a clear multi-laminate structure seen under PPL. B: compositional differences are seen under BSE; the laminae are highlighted by bands of iron oxide. C to E: element maps for part of the same specimen, for calcium (C), iron (D) and magnesium (E). A-B: scale bar 50 μ m. C-E: scale bar 20 μ m.

Interpretation of the procuticle ultrastructure of Carboniferous specimens: The size of procuticle crystals in Carboniferous specimens is significantly larger than in Recent specimens, indicating a diagenetic neomorphic calcite recrystallisation. The difference in the size of crystals on the outer surfaces compared to those in the procuticle centre is due to there being more space for calcite growth on the external surfaces.

One of the most interesting aspects of the Carboniferous specimens is the apparent lack of crystal alignment within the procuticle, when viewed in broken shell fragments, compared to living ostracods. The reason for this discrepancy may be because the entire carapace has undergone recrystallisation. However, thin sections of Carboniferous specimens do reveal a

multi-laminate procuticle in many specimens, or remnants of this structure under CL.

Where a multi-laminate procuticle is seen under PPL or the SEM, the carapaces are either calcitic with densely packed laminae, or dolomitic with less densely packed laminae visible by iron oxide growth. The laminae that luminesce under CL do not have any detectable amounts of manganese or iron (which act as activators and inhibitors to luminescence respectively). The magnesium concentration does not affect the luminescence.

There may be trace chemical differences between laminae that are below the scale of detection of the electron microprobe. Contamination from the sediment is likely. Trace differences of iron, magnesium, strontium and manganese between laminae may be the result of holes or cracks in the carapace, through which the sediment is sampled by the electron microprobe. The largest trace amount is iron (1.4wt% FeO), and this is probably a contamination from the pyrite-bearing sediment. The microprobe beam width of 15 μm may be too large to test the carapace without incorporating sediment at the edge of it, as most of the Carboniferous specimens have a valve thickness of approximately 30 – 50 μm .

The iron oxide mineralisation along carapace laminae only occurs in ostracods composed of ferroan dolomite. It is likely that the carapace was weakened due to diagenesis and burial, which may have allowed fluid flow along relatively weak and permeable laminae and the nucleation of iron oxide crystals in these layers. The iron oxide enriched laminae have a more widely spaced structure than that seen in calcitic specimens. The cause of this is unknown, but it may be because the specimens have been more diagenetically altered. For example, extensive recrystallisation of the carapace may have weakened the original closely spaced multi-laminate template.

Summary and discussion

In summary, Carboniferous ostracods have a procuticle ultrastructure that represents diagenetic alteration and recrystallisation; most specimens have randomly oriented crystals. Rare calcitic and dolomitic carapaces with a multi-laminate shell structure retain the original ostracod multi-laminar template for the procuticle despite diagenesis.

A summary model of the differences in carapace ultrastructure between Recent and Carboniferous specimens is shown in Figure 10. The epicuticle is a few microns thick, it is smooth in Recent specimens, and absent in Carboniferous specimens. The procuticle varies in thickness between species from 20-45 μm , and in Recent specimens is composed of sub-micron scale calcite crystals, which can be foliated or laminated. In Carboniferous specimens the procuticle is composed of 2 – 3 μm size crystals at the carapace margins, and 0.5 – 1 μm size crystals in the interior. The crystals are not aligned in most specimens, but some thin sections do show an alignment.

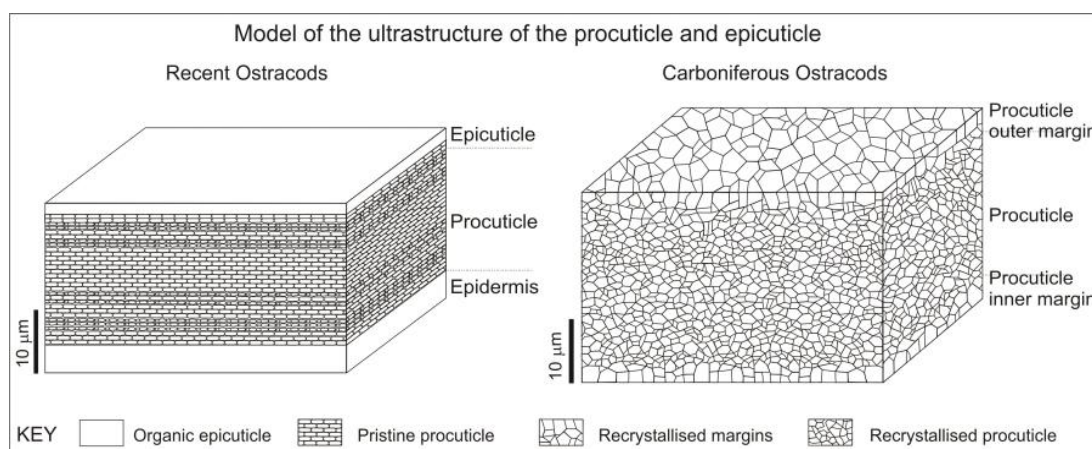


Figure 10. Model of an idealised section through the carapace of a pristine Recent ostracod and a diagenetically altered calcitic Carboniferous ostracod. In Carboniferous specimens the epicuticle and epidermis have not been preserved. Note that in the model the Carboniferous ostracod representation shows procuticle crystals with no alignment, whereas there is a laminar alignment in some specimens.

The presence of a recrystallised ultrastructure characterises diagenetically altered specimens. The preservation of a multi-laminate carapace structure in Carboniferous specimens occurs despite extensive diagenetic recrystallisation of the carapaces to ferroan dolomite. Therefore a multi-laminate procuticle cannot be taken as an indicator of pristine ostracod carapaces, and a study of the shell ultrastructure is needed to determine altered from pristine specimens.

Previous workers have divided the procuticle into two separate layers, the exocuticle and endocuticle. The Recent and Carboniferous specimens examined in this study do not show separate procuticle layers. This is also the case in some other Recent specimens, such as *Conchoecia belgica* (Bate & East 1972). Examples of foliated procuticle layers are seen in *Henryhowella asperima* (Sylvester-Bradley & Benson 1971). Multi-laminated procuticle layers are more common than foliated specimens. A multi-laminate procuticle is seen in specimens of *Conchoecia belgica* (Bate & East 1972), *Cypria ophthalmica* and *Empoelsenia pentrathrix* (Keyser 1995). The majority of myodocopes described by Sohn & Kornicker (1988) had a multi-laminate carapace structure, while some species exhibited columnal or granular crystals. A multi-laminate carapace structure is found in the chitinous (uncalcified) procuticle of *Halocypris inflata*, and is also seen in the uncalcified procuticle of *Conchoecia valdiviae* (Bate & Sheppard 1982).

It is unclear why some ostracod specimens show a more distinct multi-laminate structure than others. The presence of the multi-laminate structure in some Carboniferous specimens is likely to be due to subtle differences in preservation. It is not an indicator of differences in carapace composition or of ostracod species. No Carboniferous ostracods are from the same family as the living ostracods studied. But it is reasonable to assume that different

groups of ostracods may have a slightly different cellular template, and thus carapace ultrastructure. In this study there is some evidence for the size of procuticle crystals linked to the length of the ostracod carapace in Carboniferous specimens. Further research is needed to confirm this trend.

Conclusions

- The carapace ultrastructure of Carboniferous ostracods from the Midland Valley of Scotland was compared to Recent ostracod specimens. The epicuticle of Recent ostracods is smooth, with a sub-micron scale crystal structure. In Carboniferous specimens the epicuticle is not preserved, but the top surface of the procuticle is recrystallised by neomorphic calcite to produce equant calcite crystals of 1-3 μm size, similar to that seen in recrystallised fossil planktonic foraminifera.
- The procuticle of Recent ostracods consists of an arrangement of sub-micron size (less than 0.5 μm), equant to elongate calcite crystals, which are aligned to produce a foliated to multi-laminate ultrastructure. At the areas of curvature such as the valve margins, a multi-laminate texture is more pronounced.
- The procuticle of Carboniferous specimens is recrystallised, with an average crystal size of 1-2 μm size, larger at the valve margins. The crystals appear to be aligned fairly randomly in broken carapace fragments, but in polished thin sections some specimens have a multi-laminate texture. The laminae are fine (on a micron scale) and closely spaced, running parallel to the carapace margins. The laminae are not defined by chemical composition, but represent the original carapace structure. In

some Carboniferous ferroan dolomite ostracod carapaces, iron oxide mineralisation is present along the carapace laminae.

- In Recent and Carboniferous ostracods there is no visible differentiation of the exocuticle and endocuticle layers of the procuticle that have been recorded in other studies.
- A study of the carapace ultrastructure of ostracod fossils reveals diagenetic alteration that cannot otherwise be detected. Calcitic ostracod specimens that appeared pristine under light microscopy and low magnification scanning electron microscopy were revealed to be diagenetically altered when the carapace ultrastructure was examined. It is important to assess the carapace preservation prior to any geochemical analysis of the ostracod carapaces for palaeoenvironmental interpretations.

Chapter 7: A protocol to assess the diagenesis of Carboniferous ostracods and macrofossils, and its importance in relation to isotope-based palaeoenvironmental interpretations

Abstract

A protocol for the examination of diagenetic alteration of ostracod carapaces is proposed. This is essential prior to the stable isotope analysis of fossils for palaeoenvironmental purposes. Mississippian ostracods from the Midland Valley of Scotland have undergone seven diagenetic stages of alteration: Early burial diagenesis: 1. Replacement of the original low-magnesium calcite carapace with a diagenetic neomorphic calcite which has 1-3 μm size euhedral crystals; 2. dissolution and pitting of the carapace surface; 3. euhedral pyrite growth; 4. ferroan calcite replacement of carapaces, and growth in cavities; Later-stage, deeper burial diagenesis: 5. ferroan dolomite replacement of carapaces and growth in cavities; 6. replacement of pyrite in the sediment and carapaces by iron oxide; and 7. replacement of ferroan dolomite carapaces and cavity-filling cements by sphalerite and barite. These stages also apply to macrofossils. The oxygen and carbon isotope composition of ostracod carapaces and macrofossil shells are -12.9‰ to -0.9‰ for $\delta^{18}\text{O}$ and -6.4‰ to $+2.2\text{‰}$ for $\delta^{13}\text{C}$. The isotope data from the ostracods reflect stages of diagenesis, and not palaeoenvironmental conditions. This is most clearly seen in the oxygen isotope results, while the carbon isotope results are not significant in terms of diagenesis. The early diagenesis stage 1 calcitic ostracods have higher $\delta^{18}\text{O}$ than stage 5 ferroan dolomite ostracod valves. Stage 1 calcitic ostracod valves have oxygen isotope values similar to that of calcite precipitated from Carboniferous seawater (-3‰ $\delta^{18}\text{O}_{\text{VPDB}}$), and may represent

very early diagenesis prior to burial. A pristine calcitic specimen of the brachiopod *Productus* has an oxygen isotope value 1‰ lower than that of Carboniferous seawater calcite at $-4\text{‰ } \delta^{18}\text{O}$. This is the only specimen found not to have been diagenetically altered, and is within a marine sediment, so may reflect early Carboniferous seawater $\delta^{18}\text{O}$.

Introduction

A carapace composed of pristine calcite is critical to preserve geochemical information from the time of deposition. This study assesses the carapace ultrastructure and geochemistry to examine the preservation. The low-magnesium calcite that forms the ostracod carapace represents the isotopic composition of the waters the adult ostracod carapace was formed in. Oxygen isotopes from ostracod carapaces can be used as a salinity and temperature proxy (Chivas *et al.* 1986). As waters evaporate they become more saline, ^{16}O is preferentially lost, and thus $\delta^{18}\text{O}_{\text{water}}$ increases. Temperature also affects the fractionation of oxygen isotopes into carbonate, with a decrease in $\delta^{18}\text{O}_{\text{carbonate}}$ corresponding to an increase in temperature of about $-0.2\text{‰}/^{\circ}\text{C}$ (Chivas *et al.* 1986). On a global scale the size of the polar ice caps significantly affects the $\delta^{18}\text{O}$ composition of the oceans. For example during “icehouse” climatic periods, isotopically light water is locked at the poles, resulting in heavier $\delta^{18}\text{O}$ of the oceans.

Previous isotope studies on Paleozoic ostracods are rare, from the Ordovician (Brenchley *et al.* 2003) and the Carboniferous (Williams *et al.* 2006). In a study of the Ballagan Formation from the Carboniferous, the ostracod oxygen isotope results were interpreted in terms of a possible salinity signal, but also recognised diagenesis (Williams *et al.* 2006).

Here I hypothesise that for the Ballagan Formation and the specimens from this study little or no environmental signal is preserved, but instead a clear diagenetic signal is present.

The geochemistry of ostracod carapaces can record small scale seasonal changes in temperature and evaporation, especially in shallow water environments. Trace element concentrations of strontium and magnesium in ostracod carapaces are affected by temperature, salinity and the Mg/Ca ratio of the host water (Chivas *et al.* 1986, Wansard *et al.* 1998). Temperature is thought to be the most important variable in lacustrine and shallow marine ostracods (De Decker *et al.* 1999, Dwyer *et al.* 2002). The Mg/Ca ratio of ostracod carapace calcite has been successfully used as a palaeotemperature proxy (Chivas *et al.* 1986, Cronin *et al.* 2003, 2005, Dwyer *et al.* 1995).

Studies on living lacustrine ostracods have shown that biological effects can also be important. The so called vital effect (fractionation out of equilibrium from what is expected with experimental data) is important, and can be more than 2‰ for $\delta^{18}\text{O}$ in some ostracod species (von Grafenstein *et al.* 1999). Isotopic vital effect offsets and Sr and Mg partition coefficients are also variable between species (von Grafenstein *et al.* 1999), and within individuals of the same species (Wansard *et al.* 1998).

Ostracod carapace chemistry can be significantly altered by the processing methodology of the samples. The cleaning method can alter trace element carapace compositions (De Decker *et al.* 1999, Jin *et al.* 2006). In fact all types of processing involving acids cause some degree of isotopic shift (Keatings *et al.* 2006). Ostracods from residues sieved in distilled water were significantly isotopically lighter than those sieved in ethanol, with maximum difference of 3‰ for $\delta^{18}\text{O}$ and 1.6‰ for $\delta^{13}\text{C}$ (Mischke *et al.* 2007). The

ostracods that were sieved with water precipitated inorganic calcite crystals on the carapace while they dried. Deionised water is slightly acidic (below the carbonate stability field) and will dissolve ostracod carapaces over time (Ito 2001). The effect of oven drying is also important. Inorganic calcite growth was observed after the oven drying of foraminifera, which was 2.8‰ $\delta^{18}\text{O}$ lighter (Sperling *et al.* 2002). The oxidation of pyrite on the test led to the formation of H_2SO_4 , which dissolved the surface of the test and led to recrystallisation.

In this study Carboniferous ostracod carapaces from the Mississippian of the Midland Valley of Scotland are described and compared to Recent specimens. Carboniferous ostracods are the focus of the diagenetic assessment, although macrofossils are also important. Carboniferous ostracods are recrystallised, and are to a variable extent affected by several diagenetic stages. The diagenetic stages affecting the ostracods and macrofossils are described and interpreted in terms of a diagenetic history. Isotopic results are reported from diagenetic cements and other products of ostracod carapaces and macrofossil shells. The analysis of multiple specimens shows that $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ in the Carboniferous ostracods described here is predominantly controlled by diagenesis. However, some calcitic ostracods and rare pristine macrofossils may show a palaeoenvironmental signal.

Geological Background

Mississippian sediments of the Midland Valley of Scotland represent deposition in a range of environments from marine to non-marine, and contain a high diversity of ostracods and macrofossils (Bennett 2008, Browne *et al.* 1999, Forsyth & Chrisholm 1977, Wilson 1989).

The sediments are well dated (Table 1) using volcanic intervals and palynomorphs (Monaghan & Parrish 2005, Owens *et al.* 2005, Stephenson *et al.* 2004).

Fossils from Mississippian age rocks of the Midland Valley of Scotland were analysed to assess the presence of diagenetic materials (cements, replacements, overgrowths and minerals). Sediments and fossils are from the Inverclyde Group of Ayrshire, and the Strathclyde Group of Fife (Table 1, 2). Ostracods are more numerous than macrofossils in certain horizons, and they occur in a wide range of environments, from marine to non-marine sediments. Therefore the hypothesis that pristine ostracod carapaces may preserve isotopic signatures of different palaeoenvironments (marine versus freshwater) can be tested.

System	Series	Paly. Zones	Midland Valley of Scotland Lithostratigraphy				Group	
			Central Coalfield & Ayrshire	Fife	West Lothian	East Lothian		
Mississippian	Viséan	VF	Lawmuir Fm	Pathhead Fm	West Lothian Oil Shale Fm	Aberlady Fm	Strathclyde Group	
		NM	Kirkwood Fm	Sandy Craig Fm				
				Pittenweem Fm				
		TC	Clyde Plateau Volcanic Fm	Anstruther Fm	Gullane Fm			
		TS						
		Pu		Fife Ness Fm				
	Tournaisian		Clyde Sandstone Fm					Inverclyde Group
		CM	Ballagan Fm					
		PC	Kinneswood Fm					

Table 1. Stratigraphy of the Midland Valley of Scotland, adapted from Browne *et al.* (1999). Samples were studied from the Ballagan Formation of Ayrshire and the Fife formations of the Strathclyde Group.

The Midland Valley of Scotland has many Carboniferous igneous intrusions, which may have altered the surrounding country rock during their emplacement. Dean & Turner (1995)

used conodont CAI values to determine the influence of the intrusions in the Fife region of the Strathclyde Group. The value for East Fife was 1, indicating no influence from igneous sources. The overburden for the East Fife Carboniferous strata is calculated as 2644 m, which corresponds to a geothermal temperature of 79°C (using a modern geothermal gradient). A burial temperature of 79 °C would have been enough to dissolve the ostracod carapaces to leave only moulds in areas where there were pore waters moving through the sediments. This depth was reached during basin subsidence at the end of the Triassic (Dean & Turner 1995).

The Carboniferous was the time of an “icehouse” world with cooler ocean temperatures (Brand 1989). Carboniferous isotope data places the average value of seawater as between -3‰ and -1‰ $\delta^{18}\text{O}_{\text{PDB}}$ (Grossman 1994). Oceanographic factors that may be important in terms of isotope analysis are that the Midland Valley of Scotland was palaeoequatorial, and for most of the Mississippian had a restricted marine connection (Browne *et al.* 1999). Glacial and interglacial episodes were present in the late Mississippian in Europe, and as early as the late Devonian in South America (Fielding *et al.* 2008), the effect of these glaciations being to alter the oxygen isotope composition of seawater.

Recent Ostracods			
Ostracod species	Locality Information		
<i>Aurila woutersi</i> Horne, 1986	Porlock, Severn Estuary, donated by Dr D J Horne (Queen Mary Uni. of London)		
<i>Candonopsis tenuis</i> (Brady, 1886)	Lake Biwa, Japan, specimens donated by Dr Robin J Smith (Lake Biwa Museum)		
Carboniferous Ostracods			
Boreholes & field sections	Formation	National Grid Reference	Samples
Inverclyde Group: Heads of Ayr field section	Ballagan	NS 2933 1870	BGS collection
Strathclyde Group: Randerston field section	Anstruther	NO 6150 1125	Field samples
Anstruther borehole	Anstruther	NO 5650 0355	BGS collection
Billow Ness - Anstruther field section	Anstruther	NO 5590 0271	BGS collection
Kilconquhar borehole	Pittenweem - Pathhead	NO 4844 0304	BGS collection
Balcormo borehole	Sandy Craig	NO 5084 0408	BGS collection
Claremont borehole	Pathhead	NO 4518 1419	BGS collection
Denork borehole	Pathhead	NO 4540 1409	BGS collection
Carboniferous ostracod species: <i>Acutiangulata</i> sp. A, <i>Bairdia submucronata</i> Jones & Kirkby, 1879 <i>Carbonita</i> cf. <i>fabulina</i> (Jones & Kirkby, 1879), <i>Carbonita</i> cf. <i>inflata</i> (Jones & Kirkby, 1879), <i>Carbonita</i> sp. <i>Cavellina benniei</i> (Jones, Kirkby & Brady, 1884), <i>Cavellina</i> aff. <i>coela</i> Rome, 1973, <i>Cavellina valida</i> (Jones, Kirkby & Brady, 1884) <i>Cavellina</i> sp., <i>Geisina arcuata</i> (Bean, 1836), <i>Healdia</i> cf. <i>cuneata</i> Robinson, 1978, <i>Hollinella</i> (<i>Keslingella</i>) <i>radiata</i> (Jones & Kirkby, 1886), <i>Palaeocope</i> indet., <i>Paraparchites circularis</i> n. sp., <i>Paraparchites armstrongianus</i> (Jones & Kirkby, 1886), <i>Polycopse elegans</i> n. sp., <i>Shemonaella ornata</i> n. sp., <i>Shemonaella siveteri</i> n. sp., <i>Silenites</i> sp. A			

Table 2. Table listing the Recent and Carboniferous ostracod species used in this study. Specimen information for Recent ostracods is recorded in appendix 5. Carboniferous borehole and some field section samples are stored at the BGS in Edinburgh. Survey boreholes were taken by the British Geological Survey (BGS) from 1964-1980. Carboniferous field samples were collected as part of this study from 2005-2008.

Methodology

Carboniferous ostracod specimens were picked directly from the rock surface of borehole samples, without any chemical processing. Fossilised ostracods tend to have no organic matter (soft parts) remaining, and can be easily removed from the enclosing rock. This avoided the geochemical alteration of the ostracods by using a processing methodology.

The diagenetic protocol involved the following methods:

1. Visual analysis of whole ostracod and macrofossil specimens under a light microscope and ultrastructural analysis under the scanning electron microscope (SEM).
2. The visual analysis of polished thin sections of fossils for diagenetic cements and mineralisations under plane polarised light (PPL), SEM and cathodoluminescence (CL).
3. The geochemical analysis of polished thin sections of fossils under the SEM and the electron microprobe.

Ostracod carapaces were mounted on SEM stubs using PVA glue mixed with water, and then gold coated using an Emitech Sputter Coater K500X. Polished thin sections from Carboniferous rock samples were cut to a standard thickness of 30 μm . Individual ostracod carapaces were imbedded in araldite on a thin section slide. This section was cut to a thickness of 160 μm and polished to a 0.25 μm size grade (polished thin section standard). Specimens were analysed using both high and partial vacuum states on a Hitachi S-3600N Scanning Electron Microscope. The secondary electron (SE) detector was used for imaging the surface features such as ostracod ultrastructure. The back-scattered electron (BSE) detector was used for identifying changes in composition and for elemental mapping. It can produce semi-quantitative results derived from a cobalt standard.

For cathodoluminescence analysis, an optical microscope cold cathode vacuum setup was used at The University of Liverpool, with argon gas as an inert vacuum component. Concentrations of manganese result in a bright orange luminescence, while iron acts to inhibit the luminescence (Marshall 1988).

Carbon coated polished thin sections were analysed using a JEOL JXA-8600S electron microprobe, to produce quantitative results of ostracod carapace chemistry. The settings for analysis are an accelerating voltage of 15 kV, and a probe current of 30 nA. The smallest beam diameter of 15 μm was used, and tests were focused on thick ostracod carapaces, or thicker areas of the carapace such as the hinge or ventral commissure. 20 second count times were used for measurement of characteristic peak intensities, with 10 seconds at each of the background positions selected on either side of the peak. The quantitative results were calibrated to standards used for carbonate analysis, with an analytical error of 0.1wt%.

Ostracod carapaces were analysed at the NERC Isotope Geosciences Laboratory at the British Geological Survey in Keyworth, for carbon and oxygen stable isotopes. A weight of 40-110 μg was required for each test, and where the specimens were large enough this comprised one single ostracod valve. Articulated carapaces were avoided to reduce diagenetic carapace-filling cements, pyrite and sediment contaminations. Only adult specimens were analysed, as magnesium is preferentially incorporated into the carapace in place of calcium at the early stages of carapace calcification in juveniles (Chivas *et al.* 1986). The analyses were performed on a GV IsoPrime plural inlet mass spectrometer, plus multiprep set at 90 °C with a 15 minute reaction time. Because of the presence of high magnesium calcites and dolomites the samples were run alongside a calcite standard (KCM) and a dolomite standard (TDS). However, $\delta^{18}\text{O}$ was calculated using the standard calcite fractionation factor as the proportions of calcite-dolomite were unknown. Isotope values are reported in the usual delta notation, as per mille values, on VPBD scale. Replicate analysis of the standards resulted in +2.0‰ $\delta^{13}\text{C}$ and -1.7‰ $\delta^{18}\text{O}$, with standard deviations of 0.0-0.02 for $\delta^{13}\text{C}$ and 0.03-0.10 for $\delta^{18}\text{O}$.

Assessing the preservation of ostracod carapaces

A variety of diagenetic minerals and cements replace ostracod carapaces and macrofossil shells, and these also occur in fossil cavities and in the sediment. The following diagenetic minerals are present; calcite, ferroan calcite, ferroan dolomite, pyrite, iron oxide, barite and sphalerite. Table 3 details the composition of ostracods and macrofossils from the thin sections. A representative data set of the quantitative composition of diagenetic minerals, obtained on the electron microprobe, is shown in Table 4. There is no correlation between the fossil group, ostracod species, sediment type, age of sample, and the diagenetic product (Table 3).

Form.	Sample	Sediment	Fossil Species	Ostracods	Carapace Fill	Macrofossils	Sediment
A	EK 9601	MST	<i>Cavellina valida</i>	FD, pyrite, iron ox.	FD	x	FD, iron ox.
A	field s 12	LST	bivalves indet.	x	x	FD	FD, iron ox.
A	field s 13	LST	<i>Carbonita</i> sp.	FD	FD	FD	FD, iron ox.
A	field s 19	LST	ostracods indet.	FD	FD	FD	FD, iron ox.
A	field s 20	LST	<i>Glyptolichvinella spiralis</i>	x	x	x	FD
Pit	SE 8874	MST	<i>Naiadites</i>	x	x	FD	f pyrite
Pit	SE 8866	MST	<i>Productus</i> , crinoid columnals	x	x	FD, pyrite	e, f pyrite
Pit	SE 8821	LST	<i>Lithostrotion junceum</i>	x	barite	FD	sparce barite
Pit	SE 8751	BBI	aff. <i>Shemonaella</i>	iron ox., some FD	iron ox., some FD	x	iron ox., some FD
SC	SE 8538 A	silts	<i>Carbonita</i> cf. <i>fabulina</i>	iron ox., some FD	FD, iron ox.	x	x
SC	SE 8526	silts	<i>Shemonaella siveteri</i> n. sp.	FD, iron ox., sph.	FD	x	FD, iron ox.
SC	SE 8474	MST	<i>Cavellina</i> sp.	calcite	FD	FD	FD
SC	SE 8413 A	BBI	<i>Carbonita</i> cf. <i>inflata</i>	iron ox., some FD	FD	x	x
SC	SE 8412	BBI	<i>Paraparchites circularis</i> n. sp.	FD, barite, sph.	FD, iron ox.	x	FD, iron ox.
SC	SE 8411	BBI	<i>Paraparchites circularis</i> n. sp.	FD, iron ox.	x	x	iron oxide
SC	SE 8373	MST	<i>Paraparchites circularis</i> n. sp.	FC, some FD	FD, iron ox.	x	FD, iron ox.
SC	6E 6669	MST	ostracods indet.	calcite	x	x	x
P	EN 5329	MST	<i>Polycopse elegans</i> n. sp.	FD	FD	x	e, f pyrite
P	EN 5250	MST	multiple ostracod species	calcite, e pyrite	FC	x	e pyrite
P	EN 5250 ts2	MST	multiple ostracod species	calcite, e pyrite, sph.	FC	x	e pyrite, sph.
P	EN 5188 ts2	MST	<i>Paraparchites armstrongianus</i>	calcite	x	x	e pyrite
P	EN 4885	MST	multiple ostracod species	calcite, e, f pyrite	e pyrite	x	e, f pyrite
P	EN 4885 ts2	MST	multiple ostracod species	calcite	e pyrite, FC	calcite, FD, pyrite	e, f pyrite
P	EN 4849	MST	multiple ostracod species	calcite	e pyrite	x	e, f pyrite
P	EN 4818	MST	multiple ostracod species	calcite	x	x	sparce e, f pyrite
P	EN 4786	MST	<i>Shemonaella</i> , palaeocopes	calcite	x	x	e pyrite

Table 3. Polished thin section geochemical information, including the composition of ostracods and macrofossils, carapace filling cements and cements in the sediment. The samples are arranged in descending stratigraphic order, from oldest at the top (Anstruther Formation) to youngest (Pathhead Formation) at the bottom. Abbreviations used: Form.; Formation, A; Anstruther, Pit; Pittenweem, SC; Sandy Craig, P; Pathhead, MST; mudstone, LST; limestone, BBI; black-banded ironstone (an iron and plant-rich mudstone), FD; ferroan dolomite, FC; ferroan calcite, e;

euohedral, f; frambooidal, sph.; sphalerite, iron ox.; iron oxide, x; not present in the thin section.

Sample	Weight % element composition							Analysed Cement
	CaO	MgO	FeO	MnO	SrO	BaO	CO ₂	
EN 4885	55.7	0.4	0.3	0.0	0.2	0.2	43.3	calcitic shell
	55.2	0.4	0.4	0.1	0.1	0.2	43.6	calcitic shell
EN 4786	54.8	0.3	0.2	0.2	0.1	0.0	44.4	calcitic shell
	54.5	0.3	0.3	0.2	0.1	0.1	44.6	calcitic shell
EN 5329	26.7	11.9	10.3	0.9	0.0	0.0	50.2	FD shell
	31.5	12.6	9.5	1.2	0.0	0.0	45.3	FD carapace fill
SE 8412	35.0	9.2	9.4	0.5	0.0	0.1	45.8	FD shell
	5.3	3.3	47.8	0.5	0.1	0.1	43.0	FD & iron oxide carapace fill
SE 8751	2.9	0.8	57.2	0.9	0.0	0.1	38.1	iron oxide replaced shell
	2.5	1.2	56.4	0.7	0.1	0.0	39.0	iron oxide replaced shell
	2.6	0.9	54.2	0.8	0.0	0.0	41.5	iron oxide replaced shell

Table 4. Electron microprobe data of Carboniferous ostracod diagenetic stages. The data includes representative results of calcitic ostracod carapaces, ferroan dolomite ostracod carapaces, ferroan dolomite and iron oxide carapace filling cements, and ostracod carapaces replaced by iron oxide. Concentrations of the trace elements manganese, strontium and barium are included in the table. A full data set of semi-quantitative results from the SEM is displayed in Appendix 6.

Stages and timing of diagenesis

The position of the diagenetic cements and mineralisations relative to each other reveals seven diagenetic stages. Visual examples of these stages are shown in Figure 1. The most diagenetically altered sediment contains fossils that have undergone all seven stages, for example sample SE 8412 (Figure 1, stage 7). The diagenetic stages are as follows:

Early, shallow burial diagenesis:

1. Replacement of the ostracod carapace with euohedral micron scale low-magnesium calcite crystals.
2. Early dissolution, pitting and degradation of stage 1 ostracod carapaces (this also occurs throughout the diagenetic history).

3. Pyrite mineralization in carapace cavities, replacement of dissolved calcite carapaces, euhedral and framboidal forms. Numerous calcitic stage 1 and 2 ostracod carapaces have pyrite crystals within the carapace laminae, or growing on the inner carapace surface.
4. Replacement of ostracod carapaces by ferroan calcite, carapace-filling cements of calcite and ferroan calcite. These cements are associated with stage 3 pyrite and not any of the products of stages 5 to 7.

Late, deeper burial diagenesis:

5. Replacement of ostracod carapaces, carapace-filling cements and macrofossil shells by ferroan dolomite. Ferroan dolomite ostracod carapaces do not have the crystalline ultrastructure seen in stage 1. Carapace filling cements overprint those of ferroan calcite.
6. Replacement of pyrite in the sediment, ostracod carapaces and macrofossils by iron oxide. This only occurs in fossils or sediments with a composition of ferroan dolomite, there is no iron oxide present in calcitic specimens.
7. Replacement of ferroan dolomite carapaces and cavity-filling cements by sphalerite and barite. These mineralizations are also seen in small veins in the sediment, replacing macrofossil shells, and cross cutting iron oxide minerals.

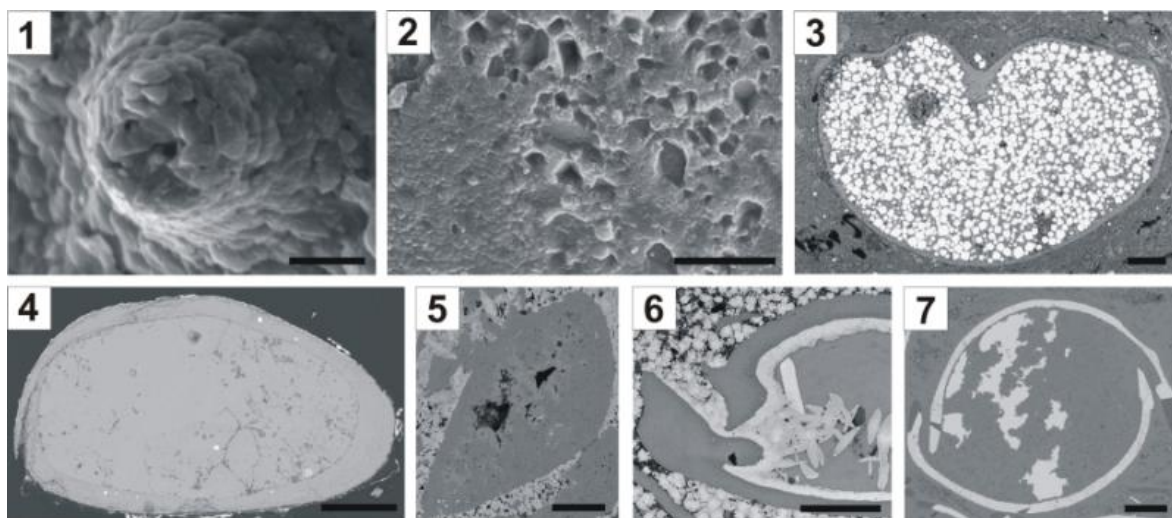


Figure 1. The sequence of diagenetic products in Carboniferous ostracods. Images are scanning electron micrographs (using secondary and back scattered electron beams). The numbers 1-7 are in order of diagenetic history. 1: Neomorphic calcite: a tuberculate pore of *Hollinella* (*Keslingella*) *radiata*, EN 4840. 2: Pitting: the external surface of *Bairdia submucronata*, EN 4885. 3: Pyritisation: A pyritised carapace fill of a palaeocope indet. juvenile, EN 4849. 4: Ferroan calcite: *Cavellina valida* with a ferroan calcite carapace fill, EN 4885. 5: Ferroan dolomite: *Carbonita* sp. ferroan dolomite carapace and carapace fill, field sample 13. 6: Iron oxide: *Paraparchites circularis* n. sp. iron oxide carapace fill, SE 8373. 7: Sphalerite and barite: *Paraparchites circularis* n. sp. carapace and fill composed of sphalerite, SE 8412. 1: scale bar 5 μm . 2-3: scale bar 20 μm . 4-7: scale bar 100 μm .

Description of diagenetic stages

1. Neomorphic calcite/ early diagenesis

Living ostracods have a smooth outer surface of the carapace, the epicuticle, which is composed of chitin and organic matter (Figure 2A, B). The Carboniferous specimens do not preserve the epicuticle, but show the top surface of the procuticle layer. This layer is recrystallised, with an ultrastructure of 1-3 μm size interlocking euhedral crystals of low-magnesium calcite (Figure 2C, D). This diagenetic calcite faithfully preserves the original carapace ornamentation such as pores, tubercles and pits (Figure 2C). The crystalline ultrastructure extends throughout the entire carapace thickness (Figure 2E, F).

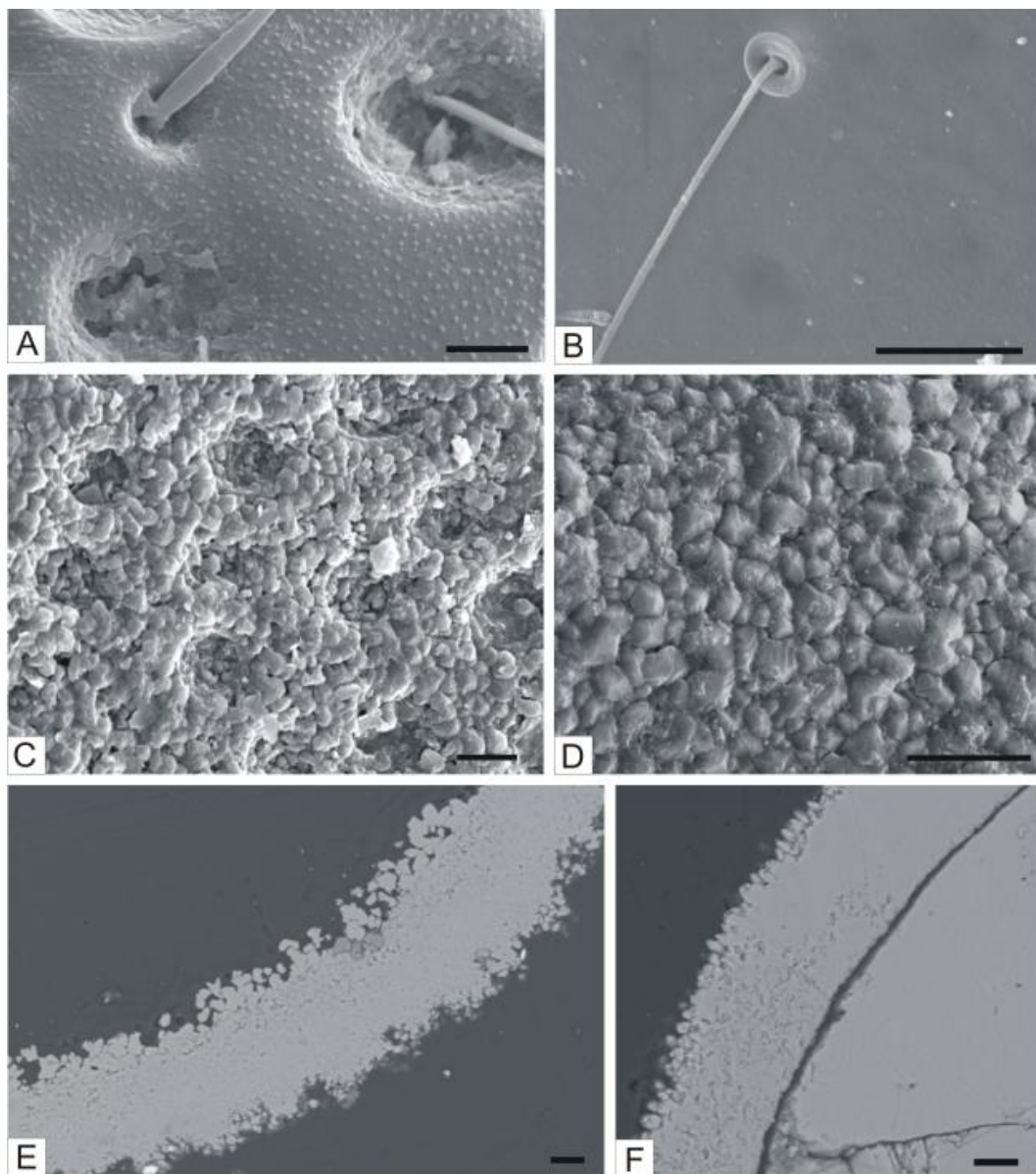


Figure 2. Stage 1 diagenesis: The carapace ultrastructure of pristine Recent ostracods compared to Carboniferous ostracods affected by stage 1 diagenesis. A, B: Recent specimens. A: *Aurila woutersi*, female, carapace, the smooth external surface of the epicuticle, with pores, setae, and a granulate ornament, CEB8. B: *Candonopsis tenuis*, male, a disk-shaped pore and setae on the epicuticle surface, CEB14. C-F: Carboniferous specimens. C: *Shemonaella ornata* n. sp., carapace, with a circular pitted reticulate ornament, and calcite crystals which have been partly dissolved, EN 4808. D: *Geisina cf. arcuata*, carapace, with faceted calcite crystals, EN 4827. E: *Shemonaella siveteri* n. sp., carapace, the posteroventral region, with large crystals on the outer and inner margins, EN 4801. F: *Cavellina aff. coela*, carapace, a crystalline ultrastructure throughout the thickness of the carapace, MPA 49788. Scale bars 10 µm.

Carboniferous calcitic ostracod carapaces have trace amounts of magnesium, iron and to a lesser extent manganese, strontium and barium (Table 5). The other diagenetic stages occur after this stage, for example pitting, and dolomitic ostracods do not have a crystalline ultrastructure.

Interpretation: When compared to Recent ostracods, it is clear that the carapace of Carboniferous specimens has been recrystallised. The calcite is a neomorphic replacement mineralisation, as it preserves surface features such as pores and tubercles, rather than destroying them. This neomorphic calcite was the earliest diagenetic stage, all other diagenetic events overprint it. The recrystallisation may have happened soon after the ostracods died, as all the original carapace features such as pores are retained. The trace element concentrations of iron, magnesium and manganese in the calcite could be the result of contamination with the sediment, due to the narrow thickness of the ostracod carapaces (average thickness of 30 μm), which were analysed with an electron beam of 15 μm diameter.

Studies on diagenetically altered planktonic foraminifera from the Cenozoic show a similar carapace ultrastructure of micrometre scale crystals throughout the test (Pearson *et al.* 2001, Pearson & Burgess 2008, Sexton *et al.* 2006). Diagenesis occurred at shallow burial depths (of less than 300 m) in open ocean pelagic oozes and chalks, with the more pristine specimens preserved in impermeable clays (Pearson *et al.* 2001). The effect of this diagenetic recrystallisation was to significantly alter the oxygen isotope signal from that of sea surface (where the forms lived) to bottom water temperatures (where the recrystallisation occurred; see Pearson *et al.* 2001, Williams *et al.* 2005a, b, 2007). The ostracods from this study are interpreted to have also been recrystallised on the sediment

surface or at shallow burial depths, on the basis of three factors; 1; the ultrastructure is directly comparable with that seen in the foraminifera, 2; the neomorphic calcite is the first stage of diagenesis, before framboidal pyrite formation, and 3; the fidelity of ornamental preservation implies an early replacement, while the original cellular template was still intact.

2. Dissolution, pitting and degradation

Most of the individual ostracod specimens analysed on the scanning electron microscope (mounted as carapaces on stubs) have undergone stages 1-2 of diagenesis. A degraded carapace surface is seen on an ultrastructural level. For example the external carapace surface of *Bairdia submucronata* has polygonal micron scale pits where individual neomorphic calcite crystals have fallen out (Figure 1, image 2). In some specimens the surface is porous on a crystalline level, and the edges of the neomorphic calcite crystals are rounded (Figure 2C).

Dissolution, pitting and degradation also affects ostracods and macrofossils throughout their diagenetic history. For example most dolomitic ostracod carapaces (stage 5) are highly degraded. Commonly the top 3 - 10 μm in thickness of the carapace has broken off in some areas, further revealing the procuticle layer.

Interpretation: Where the carapace surface has a porous texture, partial dissolution of the neomorphic calcite has occurred. Fluid flow through the sediments would cause partial dissolution of the fossil shells. The ostracod carapaces have a degraded outer surface due to successive alterations. Repeat dissolution events would have occurred through successive fluid-flow events through the sediment. The extent of degradation of fossils is localised, for

example in some areas of the Strathclyde Group cores (commonly in the Pittenweem Formation) only ostracod moulds are preserved, the entire carapace has been dissolved.

3. Pyrite mineralizations

At least 10% of the ostracods and macrofossils studied are replaced by pyrite, and the majority of thin sections contain pyrite in the sediment (Table 3). Euhedral pyrite grows on ostracod carapaces and macrofossil shells, as a cavity filling mineralization (Figure 3A, B), and is commonly disseminated within the sediment. Euhedral pyrite carapace fills are mainly associated with stage 1-2 calcitic ostracods. Euhedral pyrite is also rarely associated with ferroan dolomite ostracods and macrofossils (Figure 3B, Table 3). In these cases the order of diagenetic events is not always clear cut.

Framboidal pyritisation occurs after stages 1-2 of diagenesis, for example after the dissolution of the ostracod shell (Figure 3C). Framboidal pyrite is commonly found inside marine ostracod carapaces, and only occurs in association with marine fossils. For example a calcitic specimen of *Bairdia submucronata* from a marine horizon contains numerous framboids on the inner carapace margin (Figure 4C). In this specimen these framboids are overprinted by a later diagenetic stage of ferroan calcite carapace fill. Scattered microscopic framboids disseminated in the sediment are common in marine mudstones. The framboids are usually between 10-25 μm in diameter. One fairly large polyframboid structure with a diameter of 200 μm was recorded in a marine mudstone (Figure 3D).

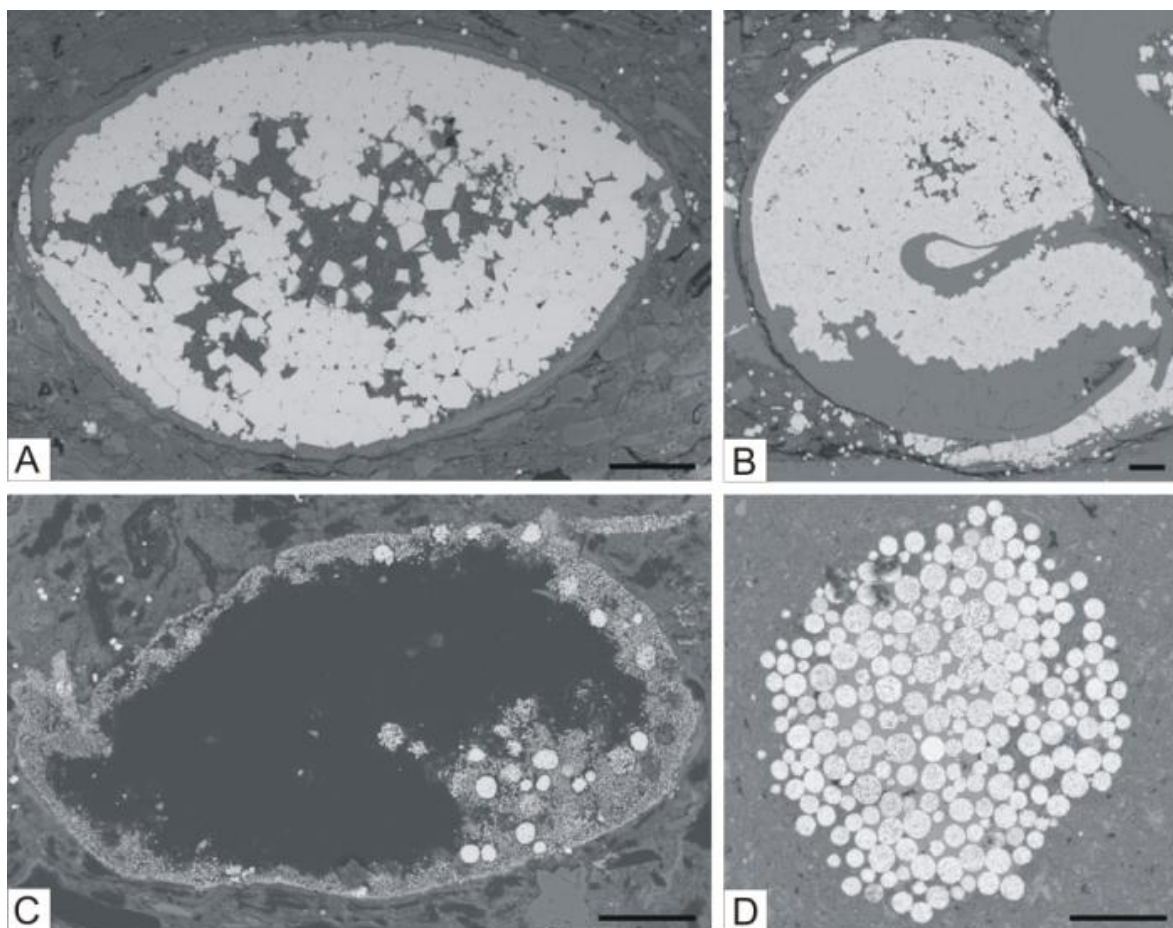


Figure 3. Stage 3 diagenesis: pyrite mineralizations on ostracods, macrofossils and in the sediment. A: ostracod indet. Juvenile, calcitic carapace with a euhedral pyrite fill, EN 5250 ts2. B: pyritised “*Spiroborbis*” macrofossil, part of which is replaced by ferroan dolomite, EN 4885 ts2. C: *Shemonaella siveteri* n. sp., juvenile, carapace, pyrite in the form of small framboids (approximately 10 µm in size) and euhedral crystals have replaced the carapace, SE 8363. D: a pyrite polyframboid, EN 4849. Scale bars 50 µm.

Interpretation: Euhedral pyrite is associated with diagenesis rather than the conditions of deposition, as it replaces ostracod and macrofossil carapaces. The presence of euhedral and framboidal pyrite in calcitic rather than ferroan dolomite ostracods indicates that it formed after stage 2 diagenesis, before deeper burial dolomitisation occurred. In rare ferroan dolomite fossil specimens that have euhedral pyrite the order of diagenetic stages is unclear, but the assumption is that the pyrite formed before the dolomite, as it is usually

associated with calcitic fossils. Euhedral pyrite can form in a number of conditions, for example when there was a restricted connection to seawater; restricted iron content in the sediments; under diagenesis; from the replacement of framboidal pyrite (Raiswell 1982).

Framboidal pyrite grows in sediments due to contact with saline waters (Raiswell 1982, Raiswell & Berner 1985, Brett & Baird 1986, Wilkin *et al.* 1996). In anaerobic bacterial decay within the top few metres of sediment, seawater sulphate is reduced to form hydrogen sulphide. This reacts with detrital iron to produce spheroidal iron monosulfides, which then react in turn with sulphur to produce framboidal pyrite.

4. Ferroan calcite cements

No macrofossil shells and only rare ostracod carapaces are composed of ferroan calcite (Table 3). The cement has sub-micron size crystals and does not preserve the stage 1 crystalline calcitic structure. Many thin sections contained ostracod carapaces with a composition of less than 1wt% FeO. Ferroan calcite carapace filling cements are fairly common, and are usually associated with framboidal pyrite (Figure 4C).

Interpretation: Ferroan calcite carapaces do not preserve the stage 1 crystalline structure, so they are a later stage event. The occurrence of pyrite in ferroan calcite carapace filling cements may lead to contamination of electron beam analytical results.

5. Ferroan dolomite cements

Many of the ostracod carapaces and almost all of the macrofossil shells in the thin sections studied are composed of ferroan dolomite (Table 3). Dolomitic ostracod carapaces have a sub-micron size crystal ultrastructure, and a carapace surface that is commonly dissolved

and degraded. For example, *Paraparchites circularis* n. sp. has a very fine crystal ultrastructure of 0.2 - 0.6 μm size (Figure 4A). Ferroan dolomite specimens of *Polycope* sp., have a smooth outer surface (Figure 4B). The stage 1 crystalline ultrastructure is no longer visible. The dolomite has a microcrystalline texture when it forms as a carapace filling cement (Figure 4E), or as crystals within the sediment (Figure 4F). Ferroan dolomite ostracod carapaces contain up to 12wt% MgO, and 10wt% FeO (Table 4). Carapace filling cements contain more magnesium and iron, and are frequently associated with iron oxide mineralization. Ferroan calcite and ferroan dolomite are present together in one thin section (specimen SE 8373; Table 3). In this case the ostracod shells are composed of ferroan calcite, and the carapace fills and cement in the sediment are ferroan dolomite. Elemental mapping reveals that ferroan dolomite grows over fragments of a broken ferroan calcite ostracod carapace.

Interpretation: The dolomitic cement replaces the stage 1 crystalline calcite in ostracod carapaces, so it is a later diagenetic stage. It occurs after ferroan calcite cements, as the dolomitic cements grow in cavities and over calcitic carapace fragments. Dolomitic cements form as the result of fluid flow through the sediment at depth.

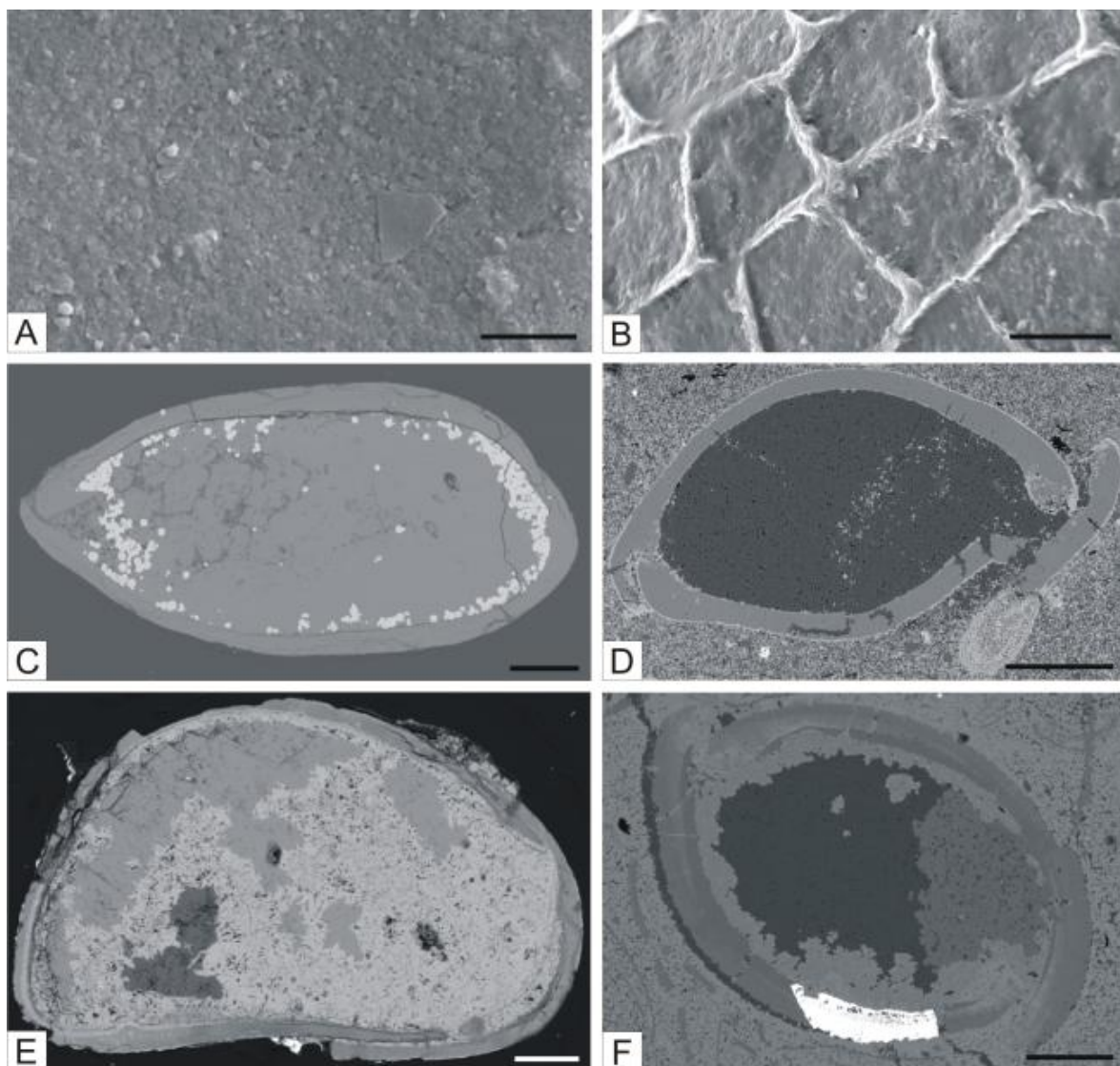


Figure 4. Diagenetic stages 4 and 5; ferroan calcite and ferroan dolomite cements. A: *Paraparchites circularis* n. sp. with a fine external carapace surface of 0.2-0.6 μm size crystals, composed of ferroan dolomite, SE 8411. B: *Polycope elegans* n. sp., carapace, smooth surface with a reticulate ornament, composed of ferroan dolomite, EN 5329. C: *Bairdia submucronata*, carapace, left lateral view, EN 4885 A. The carapace is calcitic (with 1wt% MgO), the carapace fill is ferroan calcite, there is a rim of framboidal pyrite. D: *Paraparchites circularis* n. sp., ferroan dolomite carapace, iron oxide crystals are on the exterior and interior surface of the valves, SE 8411. E: *Carbonita* cf. *fabulina*, carapace and carapace fills composed of ferroan dolomite and iron oxide, SE 8538 A. F: *Shemonaella siveteri* n. sp., ferroan dolomite carapace, SE 8526. The bright white area of the carapace is sphalerite, the carapace fill is mudstone (dark grey), ferroan dolomite (lighter grey), and iron oxide (light grey), which is also found in the sediment in a microcrystalline form. A: scale bar 3 μm . B: scale bar 20 μm . C to F: scale bars 100 μm .

6. Iron oxide mineralizations

Crystals of iron oxide are commonly found in the sediment, in fossil cavities and partially or completely coating ostracod carapaces. Samples that are rich in iron oxide do not contain pyrite, and vice versa. Only ostracod carapaces composed of ferroan dolomite have an iron oxide mineralization (for example Figure 5A). Iron oxide crystals inside the ostracod carapaces have a microcrystalline form, and they concentrate at the end of valves, and along the carapace layers in laminae parallel to the carapace margins. Iron oxide coats the internal surface of carapaces, in the form of small elongate crystals growing inwards towards the carapace cavity (Figure 5B, C). Iron oxide is also found in the centre of the carapace cavity, where it overprints the dolomitic cement (Figure 5B-D). Here the iron oxide has the form of large elongate crystals, and is often zoned with varying amounts of iron. Sample SE 8751 contains ostracods with a high iron oxide content, up to 57wt% FeO (Table 4). There may be some dolomitised carapace material left, as these carapaces have a content of up to 2.9wt% CaO, 1.2wt% MgO and 1wt% MnO.

There are different forms of iron oxide mineralisations in the sediment:

- Snowflake-shaped crystals growing between grains (Figure 5B-D). These have the same composition as elongate iron oxide crystals that infill the carapace cavity.
- Fine crystals coating sediment grains (Figure 5E).
- Sub-angular to equant-shaped crystals growing between sediment grains (Figure 5F).

- Angular to elongate crystals, zoned, covering nearly all available pore space. This is the most common in dolomitised limestone (for example Figure 5G), while in most cases the concentration of iron oxide in the sediment is variable.
- Submicron scale crystals with the appearance of a micritic-like texture covering nearly all the sediment.

Interpretation: Iron oxide mineralization on ostracod carapaces, in cavities and in the sediment originated from the diagenetic alteration of pyrite. The evidence for this is that pyrite and iron oxide content in thin sections are mutually exclusive. Pyrite commonly lines the internal surface of calcitic ostracod carapaces, where iron oxide lines the carapaces of ferroan dolomite ostracods. Iron oxide is concentrated at the end of the ostracod valves because here the calcite crystals that make up the outer lamella are the most strongly aligned to give a strong lamination. The space between these laminae may allow fluid flow, crystal nucleation and growth.

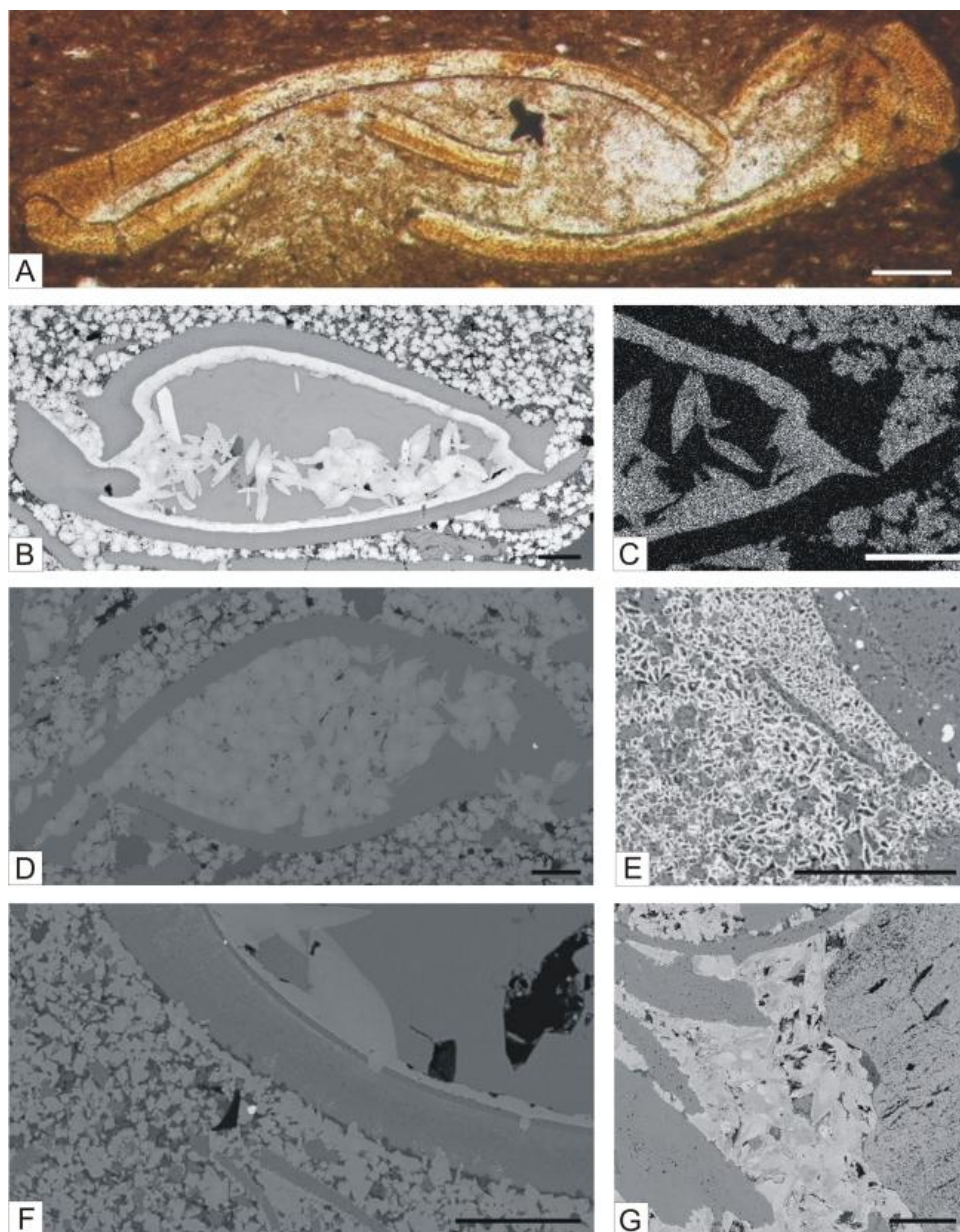


Figure 5. Stage 6 diagenesis: iron oxide mineralizations. A: *Paraparchites circularis* n. sp., crushed carapace composed of ferroan dolomite with a high amount of iron oxide mineralization (orange coloured), SE 8411. B-D: *Paraparchites circularis* n. sp. carapaces with an iron oxide carapace infill, in the form of elongate crystals, and snowflake shaped iron oxide crystals in the sediment, SE 8373. The different crystal forms have the same composition. B, C: a calcitic carapace, a slightly dolomitic carapace fill (grey), and iron oxide carapace lining and fill (white). C: element map for iron from this specimen. D: carapace with iron oxide (white) and ferroan dolomite carapace fill. E-G: Iron oxide in the sediment, overgrowing the edge of ferroan dolomite ostracod shells (in F and G). E: the sediment grains are coated in iron oxide, EK 9601. F: sub-angular to euhedral iron oxide crystals, SE 8526. G: dolomitised limestone, iron oxide crystals occupy all the pore spaces and are zoned, field sample 13. Scale bars 50 μ m.

7. Barite and sphalerite mineralization

These minerals occur in the cavities of fossils, or replacing the entire carapace (Figure 6A, B). The presence of these minerals has been recorded in three different thin sections (Table 3). A small barite vein is present in sample SE 8412 (1mm thick vein seen in thin section), with many ostracod carapaces preserved in barite and sphalerite nearby.

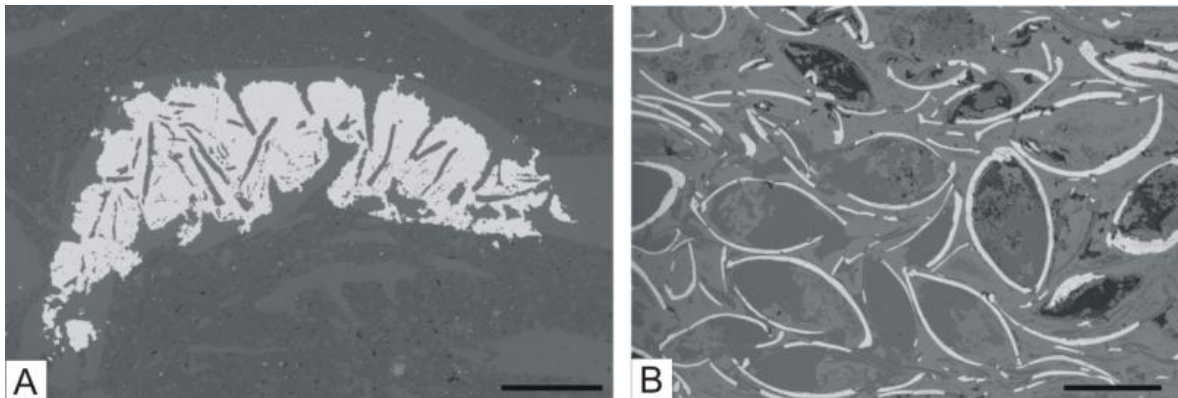


Figure 6. Stage 7 diagenesis: barite and sphalerite mineralizations. A: *Lithostrotium junceum* with a carapace composed of ferroan dolomite, and a barite mineralisation filling the central cavities, which also contains traces of boron, strontium and cobalt, SE 8821. B: *Paraparchites circularis* n. sp. carapaces and single valves composed of sphalerite, with ferroan dolomite carapace fills, SE 8412. A-B: scale bar 500µm.

Interpretation: The position of these minerals in fossil cavities indicates that they could have formed any time in the diagenetic history. However, where they are replacing ferroan dolomite (in 2 samples) and iron oxide carapaces (in 1 sample), then the mineralization occurred after diagenetic stage 6. Both these minerals can be hydrothermally derived, and the evidence of veins suggests that is a likely origin. The three samples are from the Kilconquhar core, with a core depth of over 430m between the oldest and youngest sample. The permeability of the sediments and location of volcanic intrusions would locally influence fluid flow within the sediment, and thus affect where barite and sphalerite minerals are deposited. Although Dean & Turner (1995) did not consider the rocks of the

Fife region to be altered by igneous intrusions, there may have been some local hydrothermal activity. This is most likely to have happened when the intrusions were emplaced, during the Carboniferous.

Isotope Results

A range of ostracod species, macrofossils and diagenetic carbonate minerals were sampled for isotope analysis (Table 5). The specimens were selected from all four formations of the Strathclyde Group, from different sediment types and environments. The values range from -12.9‰ to -0.9‰ for $\delta^{18}\text{O}$, and -6.4‰ to $+2.2\text{‰}$ for $\delta^{13}\text{C}$. There is a wider spread of data within the oxygen isotope range, than that of the carbon isotopes. Figure 7 shows all the isotope data, distinguishing ostracod and macrofossil results. The macrofossil shells are composed of ferroan dolomite, with the exception of *Productus* which is calcitic, and the ostracod data are from a range of different cements and mineralisations, from calcite to ferroan dolomite with iron oxide (diagenetic stages 1 to 6).

Sample	Form	Species	Composition	Components analysed	$\delta^{13}\text{C}_{\text{PDB}}$	$\delta^{18}\text{O}_{\text{PDB}}$
EN 4849	P	<i>Hollinella radiata</i>	calcite	2 single valves	+0.3	-3.6
EN 4885	P	<i>Shemonaella siveteri</i> n. sp.	calcite	1 single valve	-1.6	-3.0
EN 5250	P	<i>Shemonaella siveteri</i> n. sp.	calcite	1 single valve	-0.5	-2.0
EN 5250	P	<i>Shemonaella siveteri</i> n. sp.	calcite	single valves, multiple frags	-0.5	-1.8
EN 5250	P	<i>Shemonaella siveteri</i> n. sp.	calcite	4 single valves	-0.4	-1.6
EN 4885	P	<i>Shemonaella siveteri</i> n. sp.	calcite	single valves, multiple frags	-0.5	-3.2
EN 4885	P	<i>Shemonaella siveteri</i> n. sp.	calcite	single valves, multiple frags	-0.5	-2.6
EN 4885	P	<i>Shemonaella siveteri</i> n. sp.	calcite	single valves, multiple frags	-0.7	-3.7
EN 4885	P	<i>Shemonaella siveteri</i> n. sp.	calcite	single valves, multiple frags	-0.2	-2.6
EN 4818	P	<i>Shemonaella siveteri</i> n. sp.	calcite	single valves, multiple frags	-1.4	-2.4
EN 4818	P	<i>Shemonaella siveteri</i> n. sp.	calcite	single valves, multiple frags	-1.5	-2.4
EN 4818	P	<i>Shemonaella siveteri</i> n. sp.	calcite	single valves, multiple frags	-1.4	-1.6
EN 4818	P	<i>Shemonaella siveteri</i> n. sp.	calcite	single valves, multiple frags	-1.3	-2.0
EN 4818	P	<i>Shemonaella siveteri</i> n. sp.	calcite	single valves, multiple frags	-2.1	-2.3
EN 4818	P	<i>Shemonaella siveteri</i> n. sp.	calcite	1 single valve and 1 frag	-2.5	-1.7
EN 4818	P	<i>Shemonaella siveteri</i> n. sp.	calcite	1 single valve and 1 frag	-1.5	-2.2
EN 4818	P	<i>Shemonaella siveteri</i> n. sp.	calcite	1 single valve	-1.6	-1.7
EN 4818	P	<i>Shemonaella siveteri</i> n. sp.	calcite	1 single valve	-0.7	-0.9
EN 4885	P	<i>Cavellina valida</i>	calcite	1 single valve	-3.8	-7.0
EN 4885	P	<i>Cavellina valida</i>	calcite	shell and infilling cement (calcite)	-2.9	-6.2
EN 4885	P	<i>Cavellina valida</i>	calcite	shell and infilling cement (calcite)	-2.3	-6.0
EN 4885	P	<i>Bairdia submucronata</i>	calcite	shell and infilling cement (calcite)	-2.9	-6.4
SE 8526e	SC	<i>Carbonita</i> sp.	FD, iron oxide	single valves, multiple frags	-0.8	-8.4
SE 8411a	SC	<i>Carbonita</i> sp.	FD, iron oxide	1 single valve	-0.8	-6.6
SE 8751d	Pit	<i>Carbonita</i> sp.	FD, iron oxide	1 single valve	+2.2	-8.2
SE 8411e	SC	<i>Paraparchites circularis</i> n. sp.	FD, iron oxide	1 single valve	-0.8	-6.4
SE 8751	Pit	<i>Carbonita</i> sp.	FD, iron oxide	single valves, multiple frags	2.0	-9.4
SE 8751	Pit	<i>Carbonita</i> sp.	FD, iron oxide	single valves, multiple frags	2.0	-8.9
SE 8751	Pit	<i>Carbonita</i> sp.	FD, iron oxide	single valves, multiple frags	2.1	-8.9
SE 8751	Pit	<i>Carbonita</i> sp.	FD, iron oxide	single valves, multiple frags	1.4	-9.2
SE 8751	Pit	<i>Carbonita</i> sp.	FD, iron oxide	single valves, multiple frags	1.8	-9.3
SE 8751	Pit	<i>Carbonita</i> sp.	FD, iron oxide	single valves, multiple frags	2.0	-9.1
SE 8412	SC	<i>Shemonaella siveteri</i> n. sp.	FD	single valves, multiple frags	-0.6	-8.2
SE 8412	SC	<i>Shemonaella siveteri</i> n. sp.	FD	single valves, multiple frags	0.5	-7.4
SE 8412	SC	<i>Shemonaella siveteri</i> n. sp.	FD	single valves, multiple frags	0.3	-6.9
SE 8411	SC	<i>Paraparchites circularis</i> n. sp.	FD, iron oxide	single valves, multiple frags	-0.8	-6.3
SE 8411	SC	<i>Paraparchites circularis</i> n. sp.	FD, iron oxide	single valves, multiple frags	-0.4	-5.8
SE 8411	SC	<i>Paraparchites circularis</i> n. sp.	FD, iron oxide	single valves, multiple frags	-0.8	-6.2
SE 8411	SC	<i>Paraparchites circularis</i> n. sp.	FD, iron oxide	single valves, multiple frags	-0.9	-6.3
SE 8411	SC	<i>Paraparchites circularis</i> n. sp.	FD, iron oxide	single valves, multiple frags	-0.8	-6.8
SE 8526b	SC	<i>Carbonita</i> sp.	FD, iron oxide	1 specimen, carapace filling cement	-3.0	-11.5
SE 8526c	SC	<i>Carbonita</i> sp.	FD, iron oxide	1 specimen, carapace filling cement	-2.5	-11.9
EN 5329b	P	<i>Polycopse elegans</i> n. sp.	FD	1 specimen, shell and carapace fill	-6.3	-4.5
EN 5329c	P	<i>Polycopse elegans</i> n. sp.	FD	1 specimen, shell and carapace fill	-6.4	-4.8
SE 8526	SC	<i>Carbonita</i> sp.	FD, iron oxide	1 specimen, shell and carapace fill	-2.2	-9.9
SE 8526	SC	<i>Carbonita</i> sp.	FD, iron oxide	1 specimen, shell and carapace fill	-2.7	-10.8
EK 9601	A	<i>Cavellina</i> sp.	FD, iron oxide	1 specimen, shell and carapace fill	-0.7	-3.6
EK 9601	A	<i>Cavellina</i> sp.	FD, iron oxide	1 specimen, shell and carapace fill	0.4	-3.6
EK 9601	A	<i>Cavellina</i> sp.	FD, iron oxide	1 specimen, shell and carapace fill	-0.3	-2.9
EK 9601	A	<i>Cavellina</i> sp.	FD, iron oxide	1 specimen, shell and carapace fill	0.0	-3.1
EK 9601	A	<i>Cavellina</i> sp.	FD, iron oxide	1 specimen, shell and carapace fill	1.1	-4.3
EK 9601	A	<i>Cavellina</i> sp.	FD, iron oxide	1 specimen, shell and carapace fill	-0.1	-4.1

Sample	Form.	Species	Composition	Components analysed	$\delta^{13}\text{C}_{\text{PDB}}$	$\delta^{18}\text{O}_{\text{PDB}}$
SE 8412	SC	<i>Shemonaella siveteri</i> n. sp.	FD, iron oxide	carapace filling cement	-0.3	-9.2
SE 8412	SC	<i>Shemonaella siveteri</i> n. sp.	FD, iron oxide	carapace filling cement	0.6	-7.9
SE 8412	SC	<i>Shemonaella siveteri</i> n. sp.	FD, iron oxide	carapace filling cement	1.8	-6.8
SE 8412	SC	<i>Shemonaella siveteri</i> n. sp.	FD, iron oxide	carapace filling cement	-1.3	-12.8
SE 8412	SC	<i>Shemonaella siveteri</i> n. sp.	FD, iron oxide	carapace filling cement	1.6	-5.9
SE 8412	SC	<i>Shemonaella siveteri</i> n. sp.	FD, iron oxide	carapace filling cement	-0.4	-12.9
SE 8412	SC	<i>Shemonaella siveteri</i> n. sp.	FD, iron oxide	carapace filling cement	-0.6	-11.8
SE 8411	SC	<i>Paraparchites circularis</i> n. sp.	FD, iron oxide	1 specimen, shell and carapace fill	-1.3	-6.6
SE 8411	SC	<i>Paraparchites circularis</i> n. sp.	FD, iron oxide	1 specimen, shell and carapace fill	-1.1	-6.7
FS 12	A	bivalve indet.	FD	shell frags	-6.0	-2.8
FS 12	A	bivalve indet.	FD	shell frags	-6.0	-3.5
SE 8866	Pit	<i>Leptera</i>	FD	shell frags	-0.9	-8.2
SE 8821	Pit	<i>Lithostrotion junceum</i>	FD	shell frags	-2.2	-8.3
SE 8821	Pit	<i>Lithostrotion junceum</i>	FD	shell frags	-1.8	-9.7
SE 8821	Pit	<i>Lithostrotion junceum</i>	FD	shell frags	-1.7	-7.4
SE 8821	Pit	<i>Lithostrotion junceum</i>	FD	shell frags	-2.2	-9.0
EN 4885	P	<i>Productus</i>	calcite	shell frags	+1.2	-4.3
EN 4885	P	<i>Productus</i>	calcite	shell frags	+1.3	-4.2
EN 4885	P	<i>Productus</i>	calcite	shell frags	+1.0	-4.5
EN 4885	P	<i>Productus</i>	calcite	shell frags	+0.8	-4.4

Table 5. Carbon and oxygen stable isotope data for ostracods and macrofossils. The data are listed in order of the type of cement or fossil fragment studied, for example single valve or carapace filling cement. The composition of the analysed cement is also listed, with FD referring to ferroan dolomite. “Form.” refers to formation; P; Pathhead Formation, SC; Sandy Craig Formation, Pit; Pittenweem Formation, A; Anstruther Formation.

Most of the dolomitic ostracods and macrofossils have lighter oxygen isotope values than calcitic ostracods and macrofossils, and the calcitic ostracods have a narrower field of carbon isotopes. The calcitic ostracod carapaces which have undergone diagenetic stage 1 and 2 sit within the range of -3.7‰ to -0.9‰ for $\delta^{18}\text{O}$ and -2.5‰ to $+0.3\text{‰}$ for $\delta^{13}\text{C}$.

Calcitic ostracods of the species *Shemonaella siveteri* n. sp. and *Hollinella radiata* are from fully marine and marginal marine sediments. There is little distinction between the isotope signatures of specimens from these two different environments, but in general the fully marine ostracods have a signature that is on average lighter by 1‰ $\delta^{18}\text{O}$ (Figure 7). Note that all of the calcitic ostracods have undergone stage 1 diagenesis, and do not preserve a primary signal.

The calcitic macrofossil *Productus* has slightly lighter oxygen isotope values than calcitic ostracod carapaces (-4.4‰ to -4.2‰ $\delta^{18}\text{O}$), but heavier carbon isotope values ($+0.8\text{‰}$ to $+1.3\text{‰}$ $\delta^{13}\text{C}$). Prior analysis of *Productus* valves from the polished thin section of this sample (on the SEM and under cathodoluminescence) did not reveal any evidence of diagenesis.

All the calcitic ostracods are from the Pathhead Formation, with the exception of the *Polycope* specimen. This formation has the best preservation, and apart from this the age of the sample (and thus the burial depth of the samples) has no relation to the isotopic values (Table 5). As reported with the diagenetic stages, the sediment type the fossils were sourced from also does not have a relation to the isotope results.

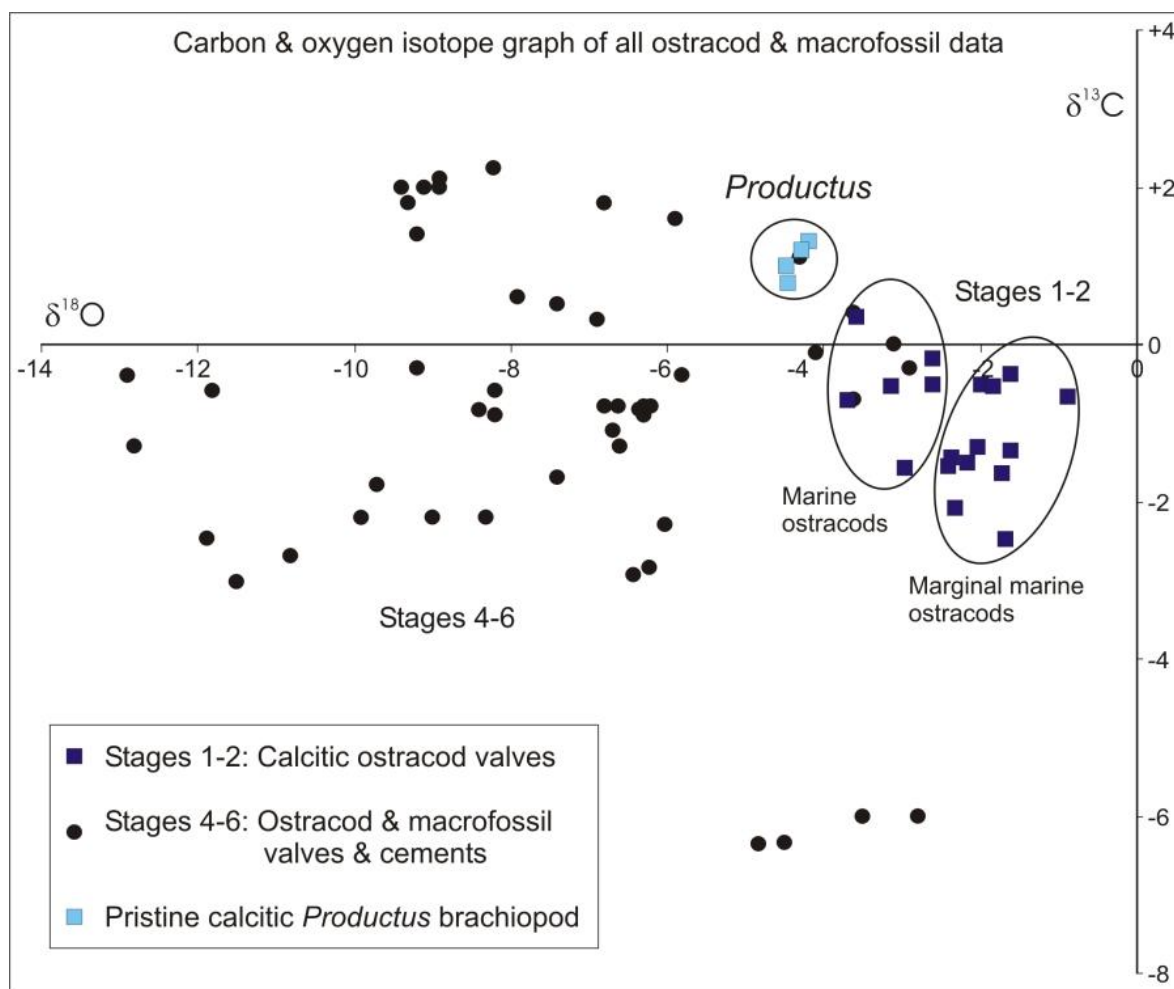


Figure 7. Stable isotope plot of all the fossil data from the Strathclyde Group. The values of *Productus* carapaces are highlighted because they are the only calcitic macrofossils tested: the others are all composed of ferroan dolomite. Ostracods with a large amount of pyrite (stage 3) were not selected for isotope analysis.

The isotopic composition of the ostracods and macrofossils plotted according to their diagenetic stages are shown in Figure 8. There is no trend between the isotope signatures of dolomitic cements and different ostracod species. There is a difference in values between the ferroan dolomite carapace replacing cement, and the carapace-filling cement, the former having a smaller range in oxygen and carbon isotopes. Also, the oxygen isotopic range of ferroan dolomite valves is narrower than dolomitic carapace-filling cements (-9.7‰ to -5.8‰ $\delta^{18}\text{O}$ compared to -2.9‰ to -12.9‰ $\delta^{18}\text{O}$). The macrofossil carapaces have lighter

carbon isotope values than the ostracod carapaces, by approximately $-2\text{‰ } \delta^{13}\text{C}$. The calcitic carapace filling cements are close to the range of ferroan dolomite ostracod carapaces and carapace filling cements, but with lighter carbon isotope values.

The presence of high concentrations of iron oxide can affect the results to give anomalous values (Figure 8). A cluster of values from ferroan dolomite ostracod carapaces has relatively heavy carbon isotopes, and light oxygen isotopes. These are ostracods from sample SE 8751, which has a very high content of iron oxide (Table 4). Two outlying results of a bivalve mollusc have significantly lighter carbon isotopes ($-6\text{‰ } \delta^{13}\text{C}$). The fossils are from a highly dolomitised limestone, with a high concentration of iron oxide crystals within the sediment. The other two anomalously light carbon isotope results are from a *Polycope elegans* n. sp. ostracod with a ferroan dolomite carapace and a carapace fill of ferroan dolomite and framboidal pyrite.

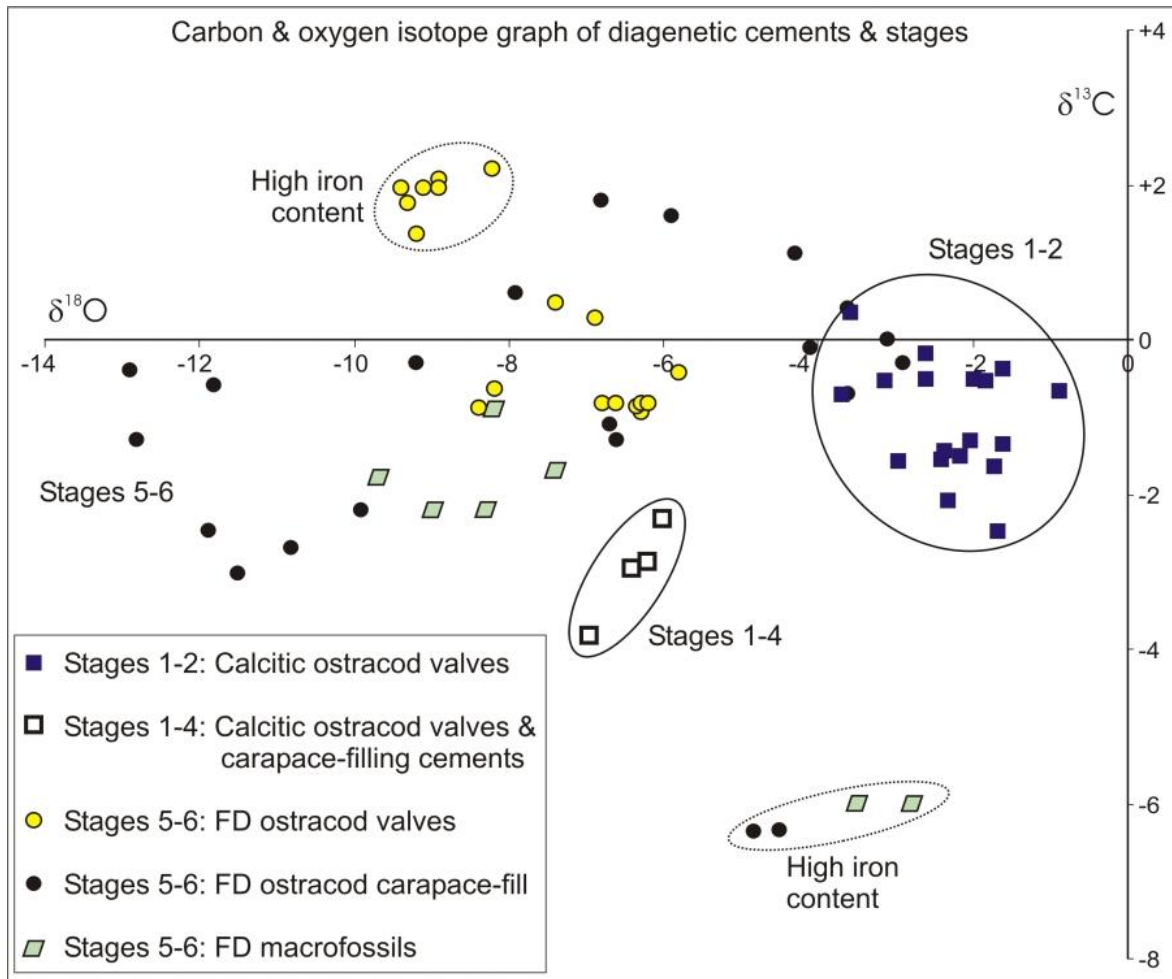


Figure 8. Stable isotope plot of ostracods and macrofossil diagenetic stages. The different calcite and ferroan dolomite (FD) cements and mineralisations are distinguished. High iron content specimens have anomalous results.

Isotope Interpretation - diagenesis

Mineralogy and the extent of diagenesis are the main controlling factors that affect the isotope results. The carbon isotope results do not reflect diagenetic stages, but the oxygen isotope results become lighter with an increasing amount of diagenesis. For example the heavier oxygen isotope values characterise calcitic ostracod carapaces, while dolomitic carapaces have lighter values. The carbon isotope values are only very variable in

specimens with high iron oxide or pyrite contents, which may reflect unusual diagenetic environments or analytical errors.

The values for the calcitic ostracod carapaces are within a fairly small isotopic range (–3.7‰ to –0.9‰ for $\delta^{18}\text{O}$ and –2.5‰ to –0.2‰ for $\delta^{13}\text{C}$). The heaviest oxygen isotope values are for stage 1 diagenesis, which from the fidelity of carapace ornament preservation and comparison with planktonic foraminifera is interpreted as an early burial event.

The wide spread of values for ferroan dolomite carapace fills compared to dolomitic shell cements reflects the diagenetic history and style of alteration. The infilling of carapace cavities can occur at any time, and happened in multiple stages. Several generations of ferroan dolomite cements have been recorded within ostracod carapace cavities. In contrast, the carapace replacement by ferroan dolomite may have occurred in one event, as the carapace itself has a dense ultrastructure and it is less open to fluid flow through pore spaces. The isotope results suggest that the shell replacement in the specimens that were analysed may have occurred at approximately the same time. This is because the results are clustered within a fairly narrow range.

Studies on benthic foraminifera and bulk carbonate have shown that diagenesis alters stable oxygen isotopes at depth, to lighter values (Schrag *et al.* 1995). In this study, the age of the specimen, and hence the burial depth of the sample, is not directly related to the diagenetic stage or isotope results. The calcitic ostracods are all from the younger Pathhead Formation, and although this formation does also contain some diagenetically altered fossils (up to stage 6), it generally has better preserved specimens. This reflects a sampling bias rather than a true diagenetic and burial depth signal.

The only other stable isotope data from Carboniferous ostracods is that from the Ballagan Formation of the Midland Valley of Scotland (Williams *et al.* 2006). The data from this study have a greater range of stable isotope values, with significantly heavier stable oxygen signatures (Figure 9). This study has elucidated that the isotope results reflect the diagenetic history of the ostracods. The results of Williams (*et al.* 2006) can now be validated in terms of diagenesis, especially for light oxygen isotope signatures, as in that study values of -9‰ or less for $\delta^{18}\text{O}$ were recognised as diagenetic signals.

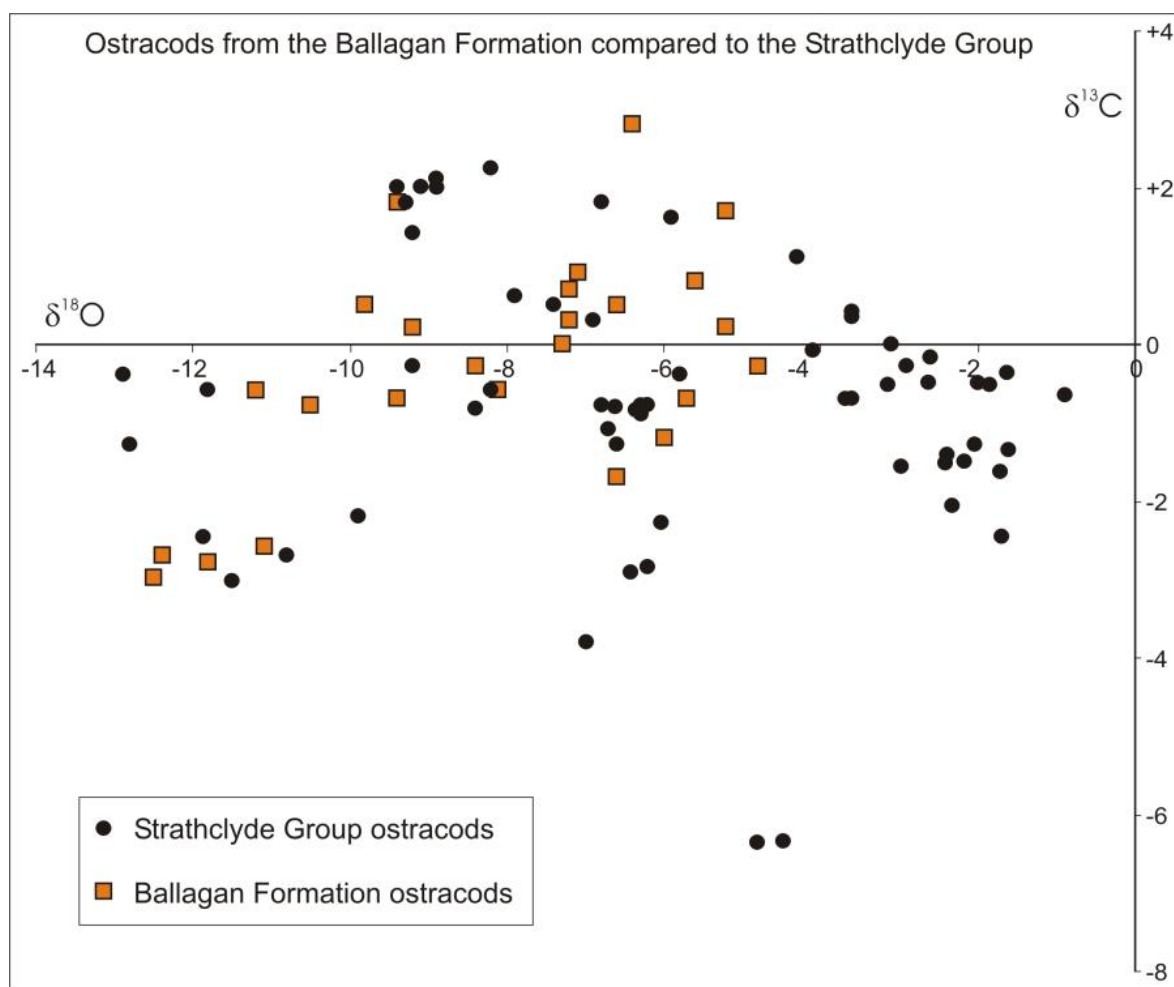


Figure 9. Isotope plot of the ostracod data from the Strathclyde Group formations compared to that of the Inverclyde Group Ballagan Formation (from Williams *et al.* 2006). The majority of the ostracod isotope results represent the effect of diagenesis.

Isotope discussion – palaeoenvironmental signals

From stages 1-2 calcitic isotope results it is likely that the environment of diagenesis was shallow burial or even pre-burial. This is because the oxygen isotope values (-3.7‰ to -0.9‰ for $\delta^{18}\text{O}$) are similar to that of Carboniferous seawater. A review of Carboniferous isotope data (Grossman 1994) gave the average value of Carboniferous seawater as between -3‰ and -1‰ $\delta^{18}\text{O}_{\text{PDB}}$. Unlike the planktonic foraminifera recrystallisation process in deep water (Pearson *et al.* 2001), the ostracods are interpreted to have lived in a shallow-water setting. They are unlikely to have bottom water temperatures different from their living conditions. This may explain why the oxygen isotope results for stage 1-2 diagenesis calcitic shells are fairly similar to that of Carboniferous seawater. Some of the ostracods tested in Williams (*et al.* 2006) were also thought to show a near-environmental signal, although the oxygen isotope results are lighter than those of this study.

Possible palaeoenvironmental signatures are present in the calcitic ostracods from different environments, if the isotope signal is interpreted as representing pre-burial waters. Marginal marine ostracods have slightly heavier oxygen isotope values (on average by $+1\text{‰}$ $\delta^{18}\text{O}$) than marine ostracods. Marginal marine waters can be enriched in $\delta^{18}\text{O}$ due to evaporation (if the water body has a higher than normal salinity), suggesting that the ostracods may have lived in an embayment or lagoon with elevated salinities. However, temperature may also be a factor, as well as unknown vital effects. The late Mississippian was a time of glaciation in western Europe (Fielding *et al.* 2008), and the effect of ice volume changes on oxygen isotopes also needs to be considered. A comparison of more fresh, brackish, marginal and marine calcitic ostracods in the future may help to resolve this issue.

The only pristine specimen tested is a specimen of a calcitic *Productus* brachiopod. Importantly it is from a marine sediment, so the $\delta^{13}\text{C}_{\text{PDB}}$ and $\delta^{18}\text{O}_{\text{PDB}}$ composition of the calcite can be used to interpret the seawater conditions in the Mississippian (assuming no vital effects). The *Productus* specimen has a range of -4.4‰ to -4.2‰ $\delta^{18}\text{O}$, so is only slightly lighter than the average seawater value. The fact that the Midland Valley of Scotland was situated in a restricted, closed sedimentary basin may account for variations in the isotope geochemistry of seawater compared to the global mean. A study of further pristine macrofossil specimens would provide further evidence for the range of seawater composition in this basin.

Conclusions

- The study documents a protocol for the examination of diagenetic alteration of ostracod carapaces. This is essential prior to the stable isotope analysis of fossils for palaeoenvironmental purposes. The methodology is applied to macrofossils, and it can be used for other fossil groups. A variety of methods were used to assess the preservation: visual assessment of specimens under a binocular microscope; study of carapace ultrastructure under the SEM; study of polished thin sections containing fossils under plane polarised light, the SEM, and CL; testing for diagenetic cements using elemental analysis under the SEM and electron microprobe.
- A history of the timing of diagenetic cement and mineral growth for ostracods is reconstructed: 1. Replacement of the original carapace low magnesium calcite with a diagenetic crystalline calcite; 2. dissolution and pitting of the carapace surface; 3. euhedral pyrite growth in cavities and on carapace surfaces; 4. ferroan calcite

replacement of calcitic carapaces, and growth in cavities; 5. ferroan dolomite replacement of carapaces and growth in cavities; 6. replacement of pyrite in the sediment and fossil carapaces by iron oxide in samples which have been substantially diagenetically altered; 7. replacement of ferroan dolomite cements by sphalerite and barite mineralizations. These stages also apply to macrofossils.

- Carbon and oxygen stable isotope results values for a range of ostracod and macrofossil carapaces are -6.4‰ to +2.2‰ for $\delta^{13}\text{C}_{\text{PDB}}$ and -12.9‰ to -0.9‰ for $\delta^{18}\text{O}_{\text{PDB}}$. The carbon isotope results do not show a clear signal. The oxygen isotope results reflect the stages of diagenesis, and not palaeoenvironmental conditions. For example stage 1 calcitic ostracods have heavier oxygen isotope values (-3.7‰ to -0.9‰ for $\delta^{18}\text{O}_{\text{PDB}}$) than stage 5 ferroan dolomite ostracod valves which are significantly lighter.
- In stage 1 of diagenesis Carboniferous ostracod carapaces are recrystallised by a neomorphic calcite of 1-3µm size euhedral crystals. This texture is comparable to the recrystallised test of planktonic foraminifera. The fidelity of ornamental preservation on the ostracod carapaces, and the overprinting of later diagenetic cements shows that this is an early stage of diagenesis. From the isotope results it is likely that the environment of diagenesis was shallow burial or even pre-burial, as the oxygen isotope values are similar to that of Carboniferous seawater.
- A pristine calcitic specimen of *Productus* has an oxygen isotope value 1‰ lighter than that of Carboniferous seawater. This is the only pristine specimen tested, and importantly it is from a marine sediment. Therefore, it is possible that the oxygen

isotope results represent palaeoceanographic isotopic conditions in the early Carboniferous.

Chapter 8: Conclusions

The aims of the study were to investigate the nature and chronology of the colonisation of non-marine environments by ostracods in the Carboniferous, by reference to various proxies that determine non-marine environments. The timing of the colonisation of non-marine environments by ostracods is in the Mississippian, with a record of freshwater ostracods approximately 20 million years earlier than previously recorded. The putative earlier non-marine invasions by ostracods are also discussed in the review chapter. The nature of non-marine colonisation may have been active or passive, and various mechanisms to achieve this such as reproductive strategies are proposed.

The objectives of the study were mostly met. Non-marine proxies such as sedimentological evidence, macrofossil data and palynology were successfully used. Ostracods were described and identified from a range of environments. Erection of a biostratigraphy was not possible due to the particular ecological ranges of the ostracods. Pristine ostracod carapaces were not present, so the original palaeoenvironmental conditions of the water bodies in which the ostracods lived could not be determined using isotopic methods. However, a diagenetic study provided a useful protocol to assess the effects of diagenesis on isotope results.

Of wider significance, this study has provided more data and interpretations about the first non-marine colonisation by the Ostracoda. The ecological tolerance ranges for key Mississippian ostracods and macrofossils has been established. A record of freshwater algal palynomorphs has provided a useful proxy for determining freshwater environments. The arthropod fragments discovered warrant further investigation, and hold potential

environmental significance if the copepod or ostracod affinities could be established. The diagenetic alteration of the ostracod carapace ultrastructure and the isotopic signature of diagenetic products will aid those seeking to analyse fossils for palaeoenvironmental reconstruction. The fact that isotope results can be directly linked to diagenetic stages is a valuable discovery.

Was glaciation a driving force for non-marine colonisation? Glacial and interglacial episodes in the late Mississippian resulted in eustatic sea level changes, the transgressions of which are observed globally (Fielding *et al.* 2008, Ross & Ross 1985). Global marine transgressions may correlate with those at the top of the Pathhead and Sandy Craig formations. The cyclothem-like cycles of sedimentation in the Mississippian of the Midland Valley of Scotland (Andrews *et al.* 1991, Browne *et al.* 1999, Kassi *et al.* 1998, 2004) and England (Barnett *et al.* 2002) provides evidence for possible eustatic sea level change. A change in eustatic sea level and continental coastlines may have acted as a driving force for animals to seek non-marine habitats which had an abundant plant food source.

Alternatively, the ostracods may have passively migrated up estuaries and across coastal floodplains during times of glacial melt and rapid sea-level rise, and over generations made the physiological changes to adapt to freshwater salinities. Regional glacial episodes may have occurred as early as the late Devonian in South America (Fielding *et al.* 2008). The first evidence of brackish ostracods and other non-marine arthropods is from about this time.

Chapter 2 - Review

The radiation of the Ostracoda from marine to non-marine environments is a key step in the evolution of the group. The nature and chronology of this transition is examined. The first non-marine environments colonized by ostracods were marginal marine to brackish.

Ostracods adapted to suit euryhaline, then freshwater salinities, through changes in osmoregulation, feeding and reproduction. Brackish ostracods are reported from the Devonian, and the first definitive freshwater ostracods occur in the late Mississippian.

There is a gap in the data of Carboniferous non-marine ostracods, especially in the Mississippian.

The recognition of palaeoenvironments of a non-marine nature requires a multi-proxy approach, such as the use of ostracods, macrofossils, sedimentology, geochemistry and palynology. These different proxies are present in the well-dated successions of the Mississippian of the Midland Valley of Scotland.

Chapter 3 – Ostracod taxonomy

Twentyfive ostracod species from the orders Myodocopida, Palaeocopida and Podocopida are described, four of which are new species.

Chapter 4 – Freshwater and brackish ostracods

The Mississippian of the Midland Valley of Scotland contains a wide range of marine to non-marine ostracods, macrofauna and sediments that make it an ideal sequence to study the non-marine radiation of ostracods. Macrofossils are used to interpret the environmental tolerance of the ostracods. Important brackish to freshwater macrofauna are the bivalves *Anthraconaia*, *Carbonicola*, *Curvirimula* and *Naiadites*, the vermiform microconchid

“*Spirorbis*”, conchostracans and fish. Common marine ostracods are *Bairdia submucronata*, *Hollinella* (*Keslingella*) *radiata* and *Polycope elegans* n. sp. Important eurytopic ostracods are *Cavellina benniei*, *Cavellina valida*, *palaeocope* sp. A and B and *Shemonaella siveteri* n. sp. Key brackish to freshwater ostracods are species of *Carbonita*, *Geisina arcuata*, and *Paraparchites circularis* n. sp. Brackish to freshwater habitats include estuaries, lakes, temporary pools and swamps, which were different in each formation. Freshwater ostracods of *Carbonita* and *Geisina arcuata* are recorded from the early Mississippian.

Chapter 5 – algal palynomorphs

A proxy for non-marine conditions are algal palynomorphs that may have lived in freshwaters, such as the spores of zygnematacean green algae. Three new types of algal palynomorph and *Botryococcus* sp. are recorded from non-marine sediments of the Strathclyde Group. The important palynofacies components of dark woody and sheet cellular material, along with arthropod fragments in these sediments indicate near-land depositional settings such as swamps and temporary pools. The algal palynomorphs are similar to living and Palaeozoic freshwater algae, and are interpreted as freshwater in origin. They are associated with some of the earliest *Carbonita* ostracods, and their discovery adds weight to the presence of a freshwater environment.

Chapter 6 – ostracod ultrastructure

Calcitic fossil ostracods may be mistaken for pristine specimens, without a study of the carapace ultrastructure. The integrity of ultrastructural preservation was assessed by comparing Carboniferous and Recent specimens. Recent ostracods have a smooth chitinous epicuticle, and a fine crystalline procuticle with a foliated to multi-laminate fabric.

Carboniferous ostracods do not preserve the epicuticle, and have a procuticle composed of equant neomorphic calcite crystals. In some specimens the procuticle has a multi-laminate texture, which is a remnant of the original carapace structure. From an ultrastructural study, Carboniferous calcitic ostracod specimens that appeared pristine under light microscopy and low magnification scanning electron microscopy were revealed to be diagenetically altered. It is important to assess the carapace preservation prior to any geochemical analysis of the ostracod carapaces for palaeoenvironmental purposes.

Chapter 7 – diagenetic alteration

A protocol for the examination of diagenetic alteration of ostracods and macrofossils is proposed. The ostracods and macrofossils have undergone seven stages of diagenetic alteration: early, shallow burial diagenesis, producing: 1. neomorphic calcite; 2. dissolution and pitting; 3. euhedral pyrite; 4. ferroan calcite. Later, deep burial diagenesis, producing: 5. ferroan dolomite; 6. replacement of pyrite by iron oxide; 7. replacement of ferroan dolomite by sphalerite and barite. The oxygen and carbon isotope data reflect stages of diagenesis, and not palaeoenvironmental conditions. For example, calcitic ostracod valves have heavier oxygen isotope values than ferroan dolomite valves, which are significantly lighter. Stage 1 diagenetic calcitic ostracod valves have oxygen isotope values similar to that of Carboniferous seawater ($-3\text{‰ } \delta^{18}\text{O}_{\text{PDB}}$). The neomorphic calcite of stage 1 is interpreted as an early diagenetic stage, which may have occurred prior to burial.

Future work

There can never be a complete result to a project of this nature, as more discoveries of non-marine ostracods can only widen the scope of knowledge and the number of questions to be tested. There are additional sections in the Midland Valley of Scotland which contain potential non-marine ostracods. Globally there is less known about non-marine ostracods in the Mississippian than in the Pennsylvanian. A key question is when were the first darwinulids? They are a diverse extant freshwater group, common in the Pennsylvanian and with unresolved origins.

The non-marine colonisation of other invertebrate groups such as bivalves is an interesting ongoing area of research. Another research area for future investigation is the types of environments that ostracods were first colonising, for example coal swamps, where there may be have even been semi-terrestrial ostracods. No ostracods were found in pure coals in this study, but ostracods are common in the Pennsylvannian Coal Measures, so there is the potential for future study and investigation of possible semi-terrestrial ostracods.

The processing of further samples for arthropods to retain larger fragments may provide taxonomic identifications and environmental information. The study of further palynological samples would provide more information on freshwater environments, as many of the samples in this study were degraded. A higher resolution analysis on a single non-marine ostracod-rich succession would be valuable. If more palynological samples were processed from ostracod-bearing sediments it is possible that ostracod appendages or other soft tissues may be recovered.

For the shell ultrastructure a study of a wider range of Recent groups compared to fossil specimens would be useful. The most relevant for extinct ostracods may be a study of

Recent Myodocopa, since the discovery of Palaeozoic soft-parts from supposed palaeocopes has revealed a myodocopid animal. The etching of Recent ostracods in hydrogen peroxide to dissolve any remaining organic material may also provide a good comparison with Carboniferous specimens. Different analytical techniques such as Transmission Electron Microscopy may give further knowledge as to the ultrastructure of the outer lamella and the recrystallisation processes.

Future isotope analysis of any pristine calcitic non-marine ostracods (none were found in this study) would be essential to advance any palaeoenvironmental interpretations. So would an analysis of further pristine macrofossils, to compare with the ostracod results. This is a very interesting research area that has wider applications to other fossil groups and geological periods.

The timing and nature of the non-marine colonisation of ostracods as a philosophical inquiry can be taken much further. The wider context of the non-marine invasion of other animal groups and the driving forces behind this event are the broad philosophical questions that the ostracod story is just a small part of. The start of the Carboniferous glaciation event as a possible driving force for non-marine colonisation is an exciting avenue for further research.

Appendices

Chapter 1 & 2

Appendix 1. A CD-Rom containing a PDF file of Bennett (2008), the published article from which chapter 2 is based on.

Chapters 3 & 4

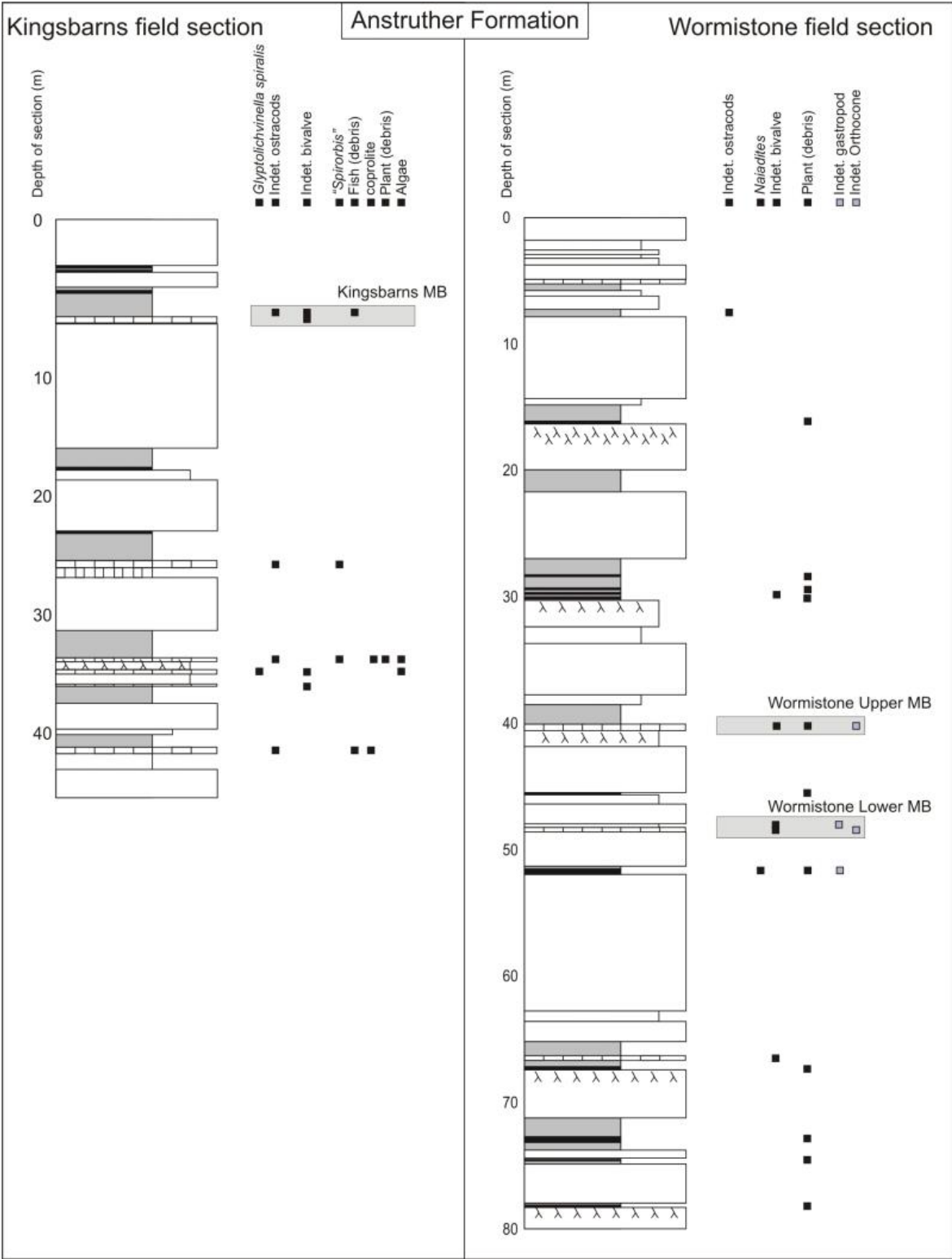
Appendix 2. An Excel file on the CD-Rom containing information on Midland Valley of Scotland borehole and field sample samples from this study. This includes sedimentological and palaeontological information, for example type specimen numbers.

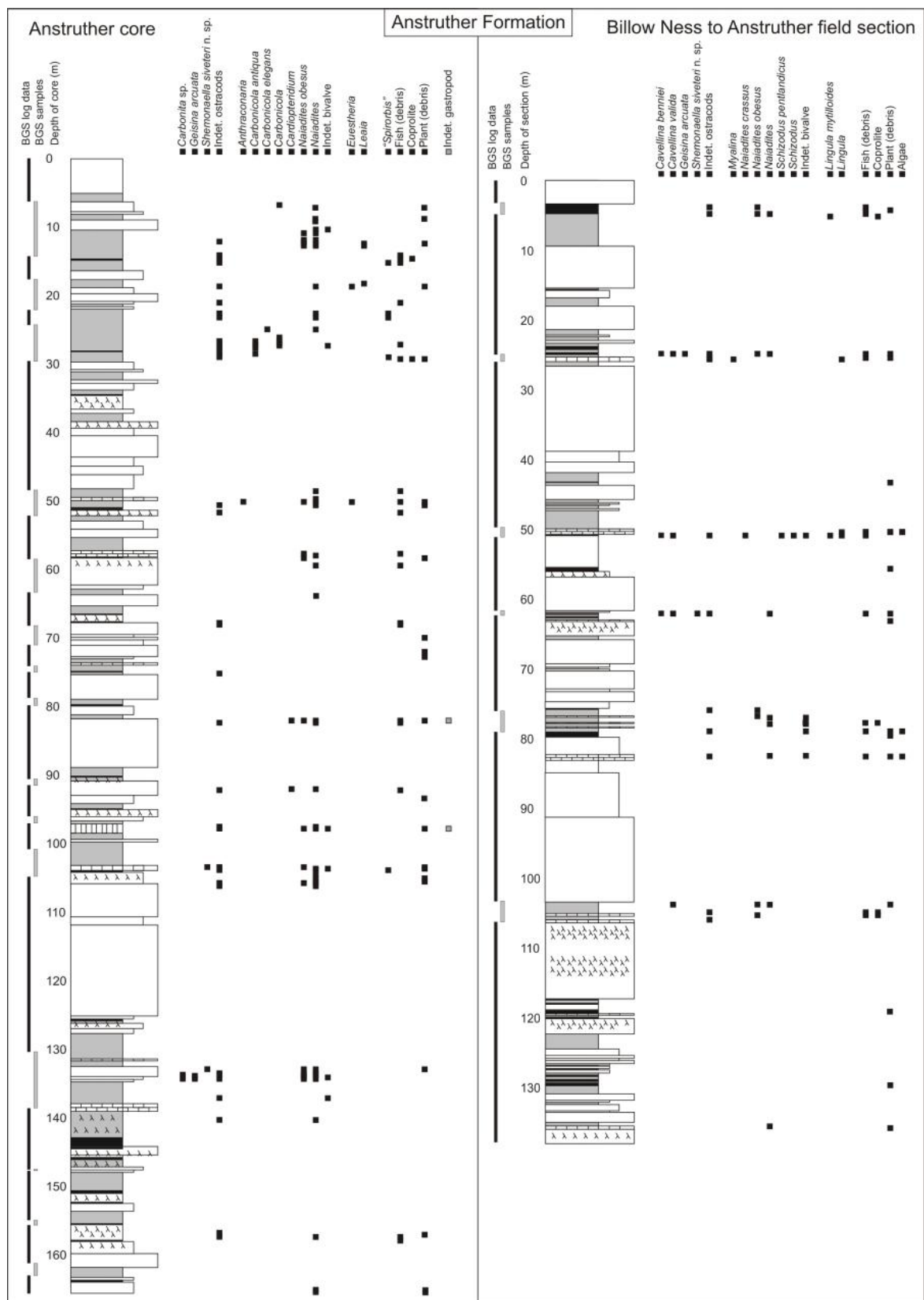
Chapter 4

Non-marine fauna of interest	Marine		Marginal marine						Brackish			Brackish to fresh			Freshwater					
	Marine macrofauna	Marine ostracods	Palaeocopes	Sanguinolites	Schizodus	Shemonaella	Cavellina	Lingula	Curvirimula	Naiadites	"Spirorbis"	Fish (debris)	Coprolites	Geisina	Anthraconaia?	Carbonicola	Cardiopteridium	Carbonita	Spinicaudata	Plant (debris)
<i>Anthraconaia?</i>	0	0	0	0	0	0	0	0	0	2	0	1	0	0	x	0	0	0	0	0
<i>Carbonicola</i>	1	0	0	0	1	0	0	0	0	0	0	2	0	0	0	x	0	0	0	5
<i>Cardiopteridium</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	x	0	0	1
<i>Curvirimula</i>	1	0	0	0	0	0	0	0	x	0	18	17	0	0	0	0	0	0	0	21
" <i>Spirorbis</i> "	3	0	0	1	2	0	0	0	17	12	x	21	1	0	0	0	0	0	0	11
<i>Naiadites</i>	6	0	0	0	5	0	0	14	0	x	12	12	1	0	1	0	1	0	5	25
Fish (indet.)	3	0	0	0	3	0	0	7	16	15	20	x	7	0	1	2	0	0	4	33
Spinicaudata	0	0	0	0	0	0	0	0	0	6	0	4	0	0	0	0	0	0	x	11
<i>Lingula</i>	39	0	0	2	6	0	0	x	0	13	0	9	0	0	0	0	0	0	2	2
<i>Myalina</i>	3	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Sanguinolites</i>	22	0	0	x	2	0	0	2	0	0	1	0	0	0	0	0	0	0	0	1
<i>Schizodus</i>	15	0	0	1	x	0	0	6	0	4	2	3	0	0	0	1	0	0	0	3
<i>Carbonita</i>	0	0	0	0	1	1	3	1	1	11	4	3	0	7	0	0	0	x	0	3
<i>Cavellina</i>	16	12	16	1	0	14	x	0	1	15	1	3	1	1	0	0	0	2	1	5
<i>Geisina</i>	2	1	0	0	0	2	2	1	0	10	0	1	0	x	0	0	0	0	0	1
<i>Shemonaella</i>	21	6	14	2	0	x	16	3	9	22	4	6	1	2	0	0	0	1	1	2

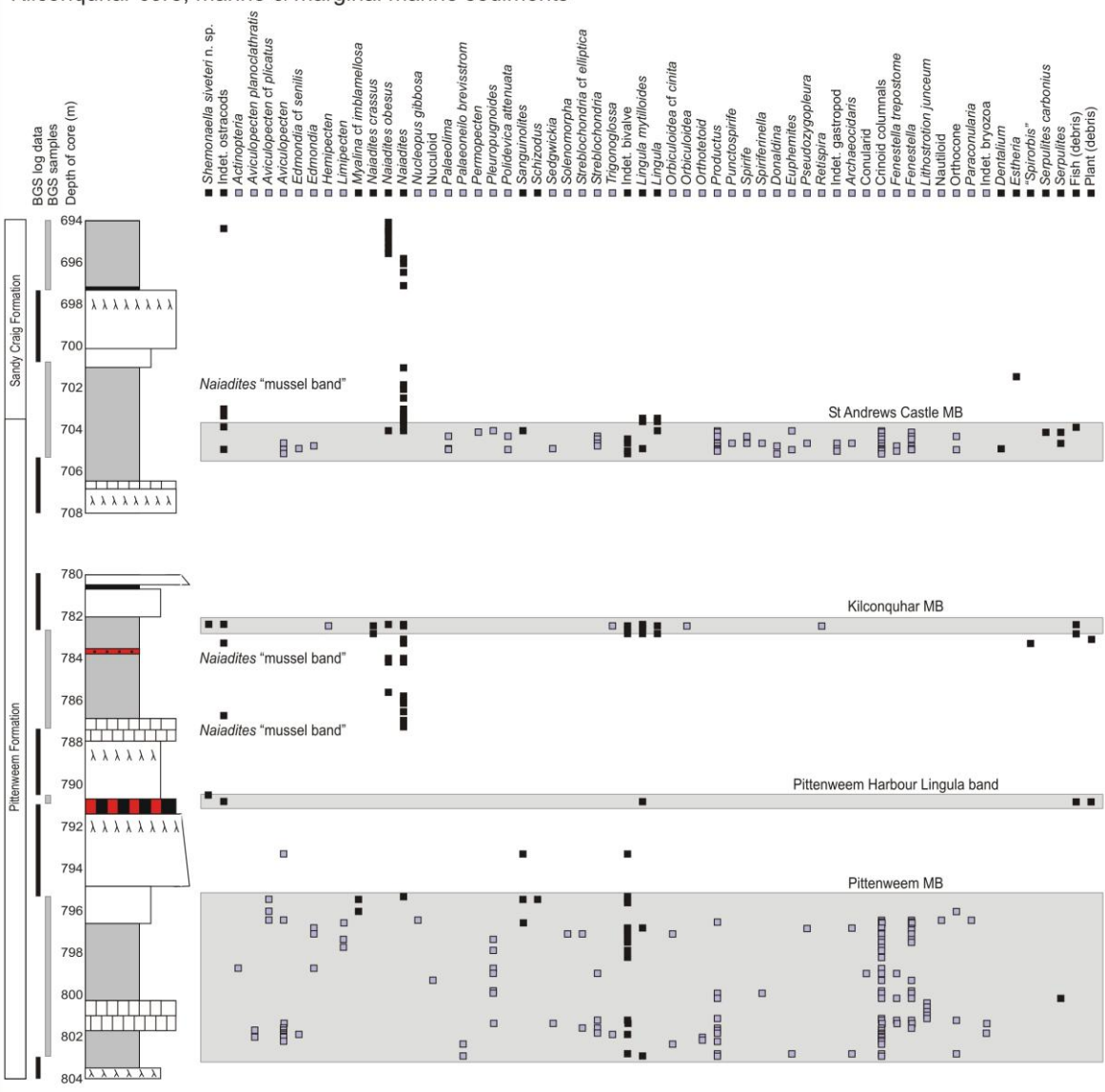
Appendix 3. Faunal associations of common marginal marine, brackish and freshwater macrofossils and ostracods from the Strathclyde Group. The numbers represent the frequency which the fauna occur in the same assemblage. An x refers to where the same fauna crosses on the chart, for example the association of *Cavellina* with *Cavellina*, which is not included in the analysis. This data is plotted on Figures 4 and 16 of Chapter 4.

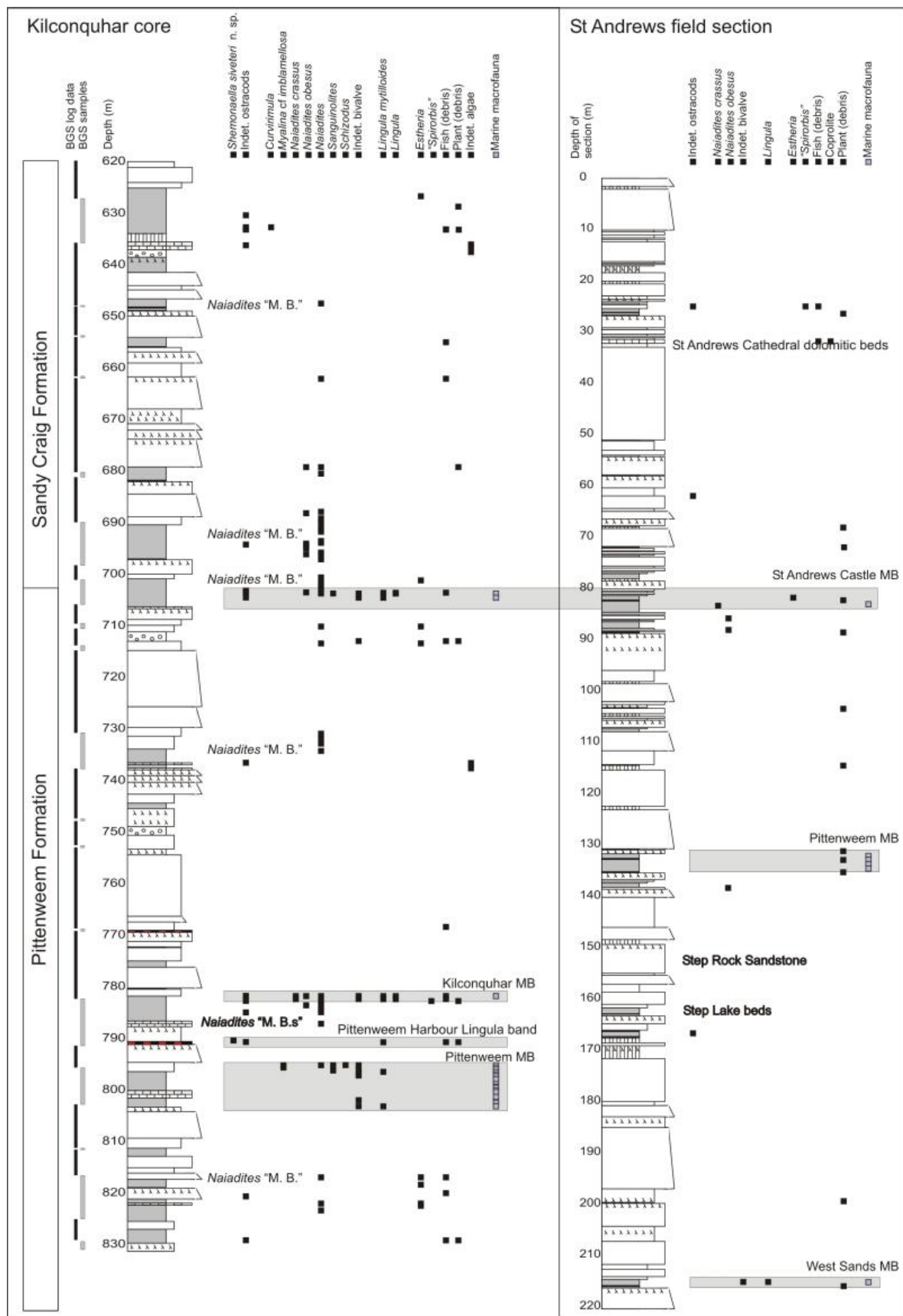
Appendix 4. Sedimentary logs: Graphical logs with faunal occurrences, supplementary to those figured in Chapter 4.

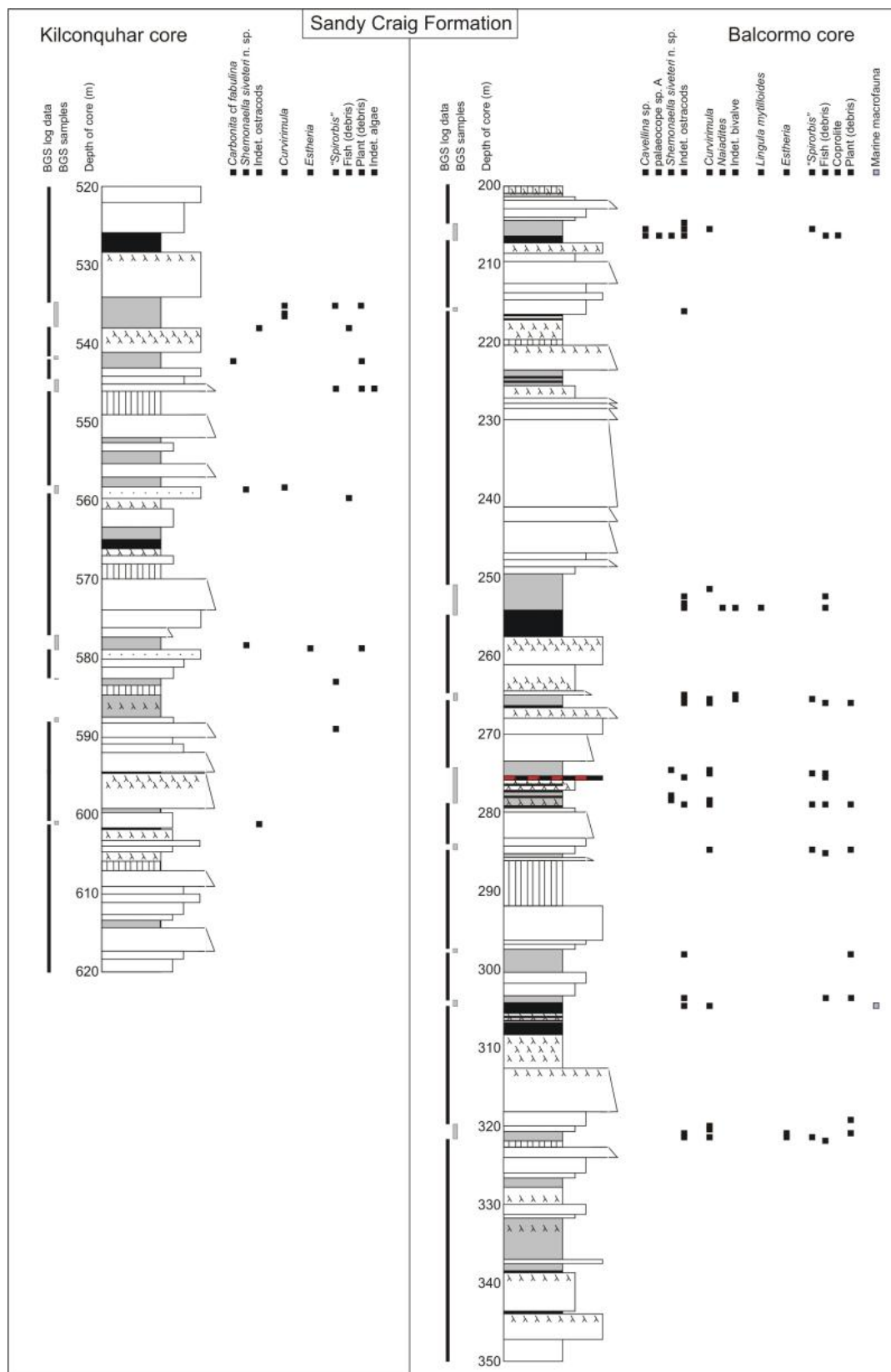


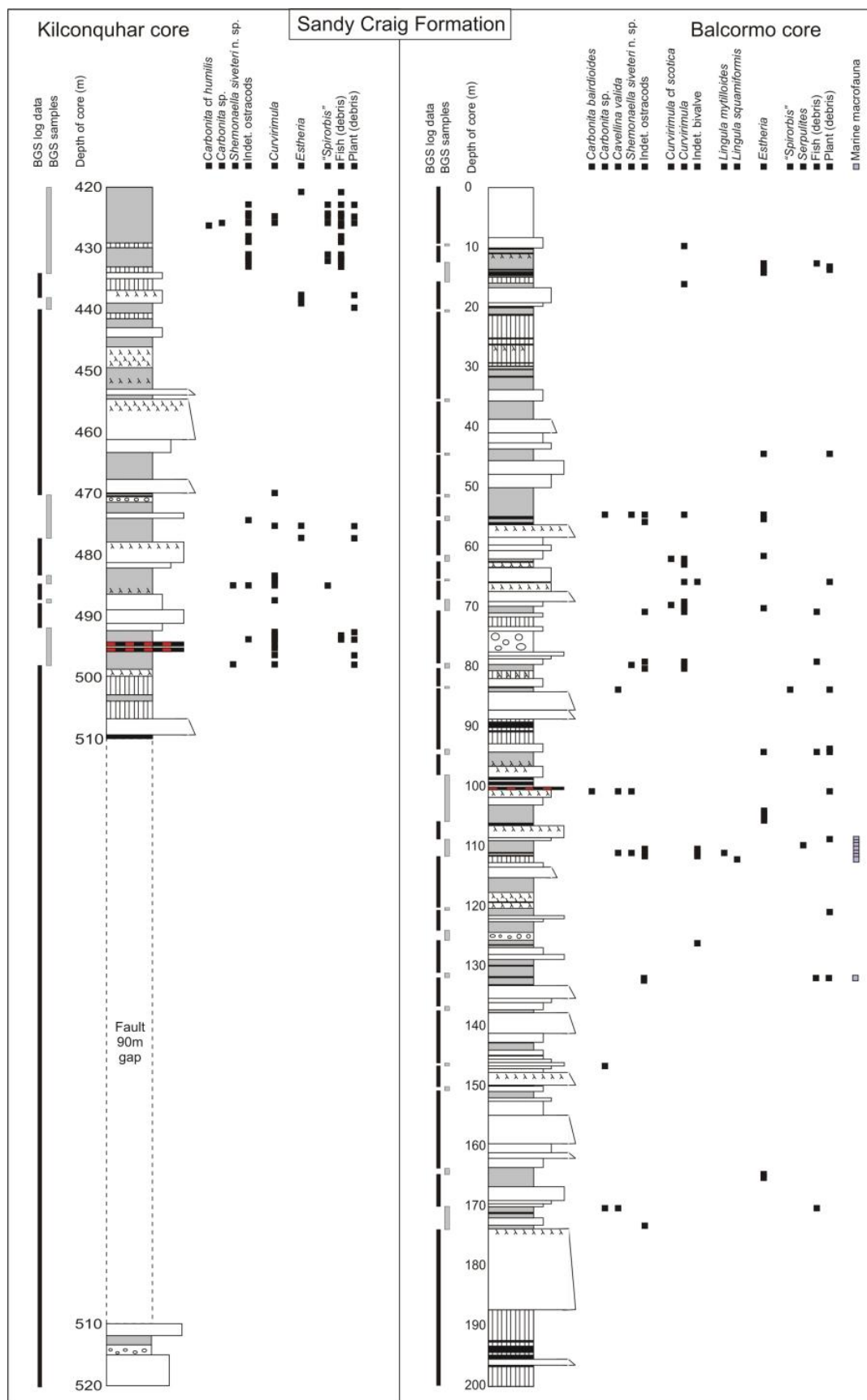


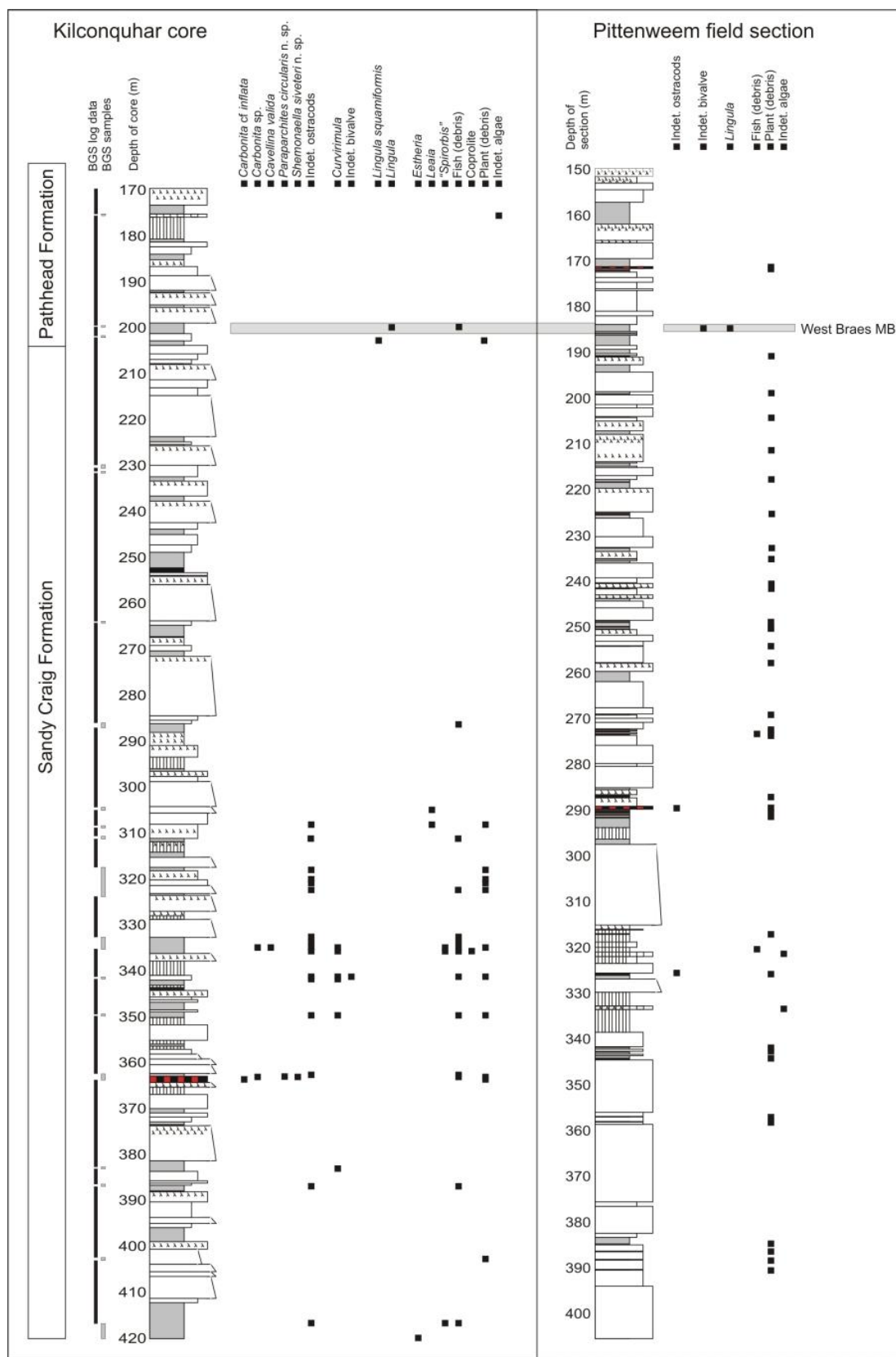
Kilconquhar core, marine & marginal marine sediments

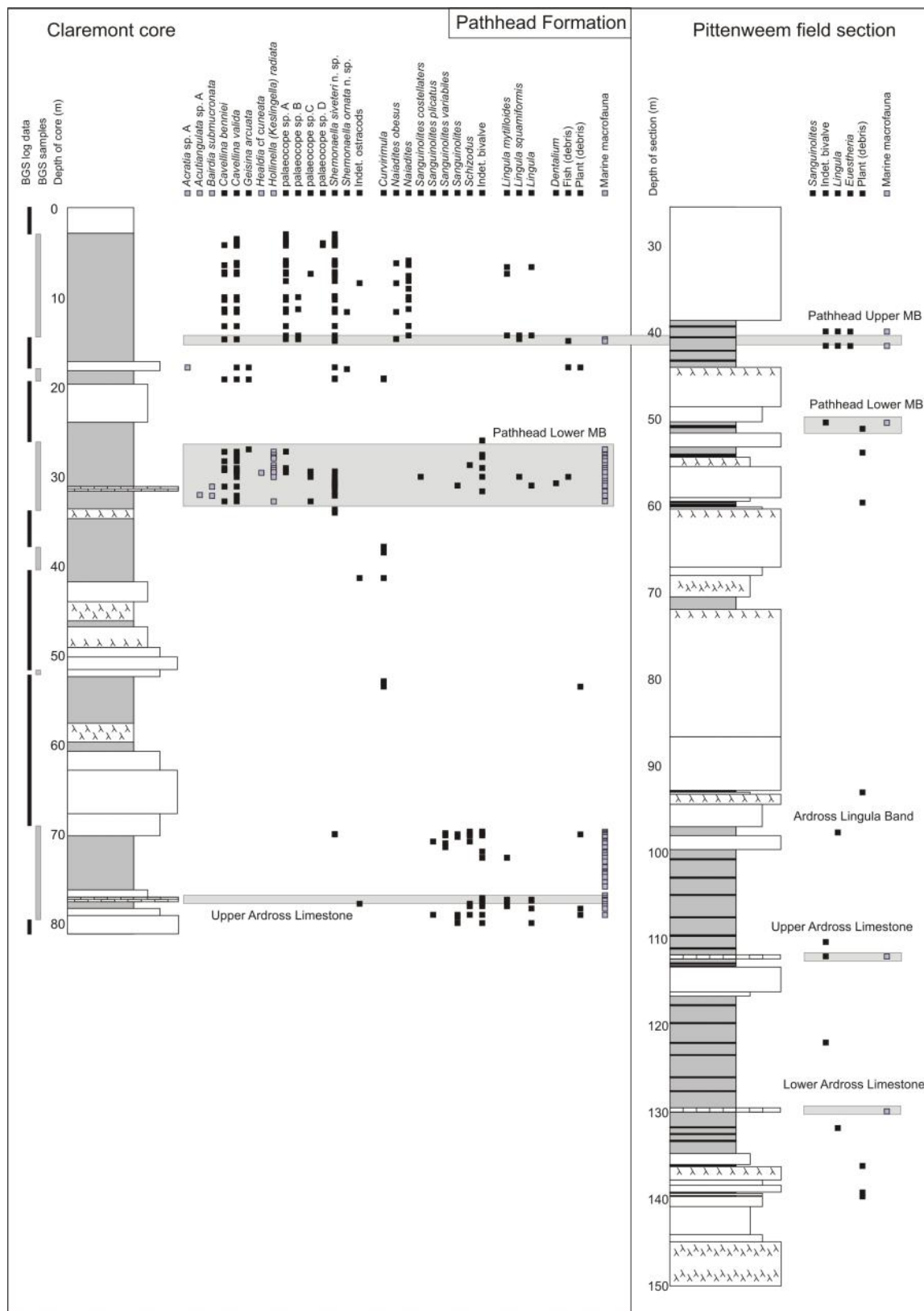




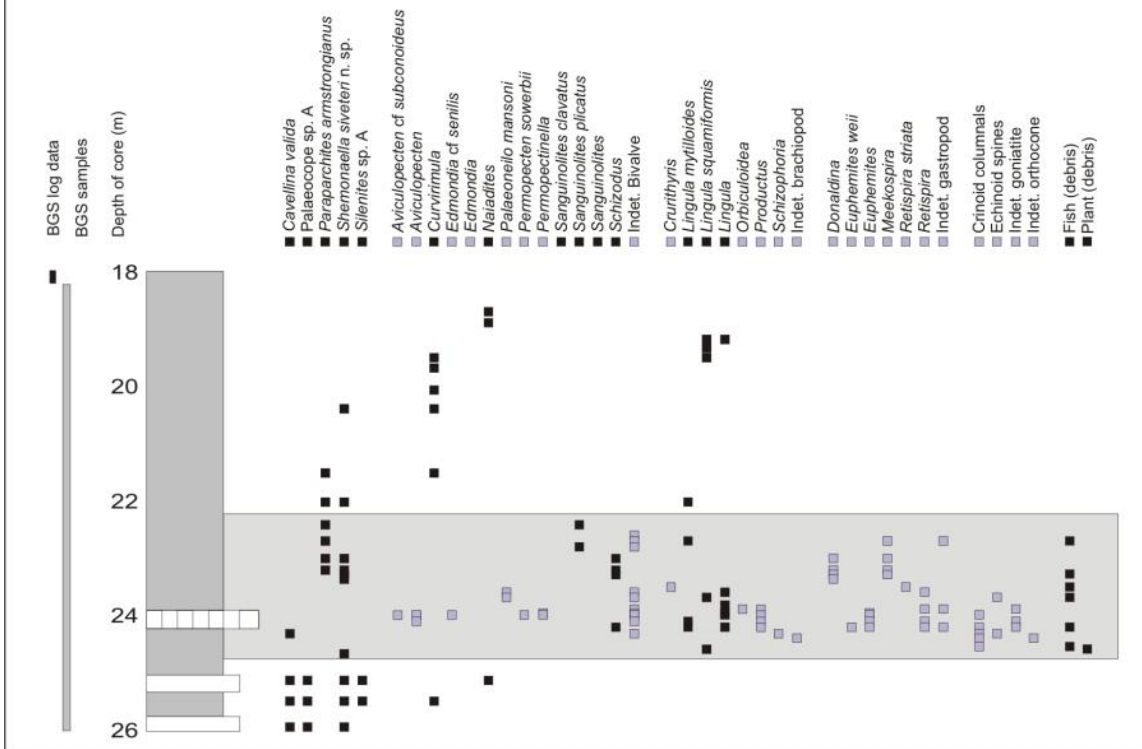


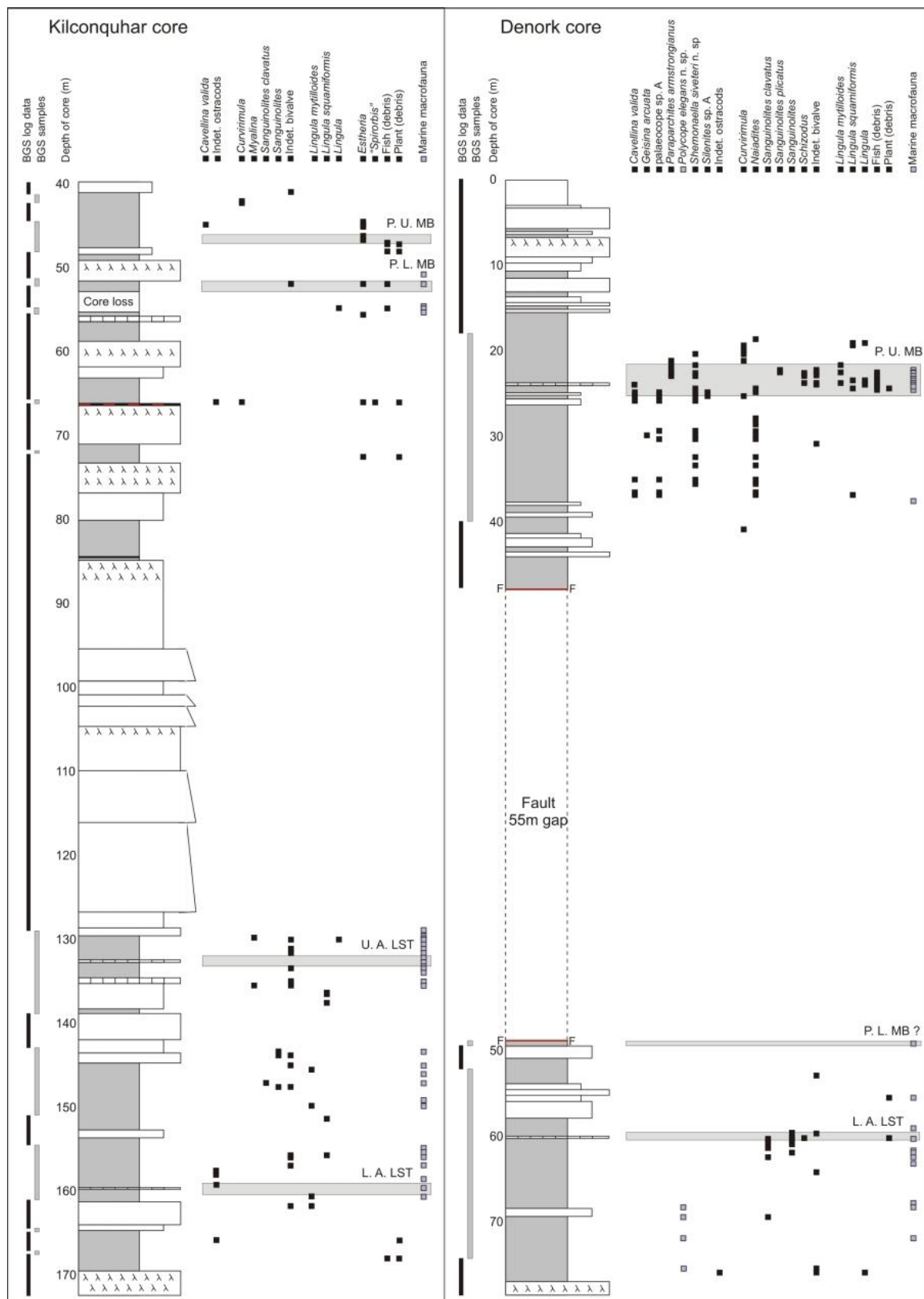






Denork core, Pathhead Formation Pathhead Upper Marine Band





Chapter 6

Fig.	Species	Location	Sex	Material	Specimen no.
*	<i>Aurila woutersi</i>	Porlock, Severn Estuary	female	carapace	CEB8
*		Porlock, Severn Estuary	female	carapace	CEB9
*	<i>Bradleystrandesia fuscata</i>	temporary pond, Flatford Mill	female	carapace	CEB10
*		temporary pond, Flatford Mill	female	single valve	CEB11
		temporary pond, Flatford Mill	female	single valve	CEB12
*	<i>Candona candida</i>	River Stour, Flatford Mill	female	right valve	CEB13
*	<i>Candonopsis tenuis</i>	Lake Biwa, Japan	male	carapace	CEB14
		Lake Biwa, Japan	female	carapace	CEB15
		Lake Biwa, Japan	female	carapace	CEB16
*	<i>Cyprideis torosa</i>	salt marsh, Pegwell Bay	male	carapace	CEB17
		salt marsh, Pegwell Bay	male	carapace	CEB18
		salt marsh, Pegwell Bay	?	carapace	CEB19
		salt marsh, Pegwell Bay	?	carapace	CEB20
		salt marsh, Pegwell Bay	?	carapace	CEB21
		salt marsh, Pegwell Bay	?	carapace	CEB22
		salt marsh, Pegwell Bay	?	carapace	CEB23
		salt marsh, Pegwell Bay	?	carapace	CEB24
		salt marsh, Pegwell Bay	?	carapace	CEB25
		salt marsh, Pegwell Bay	?	carapace	CEB26
		salt marsh, Pegwell Bay	?	carapace	CEB27
		salt marsh, Pegwell Bay	?	carapace	CEB28
		salt marsh, Pegwell Bay	?	carapace	CEB29
		salt marsh, Pegwell Bay	?	carapace	CEB30
*	<i>Cythere lutea</i>	rock pool, Foreness Point	male	carapace	CEB31
		rock pool, Foreness Point	male	carapace	CEB32
		rock pool, Foreness Point	male	carapace	CEB33
		Blue Anchor, Severn Estuary	female	carapace	CEB34
		Blue Anchor, Severn Estuary	male	carapace	CEB35
		Blue Anchor, Severn Estuary	female	single valve	CEB36
		rock pool, Foreness Point	male	carapace	CEB37
		rock pool, Foreness Point	female	carapace	CEB38
		rock pool, Foreness Point	female	carapace	CEB39
		rock pool, Foreness Point	female	carapace	CEB40
		rock pool, Foreness Point	male	carapace	CEB41
		rock pool, Foreness Point	male	carapace	CEB42
*	<i>Eucypris virens</i>	temporary pond, Flatford Mill	female	single valve	CEB43
		temporary pond, Flatford Mill	female	single valve	CEB44
*	<i>Fabaeformiscandona japonica</i>	Lake Biwa, Japan	female	carapace	CEB45
		Lake Biwa, Japan	female	carapace	CEB46
		Lake Biwa, Japan	female	carapace	CEB47
		Lake Biwa, Japan	female	carapace	CEB48
*	<i>Hemicythere villosa</i>	Blue Anchor, Severn Estuary	male	carapace	CEB49
		Blue Anchor, Severn Estuary	female	carapace	CEB50
		Blue Anchor, Severn Estuary	male	carapace	CEB51
		Blue Anchor, Severn Estuary	female	carapace	CEB52
	<i>Heterocythereis albomaculata</i>	rock pool, Foreness Point	male	carapace	CEB53
		Porlock, Severn Estuary	male	carapace	CEB54
		Porlock, Severn Estuary	female	carapace	CEB55
	<i>Hirshmannia viridis</i>	rock pool, Foreness Point	female	carapace	CEB56
*	<i>Pseudocandona sucki</i>	River Stour, Flatford Mill	?	carapace	CEB57
		River Stour, Flatford Mill	?	single valve	CEB58

Appendix 5. Specimen numbers of Recent ostracods used in Chapters 6 and 7. Fig. refers to specimens that are figured in Chapters 6 and 7, highlighted with a star.

Chapter 7

Form.	Sample	Fossil	Ca	Mg	Fe	O	Mn	Analysed Area & Cement
A	EK 9601	<i>Cavellina</i> sp.	15.0	17.3	36.7	31.0	0	carapace: FD
			36.9	16.7	15.5	30.9	trace	carapace fill: FD
			2.9	1.8	65.8	29.5	0	iron oxide in sediment
A	field s 13	<i>Carbonita</i> sp.	39.2	17.7	12.2	30.9	0	carapace: FD
			38.3	16.0	15.4	30.3	0	carapace fill: FD
		pisoliths	37.6	16.4	11.6	34.4	0	FD
			0.9	11.8	61.1	26.2	0	iron oxide in sediment
		ooliths	18.4	8.7	9.2	63.7	0	FD
			3.1	7.4	25.6	63.9	0	sediment: FD
Pit	SE 8874	<i>Naiadites</i>	39.7	15.4	14.7	30.2	0	shells: FD
Pit	SE 8821	<i>Lithostrotion junceum</i>	41.8	14.9	13.1	30.2	0	shells: FD
Pit	SE 8751	aff. <i>Shemonaella</i>	3.8	4.5	74.2	16.5	1%	carapace fill, sed.: FD, iron oxide
			3.5	7.4	79.9	8.2	1%	iron oxide on shells
SC	SE 8538 A	<i>Carbonita</i> cf. <i>fabulina</i>	1.6	5.6	49.8	43.1	0	iron oxide on shells
			1.74	4.6	44.52	49.1	trace	carapace fill: FD
			44.5	0	2.3	53.2	0	carapace fill: iron oxide
SC	SE 8526	<i>Shemonaella siveteri</i> n. sp.	57.1	2.4	11.9	27.6	1%	carapace: FD
			22.6	3.2	49.1	25.1	0	iron oxide on shells
			22.7	11	38.4	27.9	0	carapace fill: FD
			6.5	6.7	62	24.8	0	iron oxide in sediment
SC	SE 8474	<i>Cavellina</i> sp.	69.9	0.2	0.8	29.1	0	carapace: calcite
			40.4	12.5	15.8	31.3	0	carapace fill: FD
		macrofossils indet.	64.3	2.8	3.4	29.5	0	shells: FD
			65.8	3.1	2.0	29.1	0	sediment: FD
SC	SE 8413 A	<i>Carbonita</i> cf. <i>inflata</i>	3.3	5.0	45.1	46.6	trace	carapace: FD
			23.8	9.0	10.7	56.5	0	carapace fill: FD
			2.52	1.51	48.9	44.2	2.9%	iron oxide on shells
SC	SE 8412	<i>Paraparchites circularis</i> n. sp.	41.9	12.8	15.5	29.8	0	carapace: FD
			42.7	11.6	16	29.7	trace	carapace fill: FD
			6.5	3.6	64.4	25.5	trace	carapace fill, in sed.: iron oxide
SC	SE 8411	<i>Paraparchites circularis</i> n. sp.	35.3	12.2	23.2	28.3	1%	carapace: FD
			19.2	8.3	45.3	26.2	1%	iron oxide on shells
SC	SE 8373	<i>Paraparchites circularis</i> n. sp.	59.7	1.4	7.4	31.5	0	shells: FD
			47.9	6.4	15	30.7	0	carapace fill: FD
			11.4	6.8	53.2	28.6	trace	carapace fill, in sed.: iron oxide
			10.8	4.5	54.7	26.9	3.1	iron oxide in sediment
SC	6E 6669	ostracods indet.	71.5	0	0	28.5	0	carapace: calcite
P	EN 5329	<i>Polycopse elegans</i> n. sp.	44.7	21.3	13.7	19.3	1%	carapace: FD
			49.2	21.8	13.3	16.7	1%	carapace fill: FD
P	EN 5250	multiple ostracod species	71.1	0.3	0	28.6	0	carapace: calcite
			63.9	0	3.7	32.4	0	carapace fill: FC
P	EN 4885	multiple ostracod species	70.5	0.8	0	28.7	trace	carapace: calcite
		macrofossils indet.	70.1	0.6	0.5	28.8	0	shells: calcite
P	EN 4885 A	<i>Cavellina valida</i>	40.3	0.6	0	59.1	0	carapace: calcite
			43.3	0.5	2.1	54.0	0	carapace fill: FC
P	EN 4818	multiple ostracod species	70.6	0.8	0	28.6	0	carapace: calcite

Appendix 6. Summary of SEM semi-quantitative data for fossil bearing thin sections. Values are reported in weight percentage, trace quantities of elements such as Al and Si are included in the oxygen percentage. The values are the mean of the total analysis of that cement in the thin section. Abbreviations used: Form.; Formation, A; Anstruther, Pit; Pittenweem, SC; Sandy Craig, P; Pathhead, FD; ferroan dolomite, FC; ferroan calcite.

Bibliography

- Aladin, N.V. & Potts, W.T.W. 1996. The osmoregulatory capacity of the Ostracoda. *Journal of Comparative Physiology B*, **166**, 215-222.
- Anderson, F.W. 1970. Carboniferous ostracoda the genus *Carbonita* Strand. *Bulletin of the Geological Survey of Great Britain*, **32**, 69-121.
- Anderson, L.I., Dunlop, J.A., Eagar, R.M.C., Horrocks, C A. & Wilson, H.M. 1999. Soft-bodied fossils from the roof shales of the Wigan Four Foot coal seam, Westoughton, Lancashire, UK. *Geological Magazine*, **135**, 321-329.
- Andrews, J.E., Turner, M.S., Nabi, G. & Spiro, B. 1991. The anatomy of an early Dinantian terraced floodplain: palaeo-environment and early diagenesis. *Sedimentology*, **38**, 271-287.
- Archer, A.W. & Maples, C.G. 1984. Trace-fossil distribution across a marine-to-nonmarine gradient in the Pennsylvanian of southwestern Indiana. *Journal of Paleontology*, **58**, 448-466.
- Athersuch, J., Gooday, A.J., Pollard, J.E. & Riley, N.J. 2009. Carboniferous. In: J.E. Whittaker & M.B. Hart (eds) *Ostracods in British Stratigraphy*. The Micropalaeontological Society Special Publications. The Geological Society, London, 111-153.
- Ballèvre, M. & Lardeux, H. 2005. Signification paléoécologique et paléogéographique des bivalves du Carbonifère inférieur du bassin d'Ancenis (Massif armoricain). *Paléontologie systématique*, **4**, 109-121.

- Barnett, A.J., Burgess, P.M. & Wright, V.P. 2002. Icehouse world sea-level behaviour and resulting stratal patterns in the late Viséan (Mississippian) carbonate platforms: integration of numerical forward modelling and outcrop studies. *Basin Research*, **14**, 417-438.
- Bartram, K.M., Jeram, A.J. & Selden, P.A. 1987. Arthropod cuticles in coal. *Journal of the Geological Society, London*, **144**, 513-517.
- Bate, R.H. & East, B.A. 1972. The structure of the ostracode carapace. *Lethaia*, **5**, 177-194.
- Bate, R.H. & Sheppard, L.M. 1982. The shell structure of *Halocypris inflata* (Dana, 1849). In: Bate, R.H., Robinson, E. & Sheppard L.M. (eds) *Fossil and Recent Ostracods*. Chichester, UK, Ellis Horwood, 25-50.
- Bateman, R.M., Crane, P.R., DiMichele, W.A., Kenrick, P.R., Rowe, N.P. & Speck, T. 1998. Early evolution of land plants: Phylogeny, Physiology, and Ecology of the Primary Terrestrial Radiation. *Annual Review of Ecological Systems*, **29**, 263-292.
- Batten, R.M. & Grenfell, H.R. 1996. *Botryococcus*. In: J. Jansonius and D.C. McGregor (eds) *Palynology: Principles and Applications*. 1st edition, American Association of Stratigraphic Palynologists Foundation, 205-214.
- Bean, W. 1836. Description and figures of *Unio distortus* Bean, and *Cypris concentrica* Bean, from the Upper Sandstone and shale of Scarborough, and *Cypris arcuata* Bean, from the coal formation of Newcastle. *Magazine of Natural History*, **9**, 376-377.
- Becker, G., Coen, M., Lord, A.L. & Malz, H. 1990. In the footsteps of Griffith and M'Coy or, Lower Carboniferous Ostracods from Ireland and the definition of the genus *Bairdia* M'Coy 1844 (Part 2). *Courier Forschungsinstitut Senckenberg*, **123**, 275-290.

- Becker, G., Claus-Dieter, C. & Klaus, L. 1993. Verkieselte Ostracoden vom Thüringer Ökotyp aus dem Grenzbereich Devon/Karbon des Steinbruchs Drewer (Rheinisches Schiefergebirge). *Courier Forschungsinstitut Senckenberg*, **17**, 1-130.
- Bennett, C.E. 2008. A review of the Carboniferous colonisation of non-marine environments by ostracods. *Senckenbergiana lethaea*, **88**, 37-46.
- Bennison, G.M. 1960. Lower Carboniferous non-marine lamellibranchs from East Fife, Scotland. *Palaeontology*, **3**, 137-152.
- Bennison, G.M. 1961. Small *Naiadites obesus* from the Calciferous Sandstone Series (Lower Carboniferous) of Fife. *Palaeontology*, **4**, 300-311.
- Benson, R.H. 1955. Ostracodes from the type section of the Fern Glen Formation. *Journal of Paleontology*, **29**, 1030-1039.
- Berdan, J. 1984. Leperditicopid Ostracodes from Ordovician rocks of Kentucky and nearby States and characteristic features of the Order Leperditicopida. *United States Geological Survey Professional Paper*, **1066-J**, 1-37.
- Bless, M.J.M. 1983. Late Devonian and Carboniferous ostracode assemblages and their relationship to the depositional environment. *Bulletin de la Société Belge de Géologie*, **92**, 31-53.
- Bless, M.J.M. & Jordan, H. 1970. Stratigraphical and taxonomical remarks on the ostracode genus *Hollinella* Coryell. *Mededelingen Rijks Geologische Dienst*, **21**, 81-91.
- Bless, M.J.M. & Jordan, H. 1970. Classification of palaeocopid ostracodes belonging to the families Ctenoloculinidae, Hollinellidae and Hollinidae. *C. R. Colloque sur la Palaeoecologie des Ostracodes*, 869-890.

- Bless, M.J.M. & Jordan, H. 1971. The new genus *Copelandella* from the Carboniferous - the youngest known beyrichioidean ostracodes. *Lethaia*, **4**, 185-190.
- Bless, M.J.M. & Jordan, H. 1972. Ostracodes of the family Hollinellidae. *Mededelingen Rijks Geologische Dienst, Serie C*, **3**, 8-155.
- Bless, M.J.M. & Massa, D. 1982. Carboniferous Ostracodes in the Rhadames Basin of Western Libya: Palaeoecological implications and comparison with North America, Europe and the USSR. *Revue de l'Institut Français de Pétrole*, **37**, 19-61.
- Bless, M.J.M. & Pollard, J.E. 1973. Paleoecology and Ostracode Faunas of Westphalian Ostracode Bands from Limburg, The Netherlands and Lancashire, Great Britain. *Mededelingen Rijks Geologische Dienst, Nieuwe Serie*, **24**, 21-53.
- Bless, M.J.M. & Pollard, J.E. 1975. Quantitative analysis of dimorphism in *Carbonita humilis* (Jones and Kirkby). *American Bulletin of Paleontology*, **65**, 109-127.
- Bless, M.J.M., Boonen, P., Duser, M. & Soille, P. 1981. Microfossils and depositional environment of Late Dinantian carbonates at Heibaart (Northern Belgium). *Annales de la Société Géologique de Belgique*, **104**, 135-165.
- Bless, M.J.M., Streel, M. & Becker, G. 1988. Distribution and Palaeoenvironment of Devonian to Permian ostracods assemblages in Belgium with reference to some Late Famennian to Permian marine nearshore to "Brackish-Water" assemblages dated by Miospores. *Annales de la Société Géologique de Belgique*, **110**, 347-362.
- Boardman, E.L. 1989. Coal measures (Namurian and Westphalian) Blackband Iron Formations: fossil bog iron ores. *Sedimentology*, **36**, 621-633.

- Boomer, I. & Eisenhauer, G. 2002. Ostracod faunas as palaeoenvironmental indicators in marginal marine environments. In: J.A. Holmes and A.R. Chivas (eds) *The Ostracoda: Applications in Quaternary Research*. Washington, DC, The American Geophysical Union, Geophysical monograph **131**, 135-149.
- Boomer, I., Horne, D.J. & Slipper, I.J. 2003. The use of ostracods in palaeoenvironmental studies, or what can you do with an ostracod shell? *Palaeontological Society Papers*, **9**, 153-179.
- Brand, P.J. 1996. Taxonomy and distribution of the Upper Carboniferous non-marine bivalve *Carbonicola aldamii*. *Palaeontology*, **39**, 407-411.
- Brand, U. 1989. Global Climatic Changes during the Devonian-Mississippian: Stable Isotope Biogeochemistry of Brachiopods. *Palaeogeography, Palaeoclimatology, Palaeoecology (Global Planetary Change Section)*, **75**, 311-329.
- Brand, U. 1994. Continental hydrology and climatology of the Carboniferous Joggins Formation (lower Cumberland Group) at Joggins, Nova Scotia: evidence from the geochemistry of bivalves. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **106**, 307-321.
- Brenchley, P.J., Carden, G.A., Hints, L., Kaljo, D., Marshall, J.D., Martma, T., Meidla, T. & Nolvak, J. 2003. High-resolution stable isotope stratigraphy of Upper Ordovician sequences: Constraints on the timing of bioevents and environmental changes associated with mass extinction and glaciation. *Geological Society of America Bulletin*, **115**, 89-104.

- Brett, C.E. & Baird, G.C. 1986. Comparative Taphonomy: A Key to Palaeoenvironmental Interpretation Based on Fossil Preservation. *Palaios*, **1**, 207-227.
- Browne, M.A.E., Dean, M.T., Hall, I.H.S., McAdam, A.D., Monro, S.K. & Chisholm, J.I. 1999. A lithostratigraphical framework for the Carboniferous rocks of the Midland Valley of Scotland. *BGS research report RR/99/07*.
- Buatois, L.A., Mángano, M.G., Genise, J.F. & Taylor, T.N. 1998. The ichnological record of the invertebrate invasion of non-marine ecosystems: Evolutionary trends in ecospace utilisation, environmental expansion, and behavioral complexity. *Palaios*, **13**, 217-240.
- Buatois, L.A., Gingras, M.K., Maceachern, J., Mángano, M.G., Zonneveld, J.P., Pemberton, S.G., Netto, R.G. & Martin, A. 2005. Colonization of brackish-water systems through time: evidence from the trace-fossil record. *Palaios*, **20**, 321-347.
- Burchette, T.P. & Riding, R. 1977. Attached vermiform gastropods in Carboniferous marginal marine stromatolites and biostromes. *Lethaia*, **10**, 17-28.
- Buschmina, L.S. 1959. Carboniferous ostracods from the Coal Measures of Central Kazakhstan. *Trudy Laboratorii Geologii Uglya Akademii Nauk SSSR*, **9**, 174-252.
- Buschmina, L.S. 1965. Ostracoda from the Abyshev horizon (Lower Carboniferous) of the Kuznetsk Coal Basin. *Stratigrafiya i paleontologiya Paleozoya aziatskoy chasti SSSR*, 64-98.
- Buschmina, L.S. 1968. *Early Carboniferous ostracoda of the Kuznetsk Basin*. Izdatelstvo nauka, Moscow, 1-128.

- Calder, J.H. 1998. The Carboniferous evolution of Nova Scotia. In: D. Blundell J. and A. Scott C. (eds) *Lyell: the Past is the Key to the Present*. 143rd edition, Geological Society, London. Special Publications, 261-302.
- Carbonel, P., Colin, J-P., Danielopol, D., Löffler, H. & Neustrueva, I. 1988. Paleoecology of limnic ostracodes: a review of some major topics. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **62**, 413-416.
- Chivas, A.R., De Decker, P. & Shelley, J.M.G. 1986. Magnesium and strontium in non-marine ostracod shells as indicators of palaeosalinity and palaeotemperature. *Hydrobiologia*, **143**, 135-142.
- Chivas, A.R., De Decker, P. & Shelley, J.M.G. 1986. Magnesium content of non-marine ostracod shells: a new palaeosalinometer and palaeothermometer. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **54**, 43-61.
- Clarkson, E.N.K., Harper, D.A.T. & Hoey, A.N. 1998. Basal Wenlock biofacies from the Girvan district, SW Scotland. *Scottish Journal of Geology*, **34**, 61-71.
- Cliff, S.G. & Trueman, A.E. 1929. The sequence of non-marine lamellibranchs in the Coal Measures of Nottinghamshire and Derbyshire. *Quarterly Journal of the Geological Society*, **1xxxv**, part 1, 77-109.
- Coen, M. 1989. Ostracodes of the Devonian - Carboniferous transition beds of South China. *Bulletin de la Société Belge de Géologie*, **98**, 311-317.
- Coen, M., Michiels, D. & Parisse, E. 1988. Ostracodes dinantiens de l'Ardenne. *Mémoires de l'Institut Géologique de l'Université de Louvain*, **34**, 1-42.

- Coen, M. 1990. Revision of Münster's Carboniferous ostracode species. *Courier Forschungsinstitut Senckenberg*, **123**, 265-273.
- Cole, J.M. & Crittenden, S. 1997. Early Tertiary basin formation and the development of lacustrine and quasi-lacustrine/marine source rocks on the Sunda Shelf of SE Asia. In: A.J. Fraser, S.J. Matthews & R.W. Murphy (eds) *Petroleum geology of Southeast Asia*. 126th edition, The Geological Society, London, Special Publications, 147-183.
- Cooper, C.L. 1946. Pennsylvanian ostracodes of Illinois. *Bulletin of the Illinois State Geological Survey*, **70**, 1-177.
- Coryell, H.N. 1928. Some new Pennsylvanian ostracodes. *Journal of Paleontology*, **2**, 87–94.
- Coryell, H.N. & Booth, R.T. 1933. Pennsylvanian Ostracoda: a continuation of the study of the Ostracoda from the Wayland Shale, Graham, Texas. *The American Midland Naturalist*, **14**, 258–279.
- Crasquin, S. 1985. Zonation par les ostracodes dans le Mississippien de l'ouest Canadien. *Revue de Paléobiologie*, **4**, 43-52.
- Crawford, T.L. 1995. Carbonates and associated sedimentary rocks of the Upper Viséan to Namurian Mabou Group, Cape Breton Island, Nova Scotia: evidence for lacustrine deposition. *Atlantic Geology*, **31**, 167-182.
- Cressey, R. & Boxshall, G. 1989. *Kabatarina pattersoni*, a fossil parasitic copepod (Dichelesthidae) from a Lower Carboniferous fish. *Micropaleontology*, **35**, 150-167.
- Cressey, R. & Patterson, C. 1973. Fossil Parasitic Copepods from a Lower Cretaceous Fish. *Science*, **180**, 1283-1285.

- Cronin, T.M., Dwyer, G.S., Kamiya, T., Schwede, S. & Willard, D.A. 2003. Medieval Warm Period, Little Ice Age and 20th century temperature variability from Chesapeake Bay. *Global and Planetary Change*, **36**, 17-29.
- Cronin, T.M., Thurnell, R., Dwyer, G.S., Saenger, C., Mann, M.E. & Vann, C. 2005. Multiproxy evidence of Holocene climate variability from estuarine sediments, eastern North America. *Palaeoceanography*, **20**, 1-21.
- Daeschler, E.B. 2000. An early actinopterygian fish from the Catskill Formation (Late Devonian, Famennian) in Pennsylvania, U.S.A. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **150**, 181-192.
- Danielopol, D.L., Ito, E., Wansard, G., Kamiya, T., Cronin, T.M. & Baltanas, A. 2002. Techniques for the study and collection of ostracoda. In: Holmes, J.A. & Chivas, A.R. (eds) *The Ostracoda: Applications in Quaternary Research*. Washington, DC, The American Geophysical Union, Geophysical Monograph, **131**, 65-97.
- Davaud, E. & Girardclos, S. 2001. Recent freshwater ooids and oncoids from western Lake Geneva (Switzerland): indications of a common organically mediated origin. *Journal of Sedimentary Research*, **71**, 423-429.
- De Decker, P. 2002. Ostracod palaeoecology. In: Holmes, J.A. & Chivas, A.R. (eds) *The Ostracoda: Applications in Quaternary Research*. Washington, DC, The American Geophysical Union, Geophysical Monograph **131**, 121-134.
- De Decker, P., Chivas, A.R. & Shelley, J.M.G. 1999. Uptake of Mg and Sr in the euryhaline ostracod *Cyprideis* determined from in vitro experiments. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **148**, 105-116.

- Dean, M.T. & Turner, N. 1995. Conodont Colour Alteration Index (CAI) values for the Carboniferous of Scotland. *Transactions of the Royal Society of Edinburgh Earth Sciences*, **85**, 211-220.
- Delo, D.M. 1930. Some Upper Carboniferous Ostracoda from the shale basin of western Texas. *Journal of Paleontology*, **4**, 152-178.
- Dennell, R. 1960. Chapter 14, Integument and Exoskeleton. In: T.H. Waterman (ed.) *The physiology of Crustacea I. Metabolism and Growth*. New York, London, Academic Press, 449-472.
- Dépêche, F. 1982. Ultrastructure of the wall of two living ostracods, *Herpetocypris chevreuxi* (Sars) and *Pontocythere elongata* (Brady), in comparison with fossil ostracods from the Middle Jurassic of Normandy. In: Bate, R.H., Robinson, E. & Sheppard, L.M. (eds) *Fossil and Recent Ostracoda*. Chichester, UK, Ellis Horwood, 61-74.
- Dewey, C.P. 1983. Ostracode palaeoecology of the Lower Carboniferous of Western Newfoundland. In: R. F. Maddocks (ed.) *Applications of Ostracoda*. University of Houston Geosciences, 104-115.
- Dewey, C.P. 1985. The palaeobiogeographic significance of lower carboniferous crustaceans (ostracodes and peracarids) from Western Newfoundland and Central Nova Scotia, Canada. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **49**, 175-188.
- Dewey, C.P. 1987. Palaeoecology of a hypersaline Carboniferous ostracod fauna. *Journal of Micropalaeontology*, **6**, 29-33.

- Dewey, C.P. 1988. Lower Carboniferous ostracodes from the Maritimes Basin of eastern Canada: A review. *Atlantic Geology*, **25**, 63-71.
- Dewey, C.P. 1992. A revision of "some ostracodes from the Pennington Formation of Alabama" (Ehrlich, 1964). *Geological Society of Alabama*, **163**, 1-15.
- Dewey, C.P. 1993. Palaeoecology of ostracodes from a Lower Carboniferous chemosynthetic community. In: McKenzie, K.G. & Jones, P.J. (eds) *Ostracoda in the Earth and Life Sciences*. Proceedings of the 11th International Symposium on Ostracoda, Warrnambool, Victoria, Australia, 1991, Rotterdam, Brookfield, A. A. Balkema, 77-89.
- Dewey, C.P. & Fåhræus, L.E. 1987. Taxonomy of Ostracoda (Crustacea) from Mississippian Strata of Maritime Canada. *Geologica et Palaeontologica*, **21**, 93-135.
- Dewey, C.P. & Puckett, T.M. 1993. Ostracodes as a tool for understanding the distribution of shelf-related environments in the Chesterian strata of the Black Warrior Basin in Alabama. In: J.C. Pashin (ed) *New Perspectives on the Mississippian System of Alabama*. A guidebook for the 30th annual field trip of the Alabama Geological Society, 61-68.
- Dewey, C.P., Puckett, T.M. & Devery, H.B. 1990. Palaeogeographical significance of ostracod biofacies from Mississippian strata of the Black Warrior Basin, northwestern Alabama: a preliminary report. In: R. Whatley & C. Maybury (eds) *Ostracoda and Global Events*. The British Micropalaeontological Society, Chapman and Hall, 527-540.

- Dineley, D.L. & Metcalf, S.J. 1999. British Carboniferous fossil fishes sites. In: D. Palmer (ed) *Fossil Fishes of Great Britain*. The Geological Conservation Review Series, Peterborough, UK, Joint Nature Conservation Committee, 265-312.
- Dojiri, M. & Cressey, R.F. 1987. Revision of the Taeniacanthidae (Copepoda: Poecilostomatoida) Parasitic on Fishes and Sea Urchins. *Smithsonian Contributions to Zoology*, **447**, 1-250.
- Dwyer, G.S., Cronin, T.M. & Baker, P.A. 2002. Trace Elements in Marine Ostracodes. In: J.A. Holmes & A.R. Chivas (eds) *The Ostracoda: Applications in Quaternary Research.*, Washington, DC, The American Geophysical Union, Geophysical Monograph **131**, 205-225.
- Dwyer, G.S., Cronin, T.S., Baker, P.A., Raymo, M.E., Buzas, J.S. & Corrège, T. 1995. North Atlantic deepwater temperature change during late Pliocene and late Quaternary climatic cycles. *Science*, **270**, 1347-1351.
- Eagar, R.M.C. & Belt, E.S. 2003. Succession, palaeoecology, evolution, and speciation of Pennsylvanian non-marine bivalves, Northern Appalachian Basin, USA. *Geological Journal*, **38**, 109-143.
- Eagar, R.M.C. & Peirce, H.W. 1993. A nonmarine Pelecypod assemblage in the Pennsylvanian of Arizona and its correlation with a horizon in Pennsylvania. *Journal of Paleontology*, **67**, 61-70.
- Egorov, V.G. 1950. *Ostracodes from the Frasnian of the Russian Platform, I, Kloedenillidae*. Moscow-Leningrad, VNIGRI.

- Falcon-Lang, H.J. 2005. Small cordaitalean trees in a marine-influenced coastal habitat in the Pennsylvanian Joggins Formation, Nova Scotia. *Journal of the Geological Society, London*, **162**, 485-500.
- Falcon-Lang, H.J., Benton, M.J., Braddy, S.J. & Davies, S.J. 2006. The Pennsylvanian tropical biome reconstructed from the Joggins Formation of Nova Scotia, Canada. *Journal of the Geological Society, London*, **163**, 1-16.
- Ferguson, L. 1962. The paleoecology of a Lower Carboniferous marine transgression. *Journal of Paleontology*, **36**, 1090-1107.
- Ferguson, L. 1963. The Paleocology of *Lingula squariformis* Phillips during a Scottish Mississippian marine transgression. *Journal of Paleontology*, **37**, 669-681.
- Fielding, C.R., Frank, T.D. & Isbell, J.L. 2008. The late Paleozoic ice age - A review of current understanding and synthesis of global climate patterns. *The Geological Society of America Special Paper*, **441**, 343-354.
- Floyd, J.D. & Williams, M. 2003. A revised correlation of Silurian rocks in the Girvan district, SW Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **93**, 383-392.
- Forsyth, I.H. & Chisholm, M.A. 1977. *The Geology of East Fife*. Natural Environment Research Council, Institute of Geological Sciences, Scotland, Memoirs of the Geological Survey of Great Britain.
- Frenzel, P. & Boomer, I. 2005. The Use of ostracods from marginal marine, brackish waters as bioindicators of modern and Quaternary environmental change. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **225**, 68-92.

- Freytet, P. & Verrecchia, E.P. 1998. Freshwater organisms that build stromatolites: a synopsis of biocrystallization by prokaryotic and eukaryotic algae. *Sedimentology*, **45**, 535-563.
- Freytet, P., Broutin, J. & Durand, M. 2000. Distribution and palaeoecology of freshwater algae and stromatolites: III, some new forms from the Carboniferous, Permian and Triassic of France and Spain. *Annals de Paléontology*, **86**, 195-241.
- Friedman, G.M. & Lundin, R.F. 1998. Freshwater Ostracodes from Upper Middle Devonian fluvial facies, Catskill Mountains, New York. *Journal of Palaeontology*, **72**, 485-490.
- Friend, P.F. & Moody-Stuart, M. 1970. Carbonate deposition on the river floodplains of the Wood Bay Formation (Devonian) of Spitzbergen. *Geological Magazine*, **107**, 181-195.
- Goodarzi, F. 1984. Chitinous fragments in coal. *Fuel*, **63**, 1504-1506.
- Gray, J. 1988. Evolution of the freshwater ecosystem: the fossil record. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **62**, 1-214.
- Grenfell, H.R. 1995. Probable fossil zygomatacean algal spore genera. *Review of Palaeobotany and Palynology*, **84**, 201-220.
- Guirdham, C., Andrews, J.E., Browne, M.A.E. & Dean, M.T. 2003. Stratigraphic and palaeoenvironmental significance of microbial carbonates in the Asbian Sandy Craig Formation of Fife. *Scottish Journal of Geology*, **39**, 151-168.
- Halstead, L.B. 1985. The vertebrate invasion of freshwater. *Philosophical transactions of the Royal Society of London, B*, **309**, 243-258.

- Harlton, B.H. 1933. Micropaleontology of the Pennsylvanian Johns Valley Shale of the Ouachita Mountains, Oklahoma, and its relationship to the Mississippian Caney Shale. *Journal of Paleontology*, **7**, 3-29.
- Hartley, A.J. 1993. A depositional model for the Mid-Westphalian A to late Westphalian B Coal Measures of South Wales. *Journal of the Geological Society, London*, **150**, 1121-1136.
- Hebert, B.L. & Calder, J.H. 2004. On the discovery of a unique terrestrial faunal assemblage in the classic Pennsylvanian section at Joggins, Nova Scotia. *Canadian Journal of Earth Sciences*, **41**, 247-254.
- Heckel, P.H. & Clayton, G. 2006. The Carboniferous System. Use of the new official names for the subsystems, series, and stages. *Geological Acta*, **4**, 403-407.
- Henningsmoen, G. 1953. Classification of Paleozoic straight-hinged ostracods. *Norsk Geologisk Tidsskrift*, **31**, 185–288.
- Hibbert, S. 1834. On the freshwater limestones of Burdiehouse in the neighbourhood of Edinburgh, belonging to the Carboniferous Group of rocks. With supplementary notes on freshwater limestones. *Transactions of the Royal Society of Edinburgh*, **13**, 169-241.
- Hmich, D., Schneider, J.W., Saber, H., Voight, S. & El Wartiti, M. 2006. New continental Carboniferous and Permian faunas of Morocco: implications for biostratigraphy, palaeobiogeography and palaeoclimate. In: Lucas, S.G., Cassinis, G. & Schneider, J.W. (eds) *Non-marine Permian biostratigraphy and biochronology*. 265th edition, The Geological Society, London, Special Publications, 297-324.

- Holland, W.C. 1934. The ostracodes of the Nineveh Limestone of Pennsylvania and West Virginia. *Annals of Carnegie Museum*, **22**, 343-50.
- Holmes, J.A. & Chivas, A.R. 2002. Ostracod Shell Chemistry - Overview. In: Holmes, J.A. & Chivas, A.R. (eds) *The Ostracoda: Applications in Quaternary Research*. Washington, DC, The American Geophysical Union, Geophysical Monograph **131**, 185-204.
- Horne, D.J. 2003. Key Events in the Ecological Radiation of the Ostracoda. *Palaeontological Society Papers*, **9**, 181-201.
- Horne, D.J., Cohen, A. & Martens, K. 2002. Taxonomy, Morphology and Biology of Quaternary and Living Ostracoda. *The Ostracoda: Applications in Quaternary Research*. Washington, DC, The American Geophysical Union, Geophysical Monograph **131**, 5-36.
- Horne, D.J., Smith, R.J., Whittaker, J.E. & Murray, J.W. 2004. The first British record and a new species of the superfamily Terrestricytheroidea (Crustacea, Ostracoda): morphology, ontogeny, lifestyle and phylogeny. *Zoological Journal of the Linnean Society*, **142**, 253-288.
- Ito, E. 2001. Application of stable isotope techniques to inorganic and biogenic carbonates. In: Last, W.M. & Smol, J.P. (eds) *Tracking Environmental Change Using Lake Sediments*. Volume 2, Physical and Geochemical Methods, Dordrecht, The Netherlands, Boston Kluwer Academic Publishers, 351-371.
- Jenkins, T.B.H. 1960. Non-marine lamellibranch assemblages from the Coal Measures (Upper Carboniferous) of Pembrokeshire West Wales. *Palaeontology*, **3**, 104-123.

- Jin, Z., Bickle, M., Chapman, H., Yu, J., Greaves, M., Wang, S. & Chen, S. 2006. An experimental evaluation of cleaning methods for fossil ostracod Mg/Ca and Sr/Ca determination. *Journal of Paleolimnology*, **36**, 211-218.
- Johnson, W.R. 1936. The ostracods of the Missouri series in Nebraska. *Nebraska Geological Survey Paper*, **11**, 1-52.
- Jones, P.J. 1989. Lower Carboniferous Ostracoda (Beyrichicopida and Kirkbyocopa) from the Bonaparte Basin, northwestern Australia. *Department of Primary Industries and Energy Bureau of Mineral Resources, Geology and Geophysics, bulletin* **228**, 1.
- Jones, P.J. & Chen, P.J. 2000. Carboniferous and Permian Leaiioidea (Branchiopoda: Conchostraca) from Australia: Taxonomic revision and biostratigraphic implications. *Records of the Australian Museum*, **52**, 223-244.
- Jones, T.R. 1855. Notes on Palaeozoic Bivalved Entomostraca, No II. Some British and foreign species of *Beyrichia*. *Annals and Magazine of Natural History, London*, **2**, 163-176.
- Jones, T.R. 1870. On some Bivalved Entomostraca from the Coal-measures of South Wales. *Geological Magazine*, **7**, 214-220.
- Jones, T.R. & Kirkby, J.W. 1865. Notes on Palaeozoic Bivalved Entomostraca, No. V. Münster's species from the Carboniferous Limestone. *The Annals and Magazine of Natural History, London*, series 3, **15**, 404-410.
- Jones, T.R. & Kirkby, J.W. 1867. On the Entomostraca of the Carboniferous rocks of Scotland. *Transactions of the Geological Society of Glasgow*, **2**, 213-228.

- Jones, T.R. & Kirkby, J.W. 1879 a. Description of the species of the ostracodous genus *Bairdia* McCoy, from the Carboniferous strata of Great Britain. *Quarterly Journal of the Geological Society, London*, **35**, 565-581.
- Jones, T.R. & Kirkby, J.W. 1879 b. Notes on Palaeozoic Bivalved Entomostraca, No. XII. Some Carboniferous species belonging to the genus *Carbonia*, Jones. *The Annals and Magazine of Natural History, London*, series 5, **4**, 28-40.
- Jones, T.R. & Kirkby, J.W. 1880. On the zones of marine fossils in the Calciferous Sandstone Series of Fife. *Quarterly Journal of the Geological Society, London*, **36**, 559-590.
- Jones, T.R. & Kirkby, J.W. March 1885. Notes on Palaeozoic Bivalved Entomostraca, No. XIX. On some Carboniferous Species of the Ostracodous genus *Kirkbya*, Jones. *The Annals and Magazine of Natural History, London*, series 5, **15**, 174-190.
- Jones, T.R. & Kirkby, J.W. Oct 1886. Notes on Palaeozoic Bivalved Entomostraca, No. XXII. On some undescribed species of British Carboniferous Ostracoda. *The Annals and Magazine of Natural History, London*, series 5, **18**, 249-269.
- Jones, T.R. & Kirkby, J.W. 1890. On the Ostracoda found in the shales of the Upper Coal-Measures at Slade Lane, near Manchester. *Transactions of the Manchester Geological Society*, part 3, **21**, 137-142.
- Jones, T.R. & Kirkby, J.W. 1895. Notes on Palaeozoic Bivalved Entomostraca, No. XXXII. Some Carboniferous Ostracoda from Yorkshire. *The Annals and Magazine of Natural History, London*, series 6, **16**, 452-460.

- Jones, T.R., Kirkby, J.W. & Brady, G.S. 1884. A Monograph of the British Fossil Bivalved Entomostraca from the Carboniferous Formations. Part 1, number 1. The Cypridinidae and their allies. *The Palaeontographical Society*, 1 - 56.
- Jones, T.R., Kirkby, J.W. & Brady, G.S. 1884. A Monograph of the British Fossil Bivalved Entomostraca from the Carboniferous Formations. Part 1, number 2. The Cypridinidae and their allies. *The Palaeontographical Society*, 57-92.
- Kassi, A.M., Weir, J.A., McManus, J. & Browne, M.A.E. 2004. Lithofacies and Sedimentary cycles within the Late Dinantian (late Brigantian) of Fife and East Lothian: is a sequence stratigraphical approach valid? *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **94**, 95-113.
- Kassi, A.M., Weir, J.A., Browne, M.A.E. & McManus, J. 1998. The stratigraphy and depositional context of a temporary exposure in the Anstruther Formation (Strathclyde Group), Anstruther Wester, Fife. *Scottish Journal of Geology*, **34**, 127-32.
- Keatings, K.W., Heaton, T.H.E. & Holmes, J.A. 2002. The effects of diagenesis on the trace element and stable isotope geochemistry of non-marine ostracod valves. *Journal of Paleolimnology*, **28**, 245-252.
- Keatings, K.W., Holmes, J.A. & Heaton, T.H.E. 2006. Effects of pre-treatment on ostracod valve chemistry. *Chemical Geology*, **235**, 250-261.
- Keen, M.C. 1977. Ostracod assemblages and the depositional environments of the Headon, Osborne, and Bembridge Beds (Upper Eocene) of the Hampshire Basin. *Palaeontology*, **20**, 405-445.

- Kellett, B. 1929. The ostracode genus *Hollinella*, expansion of the genus and description of some Carboniferous species. *Journal of Paleontology*, **3**, 196-217.
- Kellett, B. 1936. Carboniferous ostracods. *Journal of Paleontology*, **10**, 769-784.
- Keyser, D. 1990. Morphological changes and the function of the inner lamella layer of podocopid Ostracoda. In: Whatley, R. & Maybury, C. (eds) *Ostracoda and Global Events*. The British Micropalaeontological Society, Chapman and Hall, 399-410.
- Keyser, D. 1995. Structural elements on the surface of ostracod carapaces. In: J. Riha (ed) *Ostracoda and biostratigraphy*. Rotterdam, A. A. Balkema, 5-10.
- Knox, L.W. & Gordon, E.A. 1999. Ostracodes as indicators of brackish water environments in the Catskill Magnafacies (Devonian) of New York State. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **148**, 9-22.
- Kornicker, L.S. 1969. Relationship between the free and attached margins of the myodocopid ostracod shell. In: J.W. Neale (ed) *The taxonomy, morphology and ecology of Recent Ostracoda*. Edinburgh, Oliver and Boyd, 109-135.
- Kummerow, E. 1939. Die Ostrakoden und Phyllopoden des deutschen Unterkarbons. *Abhandu der PreuBischen Geologischen Landesanstalt, Berlin. Neue Folge, Heft 194*, **4**, 1-107.
- Kummerow, E. 1949. Über einige Süßwasser-Ostracoden des Ruhrkohlen-gebietes. *Sonderdruck aus dem Neuen Jahrbuch fuer Mineralogie, Geologie und Palaeontologie, Monatshefte*, **B**, 45-59.
- Kummerow, E. 1953. Über oberkarbonische und devonische Ostracoden in Deutschland und in der Volksrepublik Polen. *Beiheft zur Zeitschrift Geologie*, **7**, 3-75.

- Latham, M.H. 1932-33. Scottish Carboniferous Ostracoda. *Transactions of the Royal Society of Edinburgh*, **LVII**, 351-395.
- Lethiers, F. 1981. Ostracodes du Dévonien terminal de l'Ouest du Canada: systématique, biostratigraphie et paléoécologie *Geobios mémoire spécial*, **5**, 234p.
- Lethiers, F. & Damotte, R. 1993. La grande dispersion des espèces d'ostracodes (crustacea) d'eau douce à la fin de l'ère primaire. *Comptes rendus de l'Académie des sciences. Série 2, Mécanique, Physique, Chimie, Sciences de l'univers, Sciences de la Terre*, **316**, 427-433.
- Logan, B.W., Rezak, R. & Ginsburg, R.N. 1964. Classification and environmental significance of algal stromatolites. *Journal of Geology*, **72**, 68-83.
- Lundin, R.F. 1987. On *Glyptolichvinella spiralis* Jones & Kirkby. *Stereo Atlas of Ostracod Shells*, **14**, 139.
- MacNeil, A.J. & Jones, B. 2006. Palustrine deposits on a Late Devonian coastal plain - sedimentary attributes and implications for concepts of carbonate sequence stratigraphy. *Journal of Sedimentary Research*, **76**, 292-309.
- Maples, C.G. & Archer, A.W. 1989. The potential of Palaeozoic nonmarine trace fossils for paleoecological interpretations. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **73**, 185-195.
- Marshall, D.J. 1988. *Cathodoluminescence of geological materials*. London, Unwin Hyman, 146pp.
- Mauchline, J. 1998. The biology of Calanoid Copepods. In: Blaxter, J.H.S., Southward A.J. & Tyler, P.A. (eds) *Advances in Marine Biology*, **33**, 1-710.

- McCoy, F. 1844. *A synopsis of the characters of the Carboniferous Limestone fossils of Ireland*. Dublin, University Press, 207pp.
- Medeanic, S. 2006. Freshwater algal palynomorph records from Holocene deposits in the coastal plain of Rio Grande do Sul, Brazil. *Review of Palaeobotany and Palynology*, **141**, 83-101.
- Miller, M.F. & Labandeira, C.C. 2002. Slow crawl across the salinity divide: delayed colonisation of freshwater ecosystems by invertebrates. *GSA today*, **12**, 4-10.
- Mischke, S., Zhang, C. & Börner, A. 2008. Bias of ostracod stable isotope data caused by drying of sieve residues from water. *Journal of Paleolimnology*, **40**, 567-575.
- Monaghan, A.A. & Parrish, R.R. 2005. Geochronology of Carboniferous-Permian magmatism in the Midland Valley of Scotland: implications for regional tectonomagmatic evolution and the numerical time scale. *Journal of the Geological Society, London*, **162**, 1-15.
- Moore, R.C. 1929. *Basslerina*, a new holliniform ostracode genus, with description of new Pennsylvanian species from Texas and Oklahoma. *Davison University Science Laboratory Journal*, **24**, 97-113.
- Moore, R.C. (ed) *Treatise on Invertebrate Paleontology, Pt. Q, Arthropoda 3. Part Q*, Arthropoda 3, Lawrence, Kansas, USA, Geological Society of America and University of Kansas Press.
- Müller, G.W. 1894. Die ostracoden des Golfs von Neapel und der angrenzenden Meeresabschitte. *Fauna und Flora Neapel, Monograph*, **21**, 404.

- Münster, G. 1830. On some fossil species of *Cypris* and *Cythere*. *Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde*, **1**, 60-67.
- Neale, J. 1984. The Ostracoda and uniformitarianism: II. The earlier record: Cretaceous to Cambrian. *Proceedings of the Yorkshire Geological Society*, **44**, 443-478.
- Neville, A.C. 1975. Chapter 2, General structure of integument. *Biology of the arthropod cuticle*. Zoophysiology and Ecology 4/5 edition, Springer-Verlag, 7-60.
- Newman, W.A. 2005. Origin of the Ostracoda and their maxillopodan and hexapodan affinities. *Hydrobiologia*, **538**, 1-21.
- Nye, E., Feist-Burkhardt, S., Horne, D.J., Ross, A.J. & Whittaker, J.E. 2008. The palaeoenvironment associated with a partial *Iguanodon* skeleton from the Upper Weald Clay (Barremian, Early Carboniferous) at Smokejacks Brickworks (Ockley, Surrey, UK), based on palynomorphs and ostracods. *Cretaceous Research*, **29**, 417-444.
- Okada, Y. 1981. Development of cell arrangement in ostracod carapaces. *Paleobiology*, **7**, 276-280.
- Okada, Y. 1982. Structure and cuticle formation of the reticulated carapace of the ostracode *Bicornucythere bisanensis*. *Lethaia*, **15**, 85-101.
- Olempska, E. 1993. An ostracod assemblage from late Visean shales of the Cracow area. *Acta Palaeontologica Polonica*, **38**, 93-107.
- Orr, P.J. & Briggs, D.E.G. 1999. Exceptionally preserved conchostracans and other crustaceans from the Upper Carboniferous of Ireland. *Special Papers in Palaeontology*, **62**, 1-68.

- Owens, B., McLean, D., Simpson, K.R.M., Shell, P.M.J. & Robinson, R. 2005. Reappraisal of the Mississippian palynostratigraphy of the east Fife coast, Scotland, United Kingdom. *Palynology*, **29**, 23-47.
- Park, L.E. & Gierlowski-Kordesch, E.H. 2007. Paleozoic lake faunas: Establishing aquatic life on land. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **249**, 160-179.
- Pearson, P.N. & Burgess, C.E. 2008. Foraminifer test preservation and diagenesis: comparison of high latitude Eocene sites. *Geological Society, London, Special Publications*, **303**, 59-72.
- Pearson, P.N., Ditchfield, P.W., Singano, J., Harcourt-Brown, K.G., Nicholas, C.J., Olsson, R.K., Shackleton, N.J. & Hall, M.A. 2001. Warm tropical sea surface temperatures in the Late Cretaceous and Eocene epochs. *Nature*, **413**, 481-487.
- Perrier, V., Vannier, J. & Siveter, D.J. 2007. The Silurian pelagic myodocope ostracod *Richteria migrans*. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, **98**, 151-163.
- Peryt, T.M. 1983. Classification of coated grains. In: T.M. Peryt (ed) *Coated Grains*. Berlin, Springer-Verlag, 3-6.
- Pollard, J.E. 1966. A non-marine ostracod fauna from the coal measures of Durham and Northumberland. *Palaeontology*, **9**, 667-697.
- Pollard, J.E. 1969. Three ostracod-mussel bands in the Coal Measures (Westphalian) of Northumberland and Durham. *Proceedings of the Yorkshire Geological Society*, **37**, 239-276.

- Pollard, J.E. 1985. Coprolites and ostracods from the Dinantian of Foulden, Berwickshire, Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **76**, 49-51.
- Posner 1966. On the sexual features of dimorphism in the representatives of the genera *Lichvinella* and *Glyptolichvinella* from the Early Carboniferous of Volhynia and Podolia. In: Gurevich, K.Y. (ed) *Iskopaemye Ostrakody*. Kiev, 34-49.
- Příbyl, A. 1960. New information on the Upper Carboniferous freshwater and continental fauna from the Ostrava-Karviná Coal District. *Rozpravy Českoslovensé akademie věd*, **70**, 3-71.
- Raiswell, R. 1982. Pyrite texture, isotopic composition and the availability of iron. *American Journal of Science*, **282**, 1244-1263.
- Raiswell, R. & Berner, R.A. 1985. Pyrite formation in euxinic and semi-euxinic sediments. *American Journal of Science*, **285**, 710-724.
- Rebske, W.C. Bless, M.J.M., Paproth, E. & Steemans, E.P. 1985. Over enkele fossielen uit de klerf-schichten (Onder-Emsien) bij Waxweiler (Eifel, Brd) en hun leefmilieu *Grondboor en Hamer*, **5**, 142-155.
- Robinson, E. 1978. The Carboniferous. In: R.H. Bate and E. Robinson (eds) *A Stratigraphical Index of British Ostracoda*. Geological Journal Special Issue, No. 8, Liverpool, UK, 121-166.
- Rosenfeld, A. 1979. Structure and secretion of the carapace in some living ostracodes. *Lethaia*, **12**, 353-360.
- Ross, C.A. & Ross, J.R.P. 1985. Late Palaeozoic depositional sequences are synchronous and worldwide. *Geology*, **13**, 194-197.

- Roundy, P.V. 1926. Mississippian formations of San Saba County, Texas. U.S. *Geological Survey Professional Paper*, **146**, 5-8.
- Samoilova, R.B. & Smirnova, R.F. 1960. On new ostracode genera and species from the Palaeozoic of the southern part of the Moscow area basin. *Meterialy po geologii i poleznym isokpaemyn tsentralnykh rayonov europeyskoy chasti SSSR*, **3**, 64-111.
- Sars, G.O. 1866. Oversigt af norges marine ostracoder. *Forhandlinger i Videnskabs-Selskabet i Christiania*, , 1-130.
- Sars, G.O. 1888. Nye Bidrag til Kundskaben om Middlehavets Invertebratfauna. 4. Ostracoda Mediterranea. *Archiv Mathematische Naturvetenskap*, **12**, 173–324.
- Schäfer, P. 2007. Muschelkrebse (Ostracoden) aus permokarbonischen Karbonatbänken im rheinland-pfälzischen Teil des Saar-Nahe-Beckens. In: Schindler, T. & Heidtke, U.H.J. (eds) *Kohlesümpfe, Seen und Halbwüsten*. Pollichia.
- Schrag, D.P. 1999. Effects of diagenesis on the isotopic record of late Paleogene tropical sea surface temperatures. *Chemical Geology*, **161**, 215-224.
- Schrag, D.P., DePaolo, D.J. & Richter, F.M. 1995. Reconstructing past sea surface temperatures: correcting for diagenesis of bulk marine carbonate. *Geochimica et Cosmochimica Acta*, **59**, 2265-2278.
- Schultze, H.P., Maples, C.G. & Cunningham, C.R. 1994. The Hamilton Konservat-Lagerstätte: Stephanian terrestrial biota in a marginal-marine setting. *Transactions of the Royal Society of Edinburgh, Earth Sciences*, **84**, 443-451.
- Scott, H.W. 1944. Permian and Pennsylvanian fresh-water ostracodes. *Journal of Paleontology*, **18**, 141-147.

- Scott, H.W. 1959. Type species of *Paraparchites* Ulrich and Bassler. *Journal of Paleontology*, **33**, 670–674.
- Scott, H.W. 1961. Suborder Kloedenellocopina. In: Moore, R.C. (ed) *Treatise on Invertebrate Paleontology, Pt. Q, Arthropoda 3*. Part Q, Arthropoda 3, Lawrence, Kansas, USA, Geological Society of America and University of Kansas Press, Q180.
- Scott, H.W. & Summerson, C.H. 1943. Non-marine Ostracoda from the Lower Pennsylvanian in the Southern Appalachians, and their bearing on inter-continental correlation. *American Journal of Science*, **241**, 653-675.
- Searl, A. 1990. Dolomitisation of the Ardross Limestones (Dinantian), East Fife, Scotland. *Sedimentary Geology*, **69**, 77-94.
- Sexton, P.F., Wilson, P.A. & Pearson, P.N. 2006. Microstructural and geochemical perspectives on planktic foraminiferal preservation: "glassy" versus "frosty". *Geochemistry, Geophysics, Geosystems*, **7**, Q12P19, doi: 10.1029/2006GC001291.
- Shaver, R.H. 1961. *Seminolites* Coryell, 1928, p. Q363. In: R.C. Moore (ed) *Treatise on Invertebrate Paleontology, Part Q, Arthropoda 3*. Lawrence, Kansas, USA, Geological Society of America and University of Kansas Press.
- Shear, W.A., Jeram, A.J. & Selden, P.A. 1998. Centipede legs (Arthropoda, Chilopoda, Scutigeromorpha) from the Silurian and Devonian of Britain and the Devonian of North America. *American Museum of Natural History*, **3231**, 1-16.
- Shear, W.A., Selden, P.A., Rolfe, W.D.I., Bonamo, P.M. & Grierson, J.D. 1987. New terrestrial arachnids from the Devonian of Gilboa, New York (Arachnida, Trigonotarbida). *American Museum of Natural History*, **17**, 1-74.

- Shi, C.G. 1964. The Middle and Upper Devonian ostracoda from Dushan and Douyun, S. Kueichow. *Acta Palaeontologica Sinica*, **12**, 50-65.
- Siveter, D.J. 1984. Habits and Modes of life of Silurian Ostracodes. *Special Papers in Palaeontology*, **32**, 71-85.
- Siveter, D.J. 2008. Ostracods in the Palaeozoic? *Senckenbergiana lethaea*, **88**, 1-9.
- Siveter, D.J., Vannier, J.M.C. & Palmer, D. 1991. Silurian Myodocopes: Pioneer pelagic ostracods and the chronology of an ecological shift. *Journal of Micropalaeontology*, **10**, 151-173.
- Siveter, D.J., Sutton, M.D., Briggs, D.E.G. & Siveter, D.J. 2003. An Ostracode Crustacean with Soft Parts from the Lower Silurian. *Science*, **302**, 1749-1751.
- Siveter, D.J., Siveter, D.J., Sutton, M.D. & Briggs, D.E.G. 2007. Brood care in a Silurian ostracod. *Proceedings of the Royal Society B*, **274**, 465-469.
- Smith, R.J. 1999. Possible fossil ostracod (Crustacea) eggs from the Cretaceous of Brazil. *Journal of Micropalaeontology*, **18**, 81-87.
- Smith, R.J. 2000. Morphology and ontogeny of Cretaceous ostracods with preserved appendages from Brazil. *Palaeontology*, **43**, 63-98.
- Sohn, I.G. 1960. Palaeozoic species of *Bairdia* and related genera. Revision of some Palaeozoic ostracode genera. *United States Geological Survey Professional Paper* **330-A**, 1-105.
- Sohn, I.G. 1969. Revision of some of Girty's invertebrate fossils from the Fayetteville Shale (Mississippian) of Arkansas and Oklahoma - Ostracodes. *Geological Survey Professional Paper*, **606-F**, 41-59.

- Sohn, I.G. 1971. A Revision of the Paraparchitacea (A) New Late Mississippian Ostracode Genera and Species from Northern Alaska. *United States Geological Survey Professional Paper 711-A*, 1-24.
- Sohn, I.G. 1972. A revision of the Paraparchitacea (B) Late Palaeozoic Ostracode Species from the Conterminous United States. *United States Geological Survey Professional Paper 711-B*, 1-15.
- Sohn, I.G. 1977. Muscle scars of Late Palaeozoic freshwater ostracodes from West Virginia. *Journal of Research, US Geological Survey*, **5**, 135-141.
- Sohn, I.G. 1985. Latest Mississippian (Namurian A) nonmarine ostracodes from West Virginia and Virginia. *Journal of Palaeontology*, **59**, 446-460.
- Sohn, I.G. & Kornicker, L.S. 1988. Ultrastructure of Myodocopid Shells (Ostracoda). In: T. Hanai, N. Ikeya and K. Ishizaki (eds) *Evolutionary biology of Ostracoda, its fundamentals and applications*. Proceedings of the ninth International Symposium on Ostracoda, Shizuoka, Japan, 1985. Tokyo, Amsterdam, Elsevier, 243-257.
- Sperling, M., Weldeab, S. & Schmiedl, G. 2002. Drying of samples may alter foraminiferal isotopic ratios and faunistic composition. *Micropalaeontology*, **48**, 87-91.
- Stephenson, M.H., Williams, M., Monaghan, A.A., Arkley, S. & Smith, R. 2002. Biostratigraphy and palaeoenvironments of the Ballagan Formation (lower Carboniferous) in Ayrshire. *Scottish Journal of Geology*, **38**, 93-111.
- Stephenson, M.H., Williams, M., Leng, M.J. & Monaghan, A.A. 2004. Aquatic plant microfossils of probable non-vascular origin from the Ballagan Formation (Lower

- Carboniferous), Midland Valley, Scotland. *Proceedings of the Yorkshire Geological Society*, **55**, 145-158.
- Stephenson, M.H., Williams, M., Monaghan, A.A., Arkley, S., Smith, R.A., Dean, M., Browne, M.A.E. & Leng, M.J. 2004. Palynomorph and ostracod biostratigraphy of the Ballagan Formation, Midland Valley of Scotland, and elucidation of intra-Dinantian unconformities. *Proceedings of the Yorkshire Geological Society*, **55**, 131-143.
- Stephenson, M.H., Angiolini, L., Leng, M.J., Brewer, T.S., Berra, F., Jadoul, F., Gambacorta, G., Verna, V. & Al Beloushi, B. 2008. Abrupt environmental and climatic change during the deposition of the Early Permian Haushi limestone, Oman. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **270**, 1-18.
- Stevenson, J.R. 1985. Dynamics of the integument. In: Bliss, D.E. & Mantel, L.H. (eds) *The biology of Crustacea, Volume 9, Integuments, pigments and hormonal processes*. Academic Press, 2-32.
- Strand, E. 1928. Miscellanea nomenclatoria zoologica et palaeontologica. *Archiv für Naturgeschichte*, **92**, 40-41.
- Swain, F.M. 1976. Evolutionary development of cypridopsid Ostracoda. *Abhandlungen und Verhandlungen des naturwissenschaftlichen Vereins in Hamburg, Neue Folge*, **18/19** (Supplement), 103-119.
- Swartz, F.M. 1936. Revision of the Primitiidae and Beyrichiidae with new Ostracoda from the Lower Devonian of Pennsylvania. *Journal of Paleontology*, **10**, 541-586.

- Sylvester-Bradley, P.C. 1961. Suborder Metacopina. In: Moore, R.C. (ed) *Treatise on Invertebrate Paleontology*. Part Q, Arthropoda 3, Lawrence, Kansas, USA, Geological Society of America and University of Kansas Press, Q358.
- Sylvester-Bradley, P.C. & Benson, R. 1971. Terminology for surface features in ornate ostracodes. *Lethaia*, **4**, 249-286.
- Taylor, P.D. & Vinn, O. 2006. Convergent morphology in small spiral worm tubes ("*Spirorbis*") and its palaeoenvironmental implications. *Journal of the Geological Society of London*, **163**, 225-228.
- Tibert, N.E. & Dewey, C.P. 2006. *Velatomorpha*, a new healdioidean ostracode genus from the early Pennsylvanian Joggins Formation, Nova Scotia, Canada. *Micropaleontology*, **52**, 51-66.
- Tibert, N.E. & Scott, D.B. 1999. Ostracodes and agglutinated foraminifera as indicators of palaeoenvironmental change in an Early Carboniferous brackish bay, Atlantic Canada. *Palaios*, **14**, 246-260.
- Tinn, O. & Meidla, T. 2004. Phylogenetic relationships of Early-Middle Ordovician ostracods of Baltoscandia. *Palaeontology*, **47**, 199-221.
- Trewin, N.H. & Davidson, R.J. 1996. An Early Devonian lake and its associated biota in the Midland Valley of Scotland. *Transactions of the Royal Society of Edinburgh. Earth Sciences*, **86**, 233-246.
- Trueman, A. & Weir, J. 1946-1968. A monograph of British Carboniferous non-marine Lamellibranchia. *The Palaeontographical Society*, **I (XIII)**, 1-449.

- Turner, B.R., Dewey, C. & Fordham, C.E. 1997. Marine ostracods in the Lower Carboniferous fluviatile Fell Sandstone Group: evidence for base level change and marine flooding of the central graben, Northumberland Basin. *Proceedings of the Yorkshire Geological Society*, **51**, 297-306.
- Turner, S., Kemp, A. & Warren, A. 1999. First early Carboniferous lungfish (Dipnoi, Ctenodontidae) from central Queensland. *Alcheringa*, **23**, 177-183.
- Turpen, J.B. & Angell, R.W. 1971. Aspects of moulting and calcification in the ostracod *Heterocypris*. *Biological Bulletin*, **140**, 331-338.
- Ulrich, E.O. 1891. New and little known American Paleozoic Ostracoda, Pt. 3, Carboniferous species. *Cincinnati Society of Natural History, Journal*, **13**, 200–211.
- Ulrich, E.O. & Bassler, R.S. 1906. New American Paleozoic Ostracoda. Notes and descriptions of Upper Carboniferous genera and species. *Proceedings of the U.S. National Museum*, **30**, 149–164.
- Ulrich, E.O. & Bassler, R.S. 1908. New American Paleozoic Ostracoda. Preliminary revision of the Beyrichiidae, with descriptions of new genera. *Proceedings of the U.S. National Museum*, **35**, 277–340.
- Van Doninck, K., Schön, I., Martens, K. & Godderris, B. 2003. The life-cycle of the asexual ostracod *Darwinula stevensoni* (Brady & Robertson, 1870) (Crustacea, Ostracoda) in a temperate pond. *Hydrobiologia*, **500**, 331-340.
- van Greel, B. & Grenfell, H.R. 1996. Spores of *Zygnemataceae*. In: J. Jansonius & D.C. McGregor (eds) *Palynology: Principles and Applications*. 1st edition, American Association of Stratigraphic Palynologists Foundation, 173-179.

- Vannier, J. & Abe, K. 1992. Recent and early Palaeozoic myodocope ostracods: functional morphology, phylogeny, distribution and lifestyles. *Palaeontology*, **35**, 485-517.
- Vannier, J. & Abe, K. 1995. Size, body plan and respiration in the ostracoda. *Palaeontology*, **38**, 843-873.
- Vannier, J., Thiery, A. & Racheboeuf, P.R. 2003. Spinicaudatans and Ostracods (Crustacea) from the Montceau Lagerstatte (Late Carboniferous, France): Morphology and palaeoenvironmental significance. *Palaeontology*, **46**, 999-1030.
- Vannier, J., Wang, S.Q. & Coen, M. 2001. Leperditicopid arthropods (Ordovician - Late Devonian): functional morphology and ecological range. *Journal of Paleontology*, **75**, 75-95.
- Von Grafenstein, U., Erlernkeuser, H. & Trimborn, P. 1999. Oxygen and carbon isotopes in modern fresh-water ostracod valves: assessing vital offsets and autecological effects of interest for palaeoclimate studies. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **148**, 133-152.
- Wakefield, M.I. 1995. Ostracoda and palaeosalinity fluctuations in the Middle Jurassic Lealt Shale Formation, Inner Hebrides, Scotland. *Palaeontology*, **38**, 583-617.
- Wansard, G., De Decker, P. & Julia, R. 1998. Variability in ostracod partition coefficients $D(\text{Sr})$ and $D(\text{Mg})$: Implications for lacustrine palaeoenvironmental reconstructions. *Chemical Geology*, **146**, 39-54.
- Warshauer, S.M. & Smosna, R. 1977. Paleoecologic controls of the ostracode communities in the Tonoloway limestone (Silurian; Pridoli) of the Central Appalachians. In:

- Löffler, H. & Danielopol, D. (eds) *Aspects of Ecology and Zoogeography of Recent and fossil Ostracoda*. The Hague, 475-485.
- Webb, J.A. 1979. A reappraisal of the palaeoecology of conchostracans (Crustacea: Branchiopoda). *Neues Jahrbuch für Geologie und Palaeontologie. Abhandlungen*, **158**, 259-275.
- Whatley, R.C. 1983. The application of ostracoda to palaeoenvironmental analysis. In: Maddocs, R.F. (ed.) *Applications of Ostracoda*. University of Houston Geosciences, 51-77.
- Whatley, R.C. & Ballent, S.C. 1996. In search of the earliest nonmarine cypridacean ostracods: new discoveries from the Early Mesozoic of western Argentina. *GeoResearch Forum*, **1-2**, 111-118.
- Whatley, R.C., Siveter, D.J. & Boomer, I. 1993. Arthropoda (Crustacea: Ostracoda). In: Benton, M.J. (ed.) *The Fossil Record 2*. Chapman and Hall, London, 343-356.
- Wilkin, R.T., Barnes, H.L. & Brantley, S.L. 1996. The size distribution of framboidal pyrite in modern sediments: An indicator of redox conditions. *Geochimica et Cosmochimica Acta*, **60**, 3897-3912.
- Wilkinson, B.H., Pope, B.N. & Owen, R.M. 1980. Nearshore ooid formation in a modern temperate marl lake. *Journal of Geology*, **88**, 697-704.
- Williams, M. & Siveter, D.J. 1996. Lithofacies-influenced ostracod associations in the middle Ordovician Bromide Formation, Oklahoma, USA. *Journal of Micropalaeontology*, **15**, 69-81.

- Williams, M., Haywood, A.M., Hillenbrand C.D. & Wilkinson, I.P. 2005a. Efficacy of $\delta^{18}\text{O}$ data from Pliocene planktonic foraminifer calcite for spatial sea surface temperature reconstruction: comparison with a fully coupled ocean-atmosphere GCM and fossil assemblage data for the mid-Pliocene. *Geological Magazine*, **142**, 399-417.
- Williams, M., Haywood, A.M., Taylor, S.P., Valdes, P.J., Sellwood, B.W. & Hillenbrand, C-D. 2005b. Evaluating the efficacy of planktonic foraminifer calcite $\delta^{18}\text{O}$ data for sea surface temperature reconstruction for the Late Miocene. *Geobios*, **38**, 843-863.
- Williams, M., Stephenson, M.H., Wilkinson, I.P., Leng, M.L. & Miller, C.G. 2005c. Early Carboniferous (Late Tournaisian-Early Viséan) ostracods from the Ballagan Formation, central Scotland, UK. *Journal of Micropalaeontology*, **24**, 77-94.
- Williams, M., Leng, M.L., Stephenson, M.H., Andrews, J.E., Wilkinson, I.P., Siveter, D.J., Horne, D.J. & Vannier, J.M.C. 2006. Evidence that Early Carboniferous ostracods colonised coastal flood plain brackish water environments. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **230**, 299-318.
- Williams, M., Haywood, A.M., Vautravers, M., Sellwood, B.W., Hillenbrand, C.D., Wilkinson, I.P. & Miller, C.G. 2007. Relative effect of taphonomy on calcification temperature estimates from fossil planktonic foraminifera. *Geobios*, **40**, 861-874.
- Williams, M., Siveter, D.J., Salas, M.J., Vannier, J., Popov, L.E. & Pour, M.G. 2008. The earliest ostracods: the geological evidence. *Senckenbergiana lethaea*, **88**, 11-21.
- Wilson, R.B. 1989. A study of the Dinantian marine macrofossils of central Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **80**, 91-126.

- Wood, G.D., Gabriel, A.M. & Lawson, J.C. 1996. Palynological techniques – processing and microscopy. In: Jansonius, J. & McGregor, D.C. (eds) *Palynology: Principles and Applications*. American Association of Stratigraphical Palynologists Foundation, vol. 1, 29-50.
- Wright, W.B. 1930. Additions to the fauna of the Lancashire Coal Measures. *Memoirs of the Proceedings of the Manchester Literary and Philosophical Society*, **74**, 41-51.
- Yamada, S., Tsukagoshi, A. & Ikeya, N. 2005. Carapace formation of the podocopid ostracode *Semicytherura* species (Crustacea: Ostracoda). *Lethaia*, **38**, 323-325.
- Yasuhara, M. & Cronin, T.M. 2008. Climatic influences on deep-sea ostracode (Crustacea) diversity for the last three Million years. *Ecology*, **89**, 53-65.
- Zavattieri, A.M. & Prámparo, M.B. 2006. Freshwater algae from the Upper Triassic Cuyana Basin of Argentina: palaeoenvironmental implications. *Palaeontology*, **49**, 1185-1209.
- Ziegler, P.A. 1989. *Evolution of Laurussia, a study in late Palaeozoic plate tectonics*. Dordrecht, The Netherlands, Kluwer academic publishers.