

Ostracods from freshwater and brackish environments of the Carboniferous of the Midland Valley of Scotland: the early colonization of terrestrial water bodies

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Abstract – The Mississippian Strathclyde Group of the Midland Valley of Scotland yields some of the earliest non-marine ostracods. The succession records shallow marine, deltaic, estuarine, lagoonal, lacustrine, fluvial and swamp environments representing a series of staging-posts between fully marine and limnetic settings. Macrofossils and ostracods are assigned to marine, marginal marine, brackish and freshwater environments based on their faunal assemblage patterns. Key brackish to freshwater ostracods are *Geisina arcuata*, *Paraparchites circularis* n. sp., *Shemonaella ornata* n. sp. and *Silenites* sp. A, associated with the bivalves *Anthraconaia*, *Carbonicola*, *Cardiopteridium*, *Curvirimula*, *Naiadites*, the microconchid ‘*Spirorbis*’, Spinicaudata and fish. Many Platycopina and Paraparchiticopina ostracods are interpreted as euryhaline, which corresponds with their occurrence in marine to coastal plain water bodies, and supports the ‘estuary effect’ hypothesis of non-marine colonization. The success of non-marine colonization by ostracods was dependent on the intrinsic adaptations of ostracod species to lower salinities, such as new reproductive strategies and the timing of extrinsic mechanisms to drive non-marine colonization, such as sea-level change. The genus *Carbonita* is the oldest and most common freshwater ostracod, and went on to dominate freshwater environments in the Late Palaeozoic.

Keywords: ostracods, Mississippian, freshwater, palaeoenvironment, terrestrialization.

1. Introduction

The colonization of non-marine water bodies by animals was one of the major ecological radiations of life. However, there is little known about the early colonization of the non-marine realm by ostracods, which are one of the most abundant animal groups. Ostracods are numerous, widespread and diverse in non-marine and marine waters today. Ostracods occur in the fossil record from the Early Ordovician onwards (Salas, Vannier & Williams, 2007; Siveter, 2008) and appear to have been entirely marine during the Early Palaeozoic (for example see Williams *et al.* 2003). Their ecological migration from marine to freshwater aquatic environments occurred during the Late Palaeozoic, with the most complete record of this transition in the Carboniferous (Bennett, 2008). Putative brackish water ostracods have been recorded in the Silurian (Siveter, 1984; Clarkson, Harper & Hoey, 1998; Floyd & Williams, 2003), with more frequent attempts at colonizing brackish waters being recorded from the Late Devonian onwards (for example Bless, 1983; Bless, Streel & Becker, 1988; Williams *et al.* 2006).

In the Late Silurian to Devonian a non-marine macrofossil lacustrine fauna (including freshwater fish and arthropods) became established worldwide, but it was not until the Carboniferous that most non-marine terrestrial environments were colonized (Buatois *et al.* 1998). The earliest Late Palaeozoic arthropods that are possibly taxonomically ‘close’ to ostracods and which apparently colonized freshwater are leperditicopes, a group which also originated in the Early Ordovician and which are recorded from Early Devonian brackish and putative freshwater environments (Friend & Moody-Stuart, 1970; Friedman & Lundin, 1998; Knox & Gordon, 1999). The timing of non-marine colonization in the Carboniferous by invertebrate detritus-feeders can be linked to the timing of land plant evolution (Bateman *et al.* 1998; Buatois *et al.* 1998). The ‘passive’ versus ‘active’ (Gray, 1988) nature of invertebrate non-marine colonization is key to understanding the mechanism of this ostracod radiation event, that is, whether invertebrates were passively stranded in coastal plain water bodies that freshened over time or if they exploited the food available from the land and actively activity adapted to freshwater conditions.

Living non-marine ostracods belong to the podocope superfamilies Cypridoidea, Darwinuloidea and Cytheroidea, all of which have possible Late Palaeozoic origins. The Palaeozoic Carbonitoidea may be related

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to the Cypridoidea or Darwinuloidea, and a group of non-marine Cytheroidea (limnocytherids) occur in the Late Carboniferous (Carbonel *et al.* 1988; Horne, 2003). The migration from marine to freshwater by the ostracod *Carbonita* Strand, 1928 first occurred during the Carboniferous; from brackish-influenced environments in the Mississippian (Pollard, 1966; Anderson, 1970; Bless & Pollard, 1973; Sohn, 1985; Tibert & Scott, 1999), to subsequently occupy a wide range of freshwater environments by the Pennsylvanian (Schultze, Maples & Cunningham, 1994; Vannier, Thiery & Racheboeuf, 2003; Schäfer, 2007). Herein, *Carbonita* is recorded from the early Mississippian in what are interpreted as freshwater sediments. Along with darwinuloideans, the carbonitoideans radiated to a high diversity of species in the Late Carboniferous and Permian (Carbonel *et al.* 1988; Horne, 2003) and were the most successful Late Palaeozoic ostracods in freshwater environments.

This study draws on a range of palaeontological, sedimentological and palaeoecological data from the Carboniferous of the Midland Valley of Scotland (MVS) to assess: (1) the absolute range of environments that ostracods were colonizing during the Carboniferous; (2) the types of ostracods that were making this transition and whether or not their adaptation was of short-term or long-term success; and (3) the possible mechanisms, both intrinsic (genetic) and extrinsic (environmental), that were driving or facilitating this ecological shift.

2. Geological background

The Strathclyde Group of the MVS was deposited in a range of environments, from shallow marine, restricted marine lagoons and estuaries, to coastal floodplains, fluvial systems and freshwater lakes and swamps (Browne *et al.* 1999). The well-preserved and abundant macrofossils and ostracods in the Strathclyde Group make it an ideal sequence to study a marine to non-marine ecological shift during the Mississippian. At this time the MVS was situated on the margins of a restricted marine seaway at an equatorial latitude (Fig. 1). Siliciclastic sediment, sourced mainly from the highlands to the north was deposited in prograding alluvial to lacustrine deltaic systems, with infrequent marine transgressions (Browne *et al.* 1999). A study of the older (early Mississippian, Courceyan) Ballagan Formation demonstrated ostracods in hypersaline and brackish water bodies (Williams *et al.* 2005, 2006), associated with possible freshwater to brackish algal palynomorphs (Stephenson *et al.* 2004a,b).

The formations of the Strathclyde Group are correlated across Fife in Scotland using distinctive marine horizons and non-marine limestones (Browne *et al.* 1999; Wilson, 1989). The group is well dated by lava flows, lapilli-tuffs and intrusions and by the presence of spores (Monaghan & Parrish, 2005; Owens *et al.* 2005; Stephenson *et al.* 2004b; Fig. 1). The Anstruther Formation has the most non-marine limestones (Fig. 2);

the Pittenweem Formation contains fully marine and marginal marine horizons ('marine bands') belonging to the Macgregor Marine Bands (Wilson, 1989); the Sandy Craig Formation is essentially non-marine; and the Pathhead Formation contains the thickest fully marine horizons.

Twenty-five ostracod species are reported from the Strathclyde Group, belonging to the orders Podocopida, Leiocopida, Palaeocopida and Myodocopida (Table 1). Ostracods occur in a range of sediment types and faunal associations (Table 2). The single most diverse ostracod assemblage contains 14 species (Table 3). Ostracods are well preserved, with the exception of those from the Pittenweem Formation, in which most of the carapaces have been dissolved to leave only moulds, and only one species has been identified. The association of particular ostracod species within particular macrofaunal assemblages has been used to determine their ecology.

3. Methodology

The sedimentology and fauna were documented from a wide range of rock specimens together with 39 polished thin-sections (cut to a standard thickness of 30 μm) of samples derived from boreholes and field exposures. Ostracods picked from bedding plane surfaces were imaged using a Hitachi S-3600N Scanning Electron Microscope (SEM) at the University of Leicester. Some fossils were photographed on bedding plane surfaces using a Zeiss Axiocam light photography digital imaging system at the Natural History Museum, London.

A taphonomic assessment is important to interpret the ecology of macrofossils and ostracods. An ostracod thanatocoenosis is signalled by the presence of adults and juveniles of different instars, a high proportion of carapaces to single valves and the (rare) occurrence of open ('butterfly') carapaces. Mostly single or broken valves, stacked valves and a valve size bias signal a taphocoenosis (*sensu* Boomer, Horne & Slipper, 2003). In the sedimentary logs and faunal association tables (Tables 2–5, Figs 3–5), all occurrences of a particular fauna are noted. The problem of apparent ecological ranges being obscured by transportation (Horne, 2003) is addressed by reference to the supposed ecologies of particular fossils, and the taphonomy is carefully considered when assigning an ecological range to any fossil group.

4. Faunal assemblages and sedimentary environments

The faunas of the Strathclyde Group can be grouped into recurrent assemblages (Tables 4, 5) and facies (Figs 3–6):

Type 1 Assemblage: a high-diversity assemblage of 11 ostracod species and crinoids, orthocones, bryozoans, brachiopods, trilobites, goniatites, gastropods, echinoids and bivalves and the feeding-dwelling trace

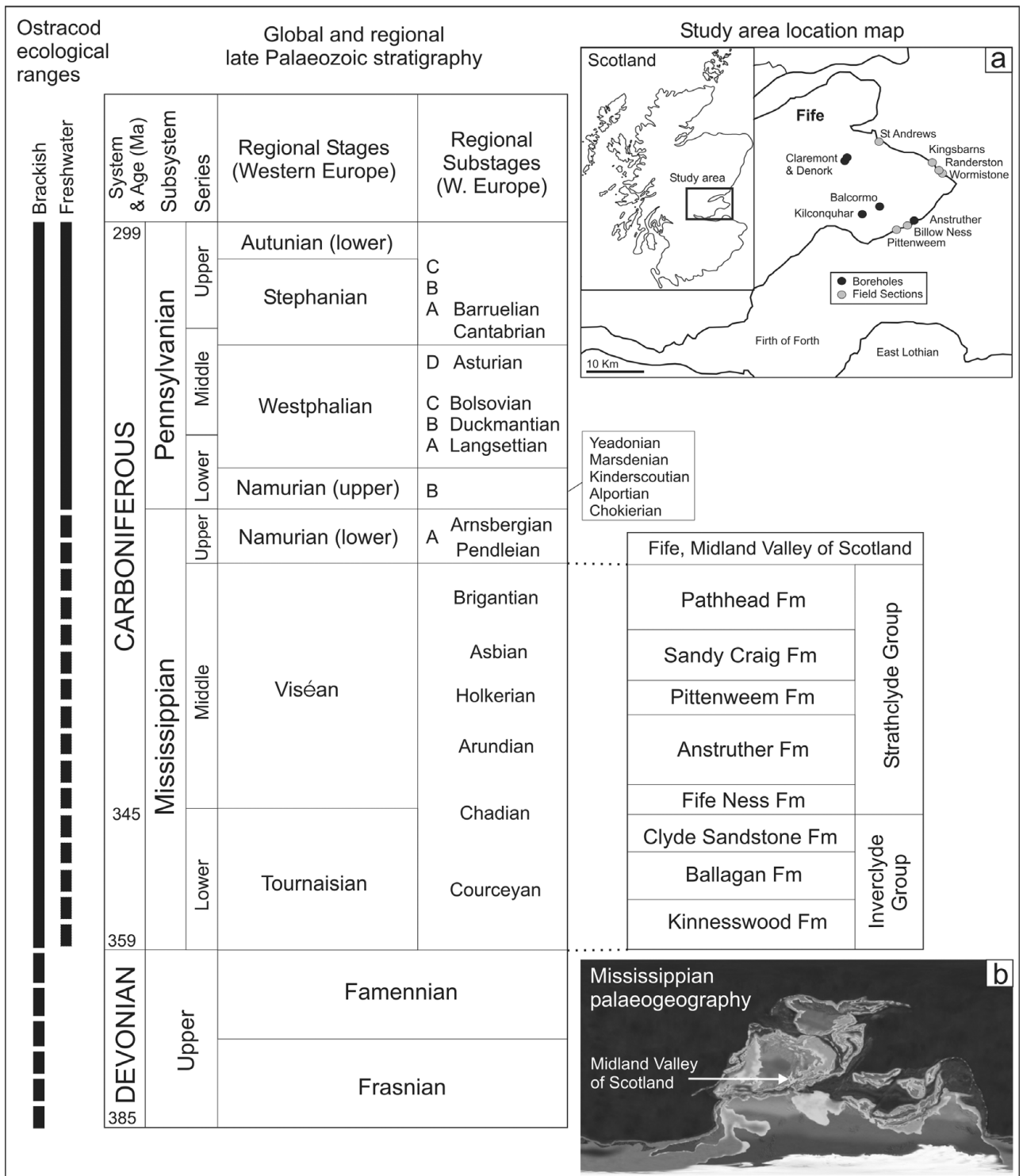


Figure 1. Late Devonian and Carboniferous lithostratigraphy for Fife in the Midland Valley of Scotland. Inset (a) shows the location map of sections studied; inset (b) shows Mississippian palaeogeography. The ecological radiation of ostracods relative to the chronostratigraphy is plotted in terms of their occurrence in brackish and freshwater, from other published records. Solid lines represent a confident age assignment for brackish or freshwater conditions, dashed lines a tentative assignment or only rare occurrence. Carboniferous stratigraphy is adapted from Heckel & Clayton (2006) for Western Europe and Browne *et al.* (1999) for Fife. Dates are from the International Commission of Stratigraphy timescale 2004. The Mississippian palaeogeographic map is for 340 Ma, downloaded from Prof. R. Blakey's website <http://jan.ucc.nau.edu/~rcb7>.

Chondrites (Table 4). The macrofaunal elements are mainly benthic, with rare nektonic elements such as cephalopods. *Hollinella (Keslingella) radiata* (Jones & Kirkby, 1886) is the most common Type 1 Assemblage ostracod species. This assemblage occurs in Facies 1

and 3a; Facies 1 is fossiliferous limestones within thick (up to 10 m) mudstone intervals or mudstones, with a diverse fauna (Fig. 3). The Pathhead Lower Marine Band has the highest faunal diversity; containing 30 macrofossil and 10 ostracod species. Only very rare

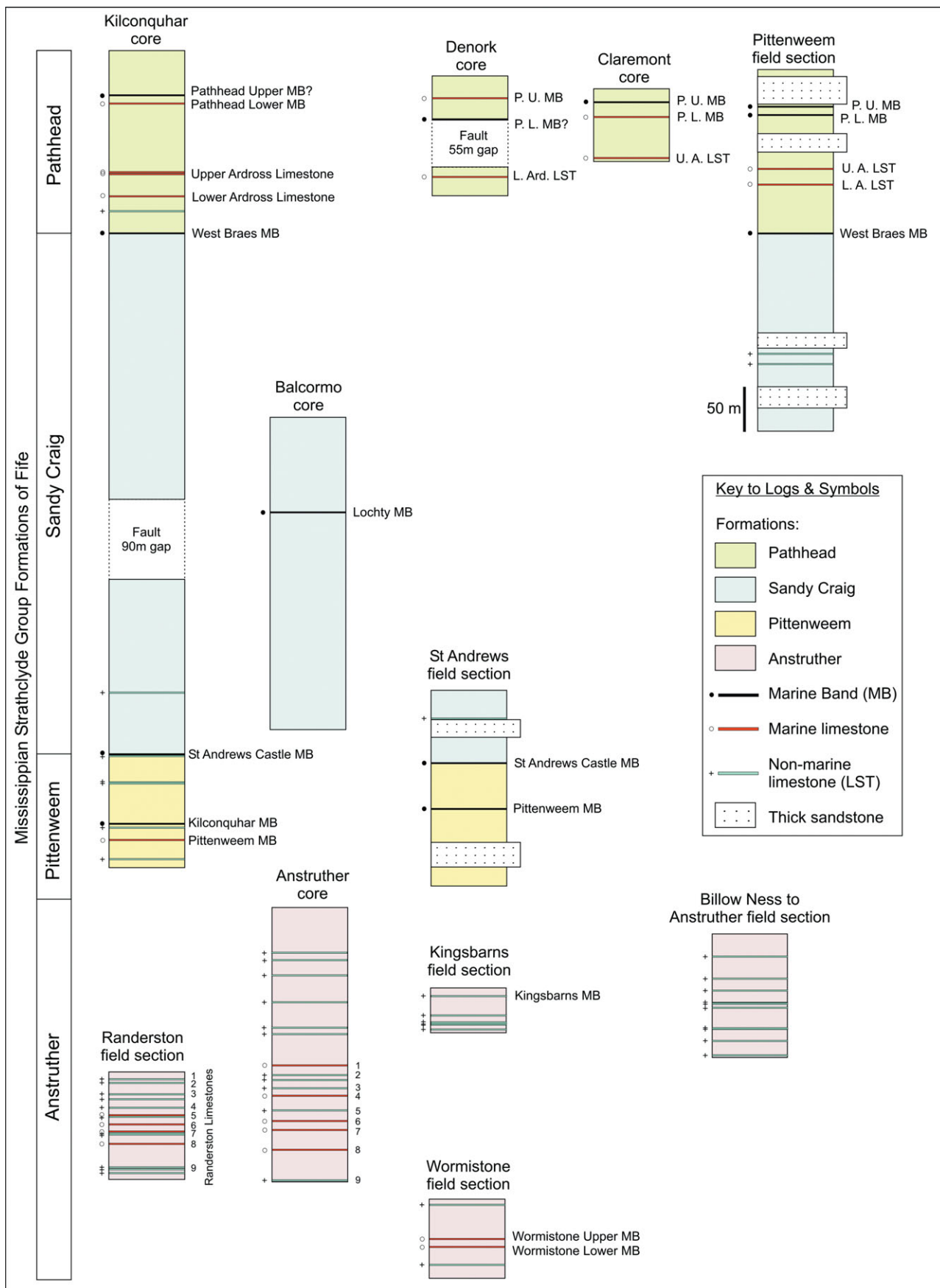


Figure 2. (Colour online) Borehole and field section correlation panel for the Strathclyde Group. Sandstone units (Facies 3a) with a thickness greater than 20 m are shown. British Geological Survey (BGS) boreholes, from 1964–1980, are stored at the BGS in Edinburgh. A sedimentary log and a list of macrofauna were described from these cores by BGS workers (additionally the Balcormo and Kilconquhar boreholes were also described by National Coal Board workers). Field samples were collected as part of this study between 2005 and 2008.

Table 1. Taxonomic scheme for the ostracods of the Strathclyde Group featured in this study. The higher classification follows Whatley *et al.* (1993), supplemented by consideration of Sohn (1985) for the Superfamily Carbonitoidea, and Dewey & Fähræus (1987) for the Family Geisinidae

Order	PODOCOPIDA	Müller, 1894
Suborder	PODOCOPINA	Sars, 1866
Superfamily	BAIRDIOIDEA	Sars, 1887
Family	BAIRDIIDAE	Sars, 1887
Genus	<i>Acratia</i>	Delo, 1930
	<i>Acutiangulata</i>	Buschmina, 1968
	<i>Bairdia</i>	McCoy, 1844
Superfamily	BAIRDIOCYPRIDOIDEA	Shaver <i>in</i> Moore, 1961
Family	BAIRDIOCYRIDIDAE	Shaver <i>in</i> Moore, 1961
Genus	<i>Silenites</i>	Coryell & Booth, 1933
Superfamily	CARBONITOIDEA	Sohn, 1985
Family	CARBONITIDAE	Sohn, 1985
Genus	<i>Carbonita</i>	Strand, 1928
Suborder	METACOPINA	Sylvester-Bradley, 1961
Superfamily	HEALDIOIDEA	Harlton, 1933
Family	HEALDIIDAE	Harlton, 1933
Genus	<i>Healdia</i>	Roundy, 1926
Suborder	PLATYCOPINA	Sars, 1866
Superfamily	KLOEDENELLOIDEA	Ulrich & Bassler, 1908
Family	CAVELLINIDAE	Egorov, 1950
Genus	<i>Cavellina</i>	Coryell, 1928
Family	GEISINIDAE	Sohn, 1961
Genus	<i>Geisina</i>	Johnson, 1936
?Superfamily	KLOEDENELLOIDEA	Ulrich & Bassler, 1908
Family	UNCERTAIN	
Genus	<i>Glyptolichvinella</i>	Posner, 1966
Order	LEIOCOPIDA	Schallreuter, 1973
Suborder	PARAPARCHITICOPINA	Gramm <i>in</i> Gramm & Ivanov, 1975
Superfamily	PARAPARCHITOIDEA	Scott, 1959
Family	PARAPARCHITIDAE	Scott, 1959
Genus	<i>Paraparchites</i>	Ulrich & Bassler, 1906
	<i>Shemonaella</i>	Sohn, 1971
Order	PALAEOCOPIDA	Henningsmoen, 1953
Suborder	PALAEOCOPINA	Henningsmoen, 1953
Superfamily	HOLLINOIDEA	Swartz, 1936
Family	HOLLINELLIDAE	Bless & Jordan, 1971
Genus	<i>Hollinella</i>	Coryell, 1928
Subgenus	<i>Hollinella</i>	(<i>Keslingella</i>) Bless & Jordan, 1970
Superfamily	UNCERTAIN	
Family	UNCERTAIN	
Palaeocope	sp. A – Palaeocope	sp. D
Order	MYODOCOPIDA	Sars, 1866
Suborder	CLADOCOPINA	Sars, 1866
Superfamily	POLYCOPOIDEA	Sars, 1866
Family	POLYCOPIDAE	Sars, 1866
Genus	<i>Polycope</i>	Sars, 1866

Type 1 Assemblage elements are present in Facies 3a; thick, medium–coarse-grained, quartz arenite sandstone successions (from 10–26 m in thickness), present in sections of the formations studied (Fig. 2). Structures include channel forms, parallel laminations, large-scale cross-bedding (1.5 m height planar cross-beds) and extensive convolute-bedding (some convoluted units are 10 m thick) leading to a hummocky weathering pattern. In some cases the tops of large cross-beds are convoluted.

Type 2 Assemblage: includes six ostracod species, the brachiopod *Lingula*, the bivalves *Myalina*, *Schizodus*, *Sanguinolites* and fish (Table 4). *Lingula* is most common in the Type 1 Assemblage, but also occurs in Type 2, 3 and 4 assemblages (Table 5), as do *Schizodus* and *Sanguinolites*. The assemblage is typified by an association of the ostracods *Cavellina valida* (Jones, Kirkby & Brady, 1884), *Shemonaella elongata* n. sp. and palaeocope sp. A. A Type 2 or low-diversity Type 1 Assemblage occurs in Facies 2 mudstones

and limestones, most common in the Pathhead and Pittenweem formations (Fig. 3).

Type 3 Assemblage: comprises 11 ostracod species, the most common being *Paraparchites circularis* n. sp., ‘*Spirorbis*’, the bivalves *Curvirimula scotica* and *Naiadites obesus* and fish (Table 4). *Naiadites* is the most common and ‘*Spirorbis*’ is frequently associated with *Curvirimula*, *Naiadites*, fish and plant debris (Table 5). Modern *Spirorbis* is a polychaete worm, but Palaeozoic ‘spirorbids’ are related to lophophorates (Microconchida; Taylor & Vinn, 2006), encrust hard substrates (such as stromatolites: Burchette & Riding, 1977) and were probably suspension feeders. Specimens are planispiral (230–2000 µm diameter) evolute, prostrate discoidal calcareous tubes. Type 3 Assemblage elements occur in Facies 4; mudstones and limestones such as *Naiadites* ‘mussel bands’, are particularly common in the Pittenweem (Fig. 3) and Anstruther (Fig. 4) formations. These mussel bands represent a taphocoenosis, but *Naiadites* is also

Table 2. Ostracod material, sediments and macrofaunal associations

Species	Material & Samples	Location	Sediments	Faunal Associations
<i>Acratia</i> sp. A.	1 specimen, (juv., SV, partly broken), sample EN 4818	Claremont core	mudstone	Type 3–4
<i>Acutiangulata</i> sp. A.	1 specimen (juv., C), EN 4885	Claremont core	Pathhead Lower MB	Type 1
<i>Bairdia submucronata</i>	10 specimens, EN 4884, EN 4885 and EN 4886 (Cs)	Claremont core	Pathhead Lower MB	Type 1
<i>Carbonita bairdioides</i>	A few specimens, 6E 6562 (SVs)	Balcormo core	BBI	Type 4
<i>Carbonita</i> cf. <i>fabulina</i>	1 specimen, SE 8538 (C)	Kilconquhar core	mudstone	Type 4
<i>Carbonita</i> cf. <i>humilis</i>	2 specimens, SE 8476 (Cs)	Kilconquhar core	mudstone	Type 4
<i>Carbonita</i> cf. <i>inflata</i>	1 specimen, SE 8413 (C)	Kilconquhar core	BBI	Type 4
<i>Carbonita</i> sp.	1000s of specimens at a generic level, mostly poorly preserved	Anstruther, Kilconquhar & Balcormo cores	mudstone, limestone	Types 2–4
<i>Cavellina benniei</i>	1 specimen, EN 4841 (adult, C) 3 specimens, EK 9601 (1 C, 1 SV, 1 juv. SV)	Claremont core Billow-Ness – Ans. Fs	mudstone mudstone	Type 1 none
<i>Cavellina valida</i>	1000s of specimens, mostly Cs, many juvs	Kilconquhar, Claremont & Denork cores	mudstone	Types 1–3
<i>Cavellina</i> sp.	100s of specimens	most cores and sections	mudstone	Type 2–3
<i>Geisina arcuata</i>	4 specimens, EN 4818 (SV), EN 4827 (Cs) 2 specimens EN 5257 (SV), EN 5272 (cast) 1 specimen EK 9591 (SV)	Claremont core Denork core Billow Ness – Ans. Fs	siltstone, mudstone mudstone mudstone	Types 2–4 Types 3–4 Types 3–4
<i>Glyptolichvinella spiralis</i>	1 specimen, field sample 20 (LV)	Kingsbarns section	limestone	Type 4
<i>Healdia</i> cf. <i>cuneata</i>	1 specimen, EN 4849 (juv., C)	Claremont core	Pathhead Lower MB	Type 1
<i>Hollinella</i> (K.) <i>radiata</i>	At least 20 specimens, 15 samples (Cs)	Claremont core	Pathhead Lower MB	Type 1
<i>Palaeocope</i> sp. A	100s of specimens (Cs & SVs)	Denork, Claremont & Balcormo cores	siltstone, mudstone	Types 1–4
<i>Palaeocope</i> sp. B	5 specimens, EN 4805 (3 SVs), EN 4807 (C) EL 5791 (SV)	Claremont core Anstruther core	mudstone siltstone	Types 3–4 Type 2
<i>Palaeocope</i> sp. C	3 specimens, EN 4848 (C), EN 4849 (C) & EN 4856 (juv., C)	Claremont core	Pathhead Lower MB	Type 1
<i>Palaeocope</i> sp. D	1 specimen, EN 4787 (C, specimen now lost)	Claremont core	mudstone	none
<i>Paraparchites</i> <i>arm.</i>	8 specimens, EN 5188, EN 5197 (SVs, dis. Cs, moulds)	Denork core	mudstone	Types 1–2
<i>Paraparchites</i> <i>circ.</i> n. sp.	1000s of specimens, SE 8410, 8411 and 8412 (SVs & Cs)		BBI, mudstone	Types 3–4
<i>Polycope elegans</i> n. sp.	26 specimens, EN 5329 (10 Cs, 10 moulds) EN 5328 (2 Cs, 2 SVs) EN 5327 & EN 5326 (one mould in each)	Denork core	mudstone mudstone siltstone	none Types 1–2 Type 1
<i>Shemonaella elongata</i> n. sp.	1000s of specimens, many samples, Cs & SVs	all formations	all sediments	Types 1–4
<i>Shemonaella ornata</i> n. sp.	6 specimens, EN 4818 (four SVs), & EN 4804 (2 Cs)	Claremont core	mudstone	Types 3–4
<i>Silenites</i> sp. A	3 specimens, EN 5249 (RV), EN 5250 (RV), SE 8411 (C)	Denork, Kilconquhar cores	siltstone, BBI	Types 3–4

Sample numbers refer to sedimentary rocks containing the ostracods (from BGS boreholes, stored in Edinburgh). Faunal association indicates the ostracod occurrence in particular macrofaunal assemblages.

Abbreviations: C – carapace; SV – single valve; RV – right valve; LV – left valve; juv. – juvenile; dis – disarticulated; Ans. Fs – Anstruther field section; MB – Marine Band; BBI – blackband ironstone.

present in thanatocoenosis deposits of low-abundance, monospecific or low-diversity elements of Type 3 and 4 assemblages (Fig. 4).

Type 4 Assemblage: includes 15 ostracod species, most commonly *Carbonita* sp., the bivalves *Anthraconaia*, *Carbonicola antique*, *C. elegans*, *Cardiopteridium* and the branchiopod conchostracans *Spinicaudata* (Table 4). *Curvirimula*, *Naiadites*, fish and ‘*Spirorbis*’ occur in both Type 3 and 4 assemblages. *Anthraconaia*, *Carbonicola* and *Cardiopteridium* commonly occur as low-diversity assemblages associated with *Naiadites*, plant and fish debris (Bennison, 1960, 1961 and this study). *Euestheria*, *Estheria* and *Leaia* occur in mudstones, associated with plants, fish, *Naiadites* and ostracods (Table 5). Fish debris (fragments, scales and teeth) are ubiquitous in a range of faunal associations throughout the Strathclyde Group, but occur frequently with Type 3 and 4 assemblages (Table 5). The most

complete specimen is a small fish jaw, with affinities to the actinopterygian *Rhadinichthys ferrox* Traquair (Z. Johanson pers. comm.).

Type 4 Assemblage elements are present in Facies 3b, 5, 6 and 7. Facies 3b is medium-grained, quartz arenite sandstone units (2–10 m in thickness), with *Stigmara* roots and bioturbated bases and tops of beds, common in all studied sections. Sedimentary structures include sigmoidal surfaces, trough cross-bedding, planar cross-bedding, current ripples and rare desiccation cracks. Sandstones are commonly interbedded with mudstones on a centimetre to millimetre scale. The thinner beds (commonly 1 m or less), compared to the thicker or convoluted beds of Facies 3a, can be clearly distinguished at exposure. Low-diversity ichnofossil assemblages are most common in this facies and include *Monocraterion*, *Arenicolites*, *Diplocraterion*, *Skolithos* and *Teichichnus* and *Palaeophycus* and

Table 3. Ostracod faunal associations of species from the Strathclyde Group

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
1 <i>Acratia</i> sp. A.										X	X												X	X	
2 <i>Acutiangulata</i> sp. A.			X							X														X	
3 <i>Bairdia submucronata</i>		X								X														X	
4 <i>Carbonita bairdioides</i>										X															
5 <i>Carbonita</i> cf. <i>fabulina</i>		no associations																							
6 <i>Carbonita</i> cf. <i>humilis</i>		no associations																							
7 <i>Carbonita</i> cf. <i>inflata</i>										X	X														
8 <i>Carbonita</i> sp.										X		X													
9 <i>Cavellina benniei</i>										X					X										X
10 <i>Cavellina valida</i>	X	X		X			X	X	X			X	X	X	X	X	X						X	X	
11 <i>Cavellina</i> sp.							X			X		X					X		X				X	X	
12 <i>Geisina arcuata</i>	X						X		X	X													X	X	X
13 <i>Glyptolichvinella spiralis</i>		no associations																							
14 <i>Healdia</i> cf. <i>cuneata</i>										X				X			X								
15 <i>Hollinella (Keslingella) radiata</i>									X	X			X	X	X	X								X	
16 palaeocope sp. A										X	X			X	X	X	X						X	X	X
17 palaeocope sp. B											X					X								X	
18 palaeocope sp. C										X			X	X										X	
19 palaeocope sp. D											X					X								X	
20 <i>Paraparchites armstrongianus</i>																								X	
21 <i>Paraparchites circularis</i> n. sp.																									X
22 <i>Polycope elegans</i> n. sp.		no associations																							
23 <i>Shemonaella ornata</i> n. sp.	X									X	X	X				X									X
24 <i>Shemonaella elongata</i> n. sp.	X	X	X						X	X	X	X		X	X	X	X	X	X	X					X
25 <i>Silenites</i> sp. A.										X						X						X	X	X	

These data do not include the frequency of occurrences; this information is shown for four selected non-marine ostracods in Table 5.

Planolites. Rare body fossils include *Naiadites*, fish, plants, ‘*Spirorbis*’, *Lingula*, Spinicaudata, Type 1 and Type 2 Assemblage bivalves and poorly preserved ostracods. Facies 5 sediments are mudstones, carbonaceous shales, siltstones and sandstones with plentiful plant debris; common in the Anstruther and Sandy Craig formations (Fig. 5a–h). The Type 4 Assemblage ostracods are most diverse in Facies 5.

Facies 6 sediments are blackband ironstones composed of alternating iron-rich mudstone (occasionally siltstone) laminae, black carbonaceous mudstone laminae and coal with abundant plant debris; present in sections of the Pathhead, Sandy Craig and Pittenweem formations (Fig. 5). Common fauna in this facies are Spinicaudata, *Lingula*, *Curvirimula*, fish, ‘*Spirorbis*’ and ostracods (Fig. 6a). Ostracods are mostly preserved as carapaces and occur on both ironstone and mudstone laminae, but are more common on the iron-rich laminae. *Paraparchites circularis* n. sp. occurs within a 20 cm thick blackband ironstone in great abundance, associated with plant debris, rare fish and rare *Carbonita* cf. *inflata* and *Silenites* sp. A. In this thanatocoenosis ostracod carapaces are randomly oriented; adult carapaces are most abundant, with some juveniles (Fig. 6a).

Coals and extensively rooted sandstones or siltstones (‘seat-earths’) are associated with Facies 6. No ostracods have been identified from coals although *Carbonita* is common in Pennsylvanian coal deposits elsewhere (see, for example, Bless & Pollard, 1973; Sohn, 1977; Schäfer, 2007). The ‘seat-earths’ commonly underlie shaly coal or coal beds, range in thickness from 0.1–1 m, and do not contain ostracods or macrofauna. The roots are composed of large 1 cm diameter siderite-filled vertical roots and smaller

(millimetre thick) organic branching rootlets. Thin units with remnant sedimentary structures are common in all formations and are often overlain by cross-bedded or laminated sandstones. Thicker units (1 m thick) with pervasive root structures are prominent because the roots have destroyed any sedimentary structures. Three of these thick units are identified from field exposures of the Pittenweem and Sandy Craig formations and each is overlain by coals.

Facies 7 dolomitized algal limestones are most numerous in the Anstruther Formation (Fig. 2), and are either stromatolitic or of oncoidal-type concentric form. The fauna includes ‘*Spirorbis*’, fish and plant debris, coprolites, *Naiadites*, and the ostracods *Carbonita* sp., rare *Glyptolichvinella spiralis*, *Shemonaella elongata* n. sp. and mostly indeterminate ostracods. Most limestone beds contain elements of both vertically stacked hemispheroids (stromatolites) and concentrically laminated spheroids (oncoids). Oncoids range in size (centimetres to millimetres), while stromatolites vary in form from laminated to well-formed hemispheroids. Vertically stacked hemispheroids have *Cryptozoon*-like club or columnar shapes in outline (Logan, Rezak & Ginsburg, 1964) and some are brecciated at the top (probably owing to desiccation). The basal radius of the laminae increases upwards and domes at the top (Fig. 6b). The spaces between the hemispheroids and within desiccation cracks are filled with oncoids, detrital sediment, fish fragments and abundant ostracods. Freshwater stromatolites are typically composed of a diverse community of algae and microinvertebrates (Freytet & Verrecchia, 1998). The Strathclyde Group limestones have been extensively dolomitized (Searl, 1991) and particular algal species cannot be determined.

Table 4. The macrofossils and ostracods of the Strathclyde Group, grouped into their respective assemblage types

TYPE 1 ASSEMBLAGE	TYPE 2 ASSEMBLAGE	TYPE 3 ASSEMBLAGE	TYPE 4 ASSEMBLAGE
Ostracoda <i>Acutiangulata</i> sp. A <i>Bairdia submucronata</i> <i>Cavellina benniei</i> <i>Cavellina valida</i> <i>Healdia</i> cf. <i>cuneata</i> <i>Hollinella</i> (<i>Keslingella</i>) <i>radiata</i> <i>palaeocope</i> sp. A <i>palaeocope</i> sp. C <i>Paraparchites armstrongianus</i> <i>Polycope elegans</i> n. sp. <i>Shemonaella siveteri</i> n. sp. Bivalvia <i>Actinoptera persulata</i> <i>Actinopteria</i> <i>Aviculopecten plicatus</i> <i>Aviculopecten planoclathratis</i> <i>Aviculopecten</i> cf. <i>subconoideus</i> <i>Aviculopecten</i> <i>Cypricardella</i> cf. <i>rectangularis</i> <i>Cypricardella</i> <i>Edmondia senilis</i> <i>Edmondia</i> <i>Hemipecten</i> <i>Leiptera</i> <i>Limipecten</i> <i>Linoprotonia</i> <i>Lithophaga lingualis</i> <i>Lithophaga</i> <i>Modiolus sublamellosa</i> <i>Myalina</i> <i>Naiadites crassus</i> <i>Nuculoid</i> <i>Nucleopus gibbosa</i> <i>Palaeolima</i> <i>Palaeoneilo brevisstrom</i> <i>Palaeoneilo laevirostrum</i> <i>Palaeoneilo luiniformis</i> <i>Palaeoneilo mansonii</i> <i>Paleyoldia maegregori</i> <i>Parallelodon</i> <i>Permopecten sowerbii</i> <i>Permopecten</i> <i>Permopectinella</i> <i>Polenomorpha minor</i> <i>Polenomorpha</i> <i>Polidevica attenuata</i> <i>Punctospyrifa</i> <i>Sanguinolites clavatus</i> <i>Sanguinolites costellaters</i> <i>Sanguinolites variabiles</i> <i>Sanguinolites</i> <i>Schizodus</i> <i>Sedgwickia gigantea</i> <i>Sedgwickia</i> <i>Solenomorpha</i> cf. <i>minor</i> <i>Solenomorpha</i> <i>Streblochondria elliptica</i> <i>Streblochondria</i> <i>Streblopteria ornata</i> <i>Wilkingia maxima</i> <i>Wilkingia</i> Porifera <i>Hyalostelina</i>	Brachiopoda <i>Crurithyris</i> <i>Echinocorihus</i> cf. <i>purictatus</i> <i>Lingula squariformis</i> <i>Lingula mytilloides</i> <i>Lingula</i> <i>Orbiculoidea cincta</i> <i>Orbiculoidea</i> <i>Orthotetoid</i> <i>Pleuropugnoides</i> <i>Productus</i> <i>Punctospirife</i> <i>Schizophoria</i> <i>Spirife</i> <i>Spiriferellina</i> <i>Trigonoglossa scotia</i> <i>Trigonoglossa</i> Gastropoda <i>Donaldina</i> <i>Euphemites</i> <i>Globroingulara</i> <i>Meekospira</i> <i>Murchisonid</i> <i>Naticopsis scotoburdigalensis?</i> <i>Naticopsis</i> <i>Pseudozygopleura</i> cf. <i>rugifera</i> <i>Pseudozygopleura</i> <i>Retispira decurrata</i> <i>Retispira striata</i> <i>Retispira</i> Scaphopoda <i>Dentalium</i> Cnidaria <i>Lithostrotion junceum</i> Bryozoa <i>Fenestella trepostome</i> <i>Rhabdomason</i> Echinodermata <i>Archaeocidaris</i> <i>Crinoid columnals</i> <i>Echinocidaris</i> Arthropoda <i>Trilobite fragment</i> indet. Cephalopoda <i>Beyrichoceratoides</i> <i>Goniatite fragments</i> indet. <i>Stroboceras</i> <i>Nautiloid</i> indet. <i>Orthocones</i> indet. Others <i>Conularid</i> <i>Paraconularia</i> <i>Serpulites carbonius</i> <i>Serpulites</i> Ichtnolites <i>Chondrites</i>	Ostracoda <i>Cavellina</i> sp. <i>Geisina arcuata</i> <i>palaeocope</i> sp. A <i>palaeocope</i> sp. B <i>Paraparchites armstrongianus</i> <i>Shemonaella siveteri</i> n. sp. Bivalvia <i>Myalina</i> <i>Naiadites crassus</i> <i>Naiadites obesus</i> <i>Naiadites</i> <i>Sanguinolites clavatus</i> <i>Sanguinolites costellaters</i> <i>Sanguinolites plicatus</i> <i>Sanguinolites variabiles</i> <i>Sanguinolites</i> <i>Schizodus pentlandicus</i> <i>Schizodus</i> Brachiopoda <i>Lingula squamiformis</i> <i>Lingula mytilloides</i> <i>Lingula</i> Vertebrata <i>fish fragments</i> indet. Others <i>coprolites</i> Ichtnolites <i>Arenicolites</i> <i>Diplocraterion</i> <i>Monocraterion</i> <i>Palaeophycus</i> <i>Planolites</i> <i>Skolithos</i> <i>Teichichnus</i> TYPE 3 ASSEMBLAGE Ostracoda <i>Carbonita</i> sp. <i>Cavellina benniei</i> <i>Cavellina taidonensis</i> <i>Cavellina</i> sp. <i>Geisina arcuata</i> <i>palaeocope</i> sp. A <i>palaeocope</i> sp. B <i>Paraparchites circularis</i> n. sp. <i>Shemonaella siveteri</i> n. sp. <i>Shemonaella ornata</i> n. sp. <i>Silenites</i> sp. A Bivalvia <i>Curvirimula</i> <i>Curvirimula</i> cf. <i>scotica</i> <i>Naiadites crassus</i> <i>Naiadites obesus</i> <i>Naiadites</i> Vertebrata <i>fish fragments</i> indet. Others <i>coprolites</i> <i>'Spirorbis'</i> <i>stromatolites</i>	Ostracoda <i>Carbonita</i> sp. <i>Carbonita bairdioides</i> <i>Carbonita</i> cf. <i>fabulina</i> <i>Carbonita</i> cf. <i>humilis</i> <i>Carbonita</i> cf. <i>inflata</i> <i>Cavellina benniei</i> <i>Cavellina valida</i> <i>Cavellina</i> sp. <i>Geisina arcuata</i> <i>palaeocope</i> sp. A <i>palaeocope</i> sp. B <i>Paraparchites circularis</i> n. sp. <i>Shemonaella siveteri</i> n. sp. <i>Shemonaella ornata</i> n. sp. <i>Silenites</i> sp. A Bivalvia <i>Anthraconaia?</i> <i>kirki</i> <i>Carbonicola antiqua?</i> <i>Carbonicola elegans</i> <i>Carbonicola</i> <i>Cardiopteridium</i> <i>Curvirimula</i> cf. <i>scotica</i> <i>Curvirimula</i> <i>Naiadites obesus</i> <i>Naiadites</i> Brachiopoda <i>Estheria</i> <i>Euestheria</i> <i>Leaia</i> Vertebrata <i>fish fragments</i> indet. <i>actinoptergian jaw</i> Others <i>Coprolites</i> <i>'Spirorbis'</i> <i>stromatolites</i> Plants <i>spinose megaspores</i> <i>Sphenopteris affinis</i> <i>Telangium affinae</i> ENVIRONMENT UNCERTAIN Ostracoda <i>Acratia</i> sp. A <i>Glyptolichvinella spiralis</i> <i>palaeocope</i> sp. D

Three ostracod species do not occur with other fauna and therefore have an uncertain ecology.

In the Anstruther Formation Randerston section (Fig. 6c–f) an algal limestone with both stromatolitic (Fig. 6c) and oncoidal forms (Fig. 6d, f) contains the earliest record of *Carbonita* from the Midland Valley. Some of the oncoids incorporate pisoliths and

ostracods in their centres. The ostracod assemblage is composed of 30% carapaces, whole single valves, and a range of adults and juveniles, representing a thanatocoenosis (Fig. 6f). In other areas there are abundant single valves, densely packed together,

Table 5. Faunal associations of common Strathclyde Group non-marine macrofossils and ostracods

Assemblage	Type 1		Type 2				Type 3				Type 4							
	Marine macrofauna	Marine ostracods	<i>Lingula</i>	<i>Sanguinolites</i>	<i>Schizodus</i>	<i>Cavellina</i>	<i>Shemonaella</i>	<i>Curvirimula</i>	Fish (debris)	<i>Naiadites</i>	' <i>Spirorbis</i> '	<i>Geisina</i>	<i>Anthraconaia?</i>	<i>Carbonicola</i>	<i>Cardiopteridium</i>	<i>Spinicaudata</i>	<i>Carbonita</i>	Plant (debris)
Types 2–4 fauna of interest																		
Macrofossils																		
<i>Anthraconaia?</i>	0	0	0	0	0	0	0	0	1	2	0	0	X	0	0	0	0	0
<i>Carbonicola</i>	1	0	0	0	1	0	0	0	2	0	0	0	0	X	0	0	0	5
<i>Cardiopteridium</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	X	0	0	1	
<i>Curvirimula</i>	1	0	0	0	0	0	0	X	17	0	18	0	0	0	0	0	21	
Fish (indet.)	3	0	7	0	3	0	0	16	X	15	20	0	1	2	0	4	33	
<i>Lingula</i>	39	0	X	2	6	0	0	0	9	13	0	0	0	0	2	0	2	
<i>Myalina</i>	3	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Naiadites</i>	6	0	14	0	5	0	0	0	12	X	12	0	1	0	1	5	25	
<i>Sanguinolites</i>	22	0	2	X	2	0	0	0	0	0	1	0	0	0	0	0	1	
<i>Schizodus</i>	15	0	6	1	X	0	0	0	3	4	2	0	0	1	0	0	3	
<i>Spinicaudata</i>	0	0	0	0	0	0	0	0	4	6	0	0	0	0	X	0	11	
' <i>Spirorbis</i> '	3	0	0	1	2	0	0	17	21	12	X	0	0	0	0	0	11	
Ostracods																		
<i>Carbonita</i>	0	0	1	0	1	3	1	1	3	11	4	7	0	0	0	X	3	
<i>Cavellina</i>	16	12	0	1	0	X	14	1	3	15	1	1	0	0	1	2	5	
<i>Geisina</i>	2	1	1	0	0	2	2	0	1	10	0	X	0	0	0	0	1	
<i>Shemonaella</i>	21	6	3	2	0	16	X	9	6	22	4	2	0	0	1	1	2	

Numbers represent the frequency with which the fauna occur in the same assemblage. An X refers to where the same fauna crosses, for example the association of *Cavellina* with itself. Marine macrofauna include groups such as brachiopods, bryozoa and gastropods, as defined for the Midland Valley of Scotland by Wilson (1989), and in this study as a Type 1 Assemblage. For ostracods, the occurrence data are compiled from the single or often multiple species present for that genus.

representing a taphocoenosis. Overall, the ostracod taphonomy in most algal limestone beds suggests only some limited localized transport.

Pisolithic limestones are the most common in the Anstruther Formation and can contain '*Spirorbis*', fish (debris), ostracods, rare *Lingula*, rare *Myalina* and abundant plant debris. In the Kingsbarns section a layer with irregular-shaped pisoliths (some of which contain ostracods in the centre) is overlain by siltstone packed with wood debris, including logs up to 4 m in length (Fig. 6g, h). Poorly preserved ostracods are present in both layers, with single valves composing 95 % of the assemblage.

5. Ecological interpretation of the Strathclyde Group macrofauna and ostracods

The interpretation of the ecology of the ostracods is based on macrofauna–ostracod or ostracod faunal associations, with reference to known Mississippian ostracod distribution patterns (Tables 2, 4; Fig. 7). Palaeoenvironments are interpreted based on faunal and sedimentological evidence (Fig. 8).

5.a. Type 1 Assemblage: marine

These fossil groups have been determined in the MVS as marine (Wilson, 1989). *Chondrites* is a Palaeozoic marine ichnogenus (Buatois *et al.* 2005). Most pelagic Type 1 Assemblage fossils are fragmented, while well-preserved benthic shelf faunas are the richest, and contain the most abundant fossils.

Twelve ostracod species from this assemblage are considered marine (Fig. 7). Of these, *Acutiangulata* sp. A, *Bairdia submucronata*, *Healdia* cf. *cuneata*, *Hollinella* (*Keslingella*) *radiata*, *palaeocope* sp. C and *Polycope elegans* n. sp. are considered to be stenohaline, as they are only associated with marine macrofossils. *Bairdia* is abundant in Mississippian marine assemblages (Bless, 1983; Bless, Strel & Becker, 1988), as are *Healdia* and *Hollinella* (Přibyl, 1960; Olempska, 1993; Athersuch *et al.* 2009). *Acutiangulata* is known for its possible brackish-water tolerance, in association with *Shemonaella*, *Cavellina* and '*Spirorbis*' (Athersuch *et al.* 2009; Robinson, 1978). *Polycope elegans* n. sp. is associated with marine macrofossils in a thanatocoenosis. Polycopids are supposed nektobenthic ostracods (Horne, 2003) and are reported as marine in the Mississippian (Dewey & Fähræus, 1987).

Facies 1 sediments are interpreted as near-shore, shallow marine deposits. Metres-thick successions of mudstones (containing articulated orthocones), representing fairly prolonged marine conditions, occur in the Pathhead Formation (Fig. 8), but are rare. Frequent short-lived marine transgressions are represented by thin marine mudstones overlain by coarsening-upwards successions. The low diversity of the marine ostracod fauna suggests short-lived open marine conditions. Only six species are interpreted as stenohaline and other common Mississippian marine ostracods such as *Kirkbya* and *Amphissites* (Coen, Michiels & Parris, 1988; Olempska, 1993) are absent. The tens of metres thick sandstone units of Facies 3a, with

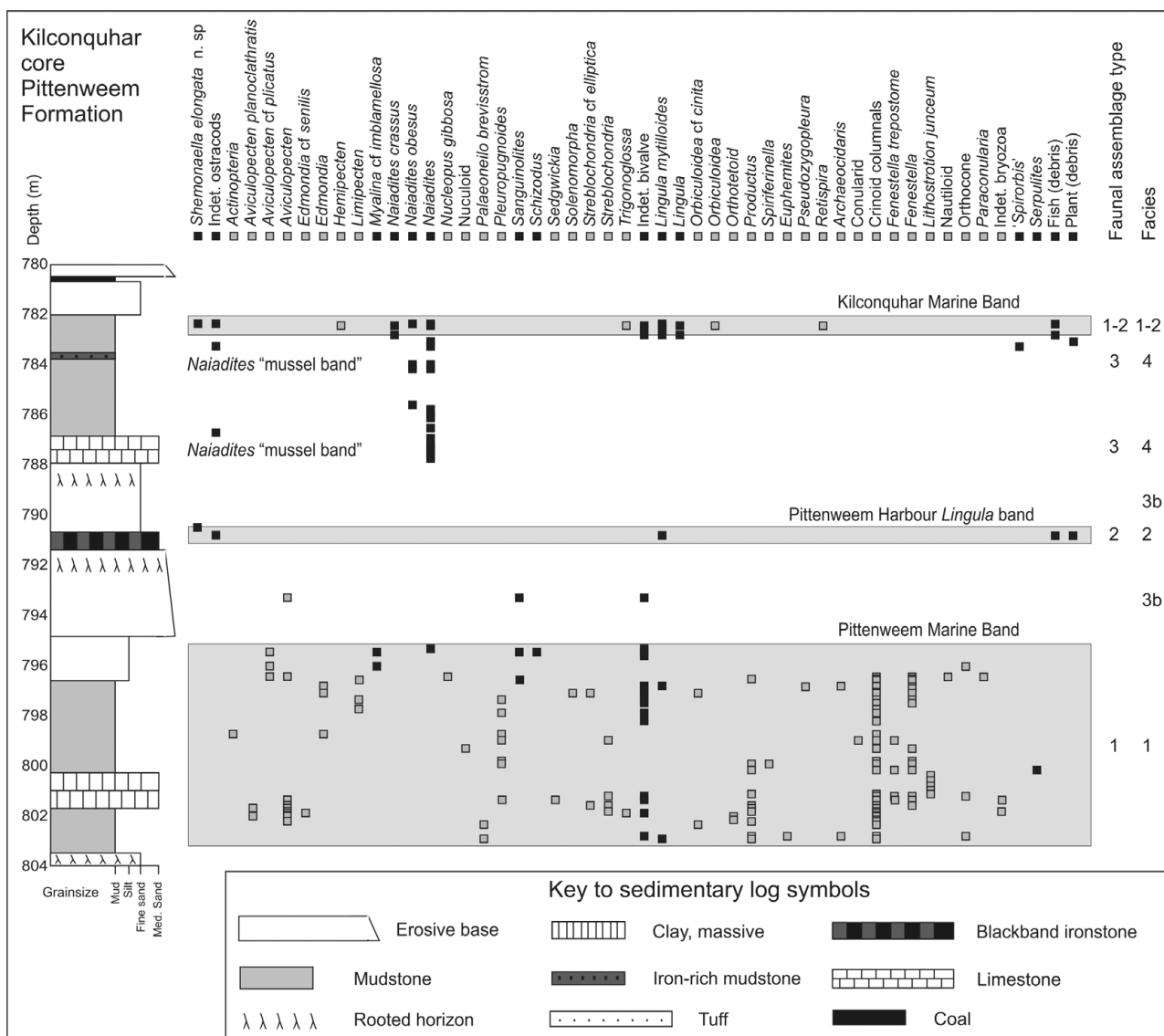


Figure 3. Sedimentary log and fauna of part of the Pittenweem Formation. Type 1 Assemblage elements are represented by a grey colour square and Type 2 to 4 assemblage elements by a black square, at the height in the core at which they occur. The sedimentary log key covers Figures 3–5.

convolute-bedding and channel forms indicate proximal deltaic mouth bar deposition, with a rare marine macrofauna incorporated at the delta front.

5.b. Type 2 Assemblage: marginal marine

The lower-diversity Type 2 Assemblage is interpreted as marginal marine. *Lingula squamiformis* from the Mississippian of the MVS has been interpreted as a brackish species (Ferguson, 1963). Here, *Schizodus*, *Sanguinolites* and *Lingula* have similar faunal associations and are interpreted as marginal marine. *Myalina* is recorded as a common freshwater bivalve by Ferguson (1962), but in the present study its associations (Table 5) determine it as marginal marine, albeit based only on low numbers of specimens.

Six species from the Type 2 Assemblage, that occur in a range of marine, marginal marine and brackish to freshwater sediments (Fig. 7), are considered as eurytopic or marginal marine. Post-Palaeozoic

ostracods of the Suborder Platycopina are exclusively marine (Horne, 2003), but the Mississippian platycopes *Cavellina*, *Geisina* and *Glyptolichvinella* are euryhaline or of uncertain ecology. At a generic level, ostracod–macrofaunal associations reveal that *Cavellina* and *Shemonaella* have a wide salinity tolerance (Table 5). In particular, the species *Cavellina valida* and *Shemonaella elongata* n. sp. are abundant (Table 2) and occur in a wide range of environments (Fig. 7) with many other ostracod species (Table 3) and are considered to be eurytopic. *Cavellina* is known for its marginal marine to brackish-water tolerance in Carboniferous environments (Robinson, 1978; Williams *et al.* 2005, 2006). Many Mississippian *Shemonaella* species are interpreted as marine (for example, Crasquin, 1985; Dewey, 1983), but some are considered as brackish (Tibert & Scott, 1999). Mississippian species of *Paraparchites* with dorsal spines occur in association with typically marine genera such as *Amphissites* and *Bairdia* (Sohn, 1969).

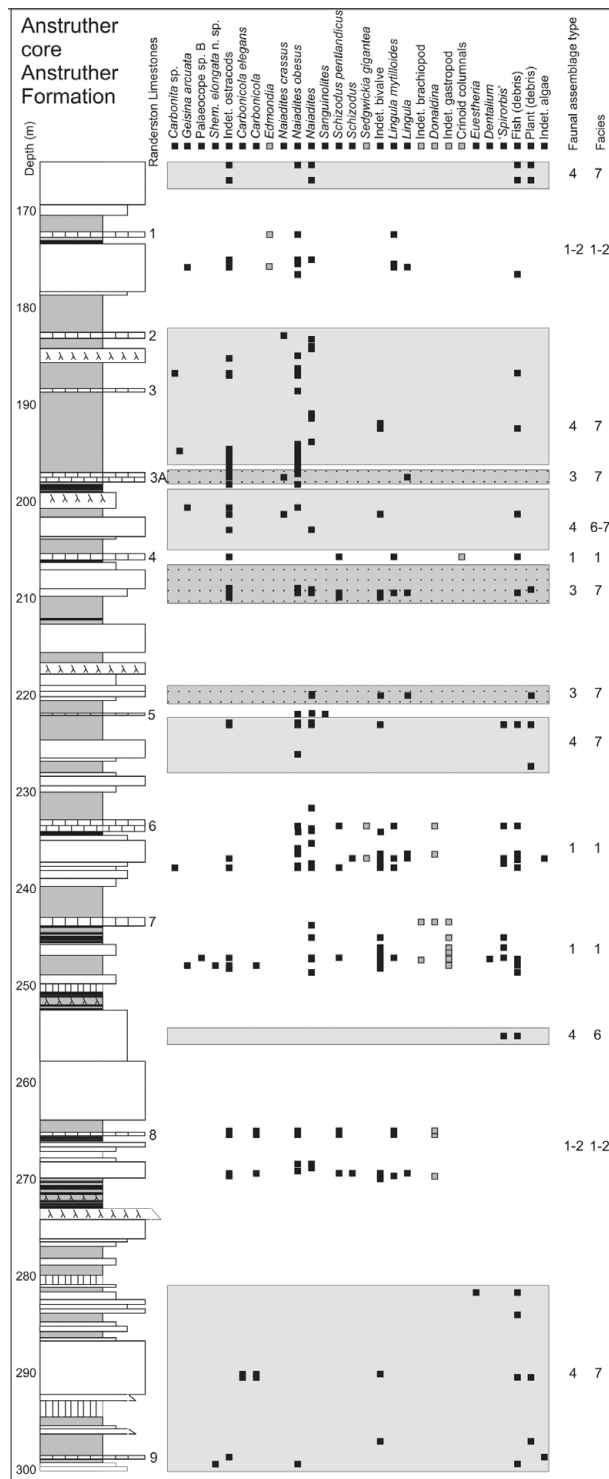


Figure 4. Sedimentary log and fauna of part of the Anstruther core (Randerston Section), Anstruther Formation. Sediments containing Type 3 and 4 assemblages are highlighted with shaded boxes in the background. The Randerston limestones 6 and 7 are typical of those containing a Type 1 Assemblage from this formation.

Here, *Paraparchites armstrongianus* is interpreted as marginal marine (Fig. 7, Table 5). Marginal marine environments include lagoons, embayments or estuaries associated with lower salinities (Fig. 8). Many ostracods are eurytopic and these environments may

have provided a pathway for marine to non-marine transitions.

5.c. Type 3 Assemblage: brackish–freshwater

Palaeozoic spirorbids are reported from freshwater, brackish, marine and hypersaline environments (Taylor & Vinn, 2006; Wilson, 1989). Here, the faunal associations of ‘*Spirorbis*’ suggest that it is brackish-water tolerant. *Curvirimula*, *Naiadites*, fish and ‘*Spirorbis*’ are interpreted to have a brackish to freshwater tolerance.

Four ostracod species are interpreted as brackish to freshwater tolerant. *Geisina arcuata* is mostly associated with brackish to freshwater (Type 3) macrofossils (Table 5), and this is a common environmental interpretation for this species in the Mississippian (Pollard, 1966, 1969; Anderson, 1970; Bless & Pollard, 1973; Bless, Streel & Becker, 1988). *Paraparchites circularis* n. sp. occurs in great abundance in black-band ironstones, which may represent opportunistic reproduction in quickly colonizing this plant-rich environment. Carboniferous species of *Paraparchites* have been recorded from environments interpreted as marine (Dewey, 1988), non-marine (Kummerow, 1953; Williams *et al.* 2005) and hypersaline (Dewey, 1983, 1987, 1988; Williams *et al.* 2005, 2006). The associations of *Shemonaella ornata* n. sp. (ostracods, *Naiadites*, fish and plant debris) indicate more brackish-water tolerance than *S. elongata* n. sp. Despite its faunal associations here, Mississippian *Silenites* has been recorded from marine sediments (Crasquin, 1985).

Naiadites is commonly associated with brackish macrofauna such as *Curvirimula* and ‘*Spirorbis*’ or occurs as a monospecific assemblage in Facies 4 sediments. Its rare occurrence in association with marine faunas may be owing to post-mortem transport. *Naiadites* mussel bands have undergone post-depositional transport by currents and wave action, as is seen in shallow marine bivalve and oyster coquinas (Wakefield, 1995). As the exact palaeoenvironmental conditions of *Naiadites* and other macrofauna are not known, there is uncertainty regarding a brackish or a freshwater interpretation.

5.d. Type 4 Assemblage: freshwater

Anthraconaia, *Carbonicola* and *Cardiopteridium* are interpreted as freshwater bivalves (Bennison, 1960, 1961). *Anthraconaia* and *Carbonicola* are commonly associated with *Naiadites* in Pennsylvanian freshwater Coal Measures (for example, Jenkins, 1960; Hartley, 1993; Brand, 1996; Eagar & Belt, 2003). *Anthraconaia*, *Carbonicola*, *Curvirimula* and *Naiadites* occur in brackish (Ballèvre & Lardeux, 2005) or lacustrine Mississippian sediments (Guirldham *et al.* 2003) and freshwater Pennsylvanian sediments (Brand, 1994; Anderson *et al.* 1999; Falcon-Lang, 2005; Falcon-Lang *et al.* 2006).

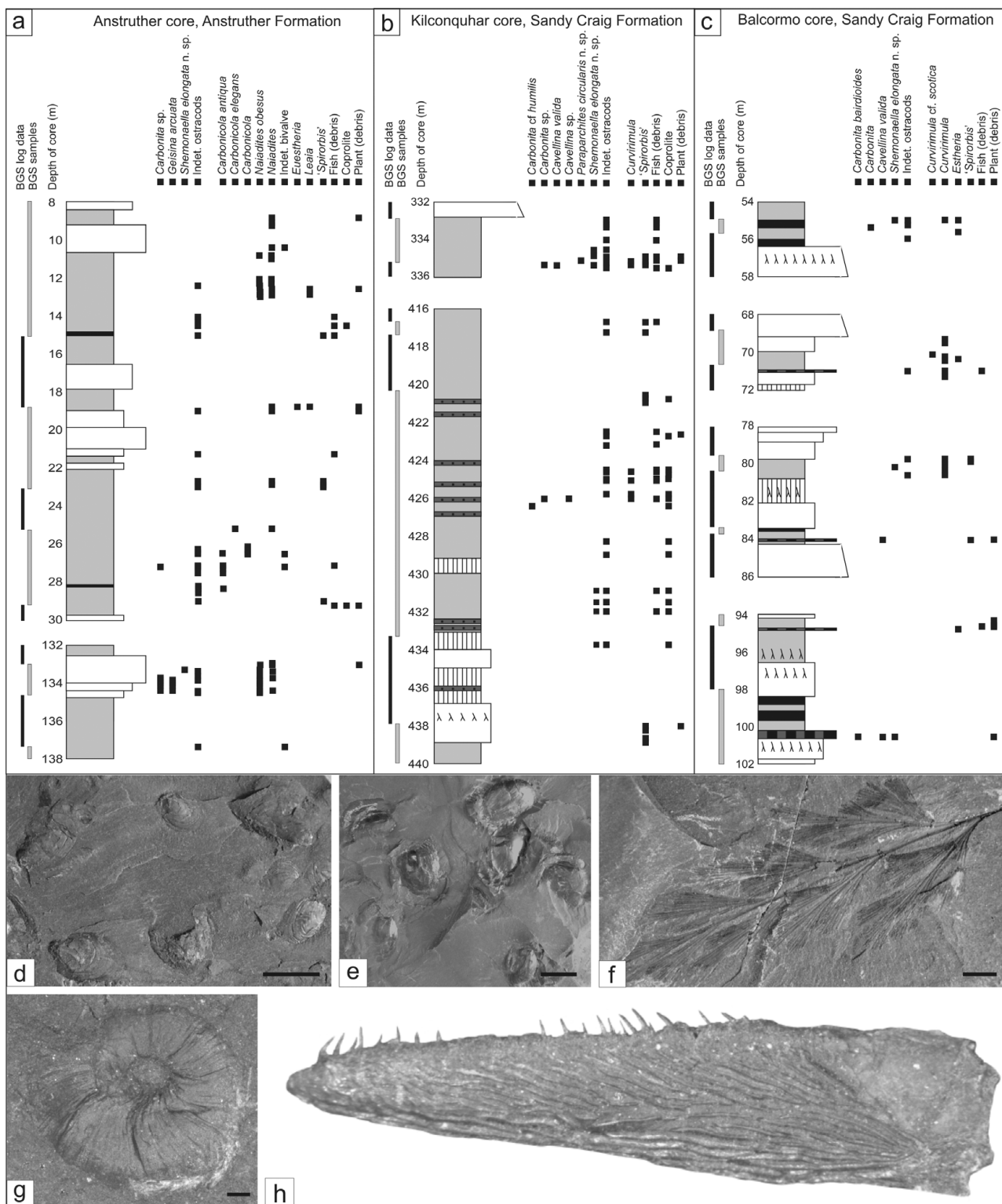


Figure 5. Sedimentary logs of Facies 5 and 6 containing ostracods (a–c) and common Type 3 and 4 assemblage macrofossils (d–h). Mudstones contain the most fossils. (d) *Curvirimula cf. scotica*, pyritized, GSE 15376. (e) *Naiadites obesus*, GSE 15378. (f) *Telangium affinae*, GSE 15380. (g) *Spirorbis*, GSE 15379. (h) Fish jaw plate with teeth, 10.5 mm in length, GSE 15382. Light photographs, scale bars 5 mm (d, f) and 0.2 mm (g). Specimens are stored in the palaeontology collection at the BGS, Edinburgh.

Extant Spinicaudata typically live in freshwater, but can tolerate salinities up to 6‰ NaCl. Late Palaeozoic Spinicaudata are found in a range of freshwater to brackish coastal plain sediments (Knox & Gordon, 1999; Jones & Chen, 2000; Park & Gierlowski-Kordesch, 2007). Some brackish water

records are interpreted as a taphocoenosis (for example Webb, 1979), and Late Palaeozoic spinicaudants mostly occur in freshwater environments, including coals and lake sediments (Orr & Briggs, 1999; Vannier, Thierry & Racheboeuf, 2003; Hmich *et al.* 2006).

The association of possible actinopterygian and sarcopterygian fish debris in Type 3 and 4 assemblages is consistent with a brackish to freshwater ecology. Freshwater actinopterygians and sarcopterygians are common in the Late Palaeozoic (for example, Daeschler, 2000; Trewin & Davidson, 1996; Turner, Kemp & Warren, 1999). In other contemporaneous MVS sedimentary rocks, fish occur in a range of water bodies, from deep-lagoonal (the Wardie Shales) to a semi-permanent lake on a coastal plain (the Foulden Beds; see Dineley & Metcalf, 1999).

Species of *Carbonita* are mostly associated with brackish to freshwater macrofossils (Table 5) and, importantly, only species of *Carbonita* occur exclusively in sediments interpreted as freshwater (Fig. 7): *Carbonita bairdioides* and *Carbonita* cf. *inflata* occur in blackband ironstones; *Carbonita* cf. *fabulina* and *Carbonita* cf. *humilis* in siltstones–mudstones associated with plant and fish debris. *Carbonita* is described from Mississippian brackish water sediments (Pollard, 1985; Sohn, 1985; Tibert & Scott, 1999). Vannier, Thiery & Racheboeuf (2003) first document unambiguous freshwater *Carbonita* from Pennsylvanian sediments deposited in an intramontane temporary pond.

The cross-bedded sandstones with sigmoidal structures of Facies 3b are interpreted as meandering fluvial channels. The low-diversity ichnofauna typify brackish to estuarine conditions (Buatois *et al.* 2005), consistent with a macrofauna of *Naiadites*, fish and plants. Over-bank deposits contain *Stigmara* roots and desiccation cracks. The mouth bar and alluvial environments are important components of the environment, but lack ostracods (Fig. 8). Facies 5 mudstones containing Type 3–4 assemblages and abundant plant debris are interpreted as freshwater inland lake or temporary pond deposits. These are present in all except the Pittenweem Formation (Fig. 8). Temporary pools or shallow lakes are a common habitat for Spinicaudata (Vannier, Thiery & Racheboeuf, 2003) and fish (Dineley & Metcalf, 1999) in the Carboniferous. The ostracod-bearing pisolithic plant-rich algal limestone is interpreted to have formed in a shallow carbonate-rich temporary pond or lake where pisoliths formed. The original ostracod ecology is uncertain owing to transport; the ostracods may have originated in a nearby freshwater swamp where wood accumulated, and were later transported to the site of deposition.

The blackband ironstones of Facies 6 represent a key depositional environment for freshwater ostracods. The macrofaunal content of these sediments favours a freshwater interpretation. Blackband ironstones are common in the Pennsylvanian Coal Measures, generally associated with upper delta-plains to alluvial floodplains and coastal plain swamps with small lakes (Boardman, 1989). The Strathclyde Group depositional setting is interpreted as a swampy wetland where plant debris had time to accumulate, creating the black laminae alternating with iron-rich mudstone–siltstone deposited in shallow water stream-fed pools. Fine grain

size suggests still-water deposition and the laminae indicate shallow to fluctuating water levels and the periodic accumulation of plant debris.

The ‘seat-earths’ present below coal beds are interpreted as exposure surfaces on a well-drained floodplain, where vegetation had time to develop. Most of these horizons are thin, and are interpreted as relatively brief periods of sub-aerial exposure. The three thicker, extensively rooted horizons are interpreted as palaeosols that developed over a longer time period, and would be classified as a spodosol (sandy forest soil; Retallack, 2001). These units are important for interpreting terrestrial conditions.

The non-marine limestones/dolostones (Facies 7) and associated sedimentary rocks of the Anstruther Formation are a key environment for early non-marine ostracods (Fig. 8). Within these lake-deltaic cycles, occasional marine transgressions occurred, but the predominance of Type 3 and 4 assemblages indicates that brackish to freshwater salinity conditions were the most prevalent. Freshwater conditions were unstable, seen in the variation of stromatolitic to oncoidal algal forms (Logan, Rezak & Ginsburg, 1964) and the presence of desiccation cracks, although the periods of exposure were short-lived enough not to result in pedogenesis (cf. MacNeil & Jones, 2006). Carboniferous freshwater algal limestones have been reported from the MVS (Guirdham *et al.* 2003), France (Freyet, Broutin & Durand, 2000) and Illinois (Scott, 1944). In the Pennsylvanian of Illinois stromatolitic limestones contain abundant indeterminate ostracods and ‘*Spirorbis*’, interpreted to have lived in a shallow water lake (Scott, 1944). Oncoidal-type grains are more problematic, as they have been described from a range of marine to non-marine settings (Davaud & Girardclos, 2001; Peryt, 1983). The algal species of the present study cannot be determined, but despite this, we know that ostracods lived in association with these algal forms and that the environment was probably freshwater.

5.e. Uncertain environment

When there is only one ostracod specimen for a particular species, with few or no associated faunas, the palaeoecology is uncertain, as in the case of *Acratia* sp. A, *Glyptolichvinella spiralis* and palaeocope sp. D. *Acratia* is reported as marine (Olempska, 1993), and *Glyptolichvinella* as marginal marine to brackish (Williams *et al.* 2005, 2006).

6. The ostracod radiation into non-marine environments

The success of the initial colonization of non-marine water bodies by ostracods was probably dependent on a number of factors, including intrinsic adaptations of ostracod species to lower salinities; extrinsic mechanisms to drive non-marine colonization, such as changing sea-levels; and a favourable aqueous

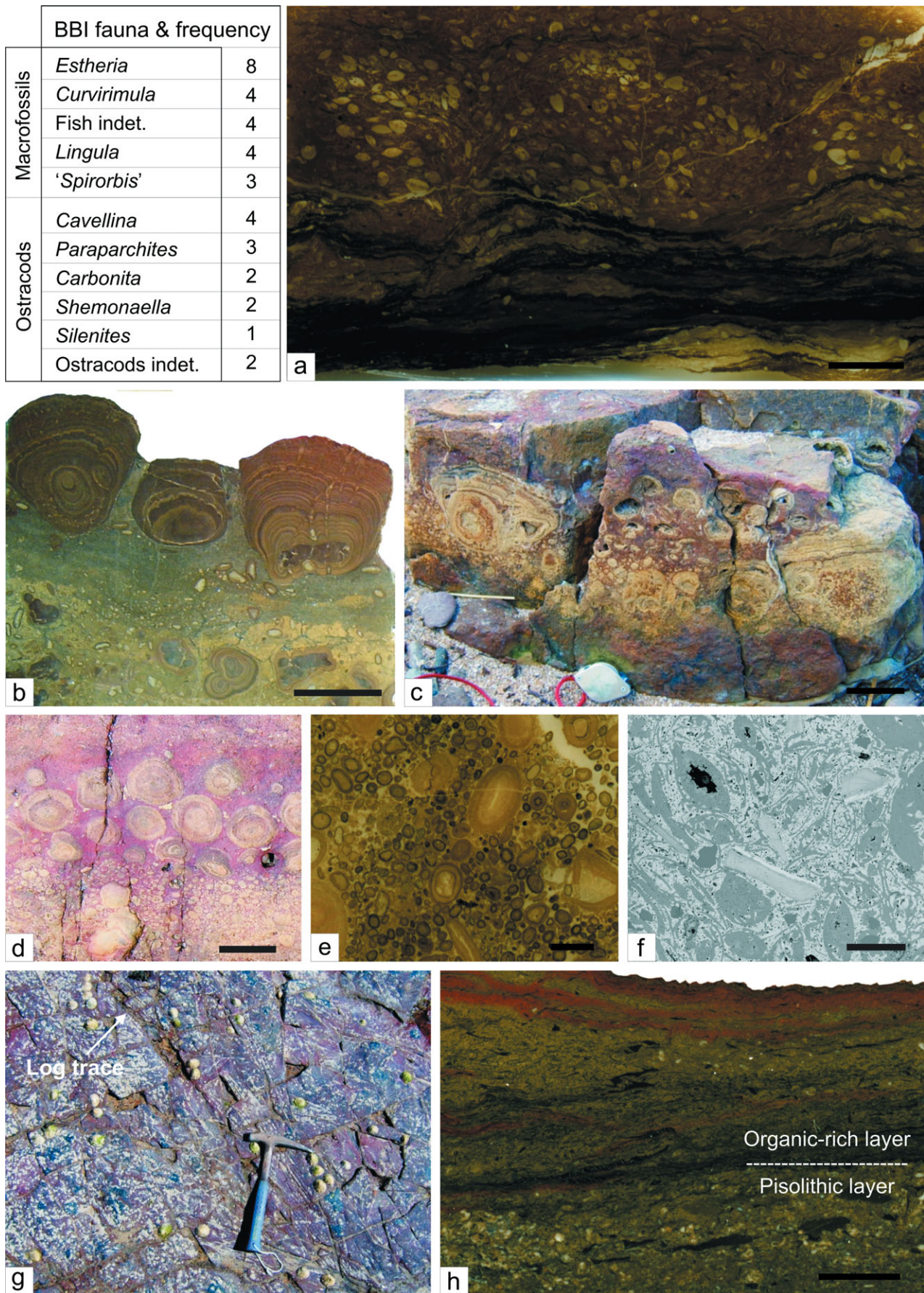


Figure 6. (Colour online) Facies 6 (blackband ironstone; BBI) and Facies 7 (algal limestones) containing ostracods. Table of fauna occurring within BBIs, the most common fauna is Spinicaudata. (a) Polished thin-section (PTS) of a BBI from the Sandy Craig Formation, containing abundant *Paraparchites circularis* n. sp., MPK 14009. (b) Well-formed stromatolites, Pittenweem Formation,

continental environment to foster ostracods in this new environment.

6.a. Intrinsic adaptations of non-marine ostracods

Of the brackish to freshwater ostracods from this study, their origin and affinity to known living freshwater ostracods is poorly resolved, particularly because all of these Carboniferous genera (*Carbonita*, *Cavellina*, *Geisina*, *Paraparchites*, *Shemonaella* and *Silenites*) became extinct by the end-Permian (Moore, 1961). The Carbonitoidea have no extant relatives or preserved soft parts for comparison. The origins of the Carbonitoidea are unknown; hypotheses link them to the marine Healdioidea (Retrum & Kaesler, 2005), Darwinulocopina or marine Sigilloidea (Horne, 2003). Retrum & Kaesler (2005) noted that the muscle scar pattern of Permian freshwater *Carbonita* is more like that of the Healdioidea than the Cytheroidea or Cypridoidea. While the Carbonitoidea have been compared to living podocopes such as *Cypridopsis* (Neale, 1984), the evidence for true cypridoideans in the Carboniferous is debated: some argue for a Late Palaeozoic origin (Lethiers & Damotte, 1993; Swain, 1976); others place the origin of the Cypridoidea in the Mesozoic (Horne 2003; Tibert *et al.* 2003; Whatley & Ballent, 1996).

Despite the problems of relating Carboniferous ostracods to living species, it is clear that important and fundamental physiological changes would be needed for ostracods to adapt to reduced salinities. Of primary importance are osmoregulation and reproductive changes, along with modifications in lifestyle. For the individual animal to survive it would have to regulate the salt intake and output. Osmoregulation takes place 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* are very successful at this and can survive in salinities of 1–40‰ NaCl (Keyser, 2005; Van Harten, 2000). Other ostracods, for example *Cavellina* species, which are interpreted as having been eurytopic herein, may have been as adaptable as *Cyprideis torosa*, although there are no visible signs to indicate how they dealt with osmoregulation, such as variation in carapace ornamentation. For Palaeozoic fossils with no preserved soft parts, inferences have to be made from the carapace. For paraparchitoidean ostracods, the strategy of having a large, thick carapace and an associated integumental circulatory system may have been beneficial in dealing with osmotic pressures caused by changing salinities. This has been

suggested for the Leperditicopida (Vannier & Abe, 1995; Vannier, Wang & Coen, 2001), which have a similarly proportioned carapace and are also adapted to non-marine environments, although it is not an exclusively freshwater adaptation.

Reproductive strategy to survive non-marine environments focuses on the ability to reproduce rapidly in often short-lived water bodies (r-strategy) and the development of desiccation-resistant eggs. Evidence for the first of these strategies comes from the hypothesis that Carboniferous paraparchitoideans may have used progenesis and parthenogenetic reproductive strategies to reproduce rapidly in hypersaline conditions (Dewey, 1987). The production of desiccation and transport-resistant resting eggs has been proposed for the Cypridoidea, which had a successful non-marine diversification the Early Cretaceous (Whatley, 1990*a,b*; Lethiers & Damotte, 1993). This adaptation would enable the survival of ostracods that lived in ephemeral water bodies such as seasonal freshwater lakes, like the resting eggs produced by the Spinicaudata of the Carboniferous Monteceau Lagerstätte, which are associated with *Carbonita* (Vannier, Thiery & Racheboeuf, 2003). Although *Carbonita* is fairly diverse in the Carboniferous (Anderson, 1970 identifies 17 species), no ostracod resting eggs have ever been found.

Possible modifications to lifestyle, such as feeding and locomotion changes, are more speculative. In the Pennsylvanian and Permian, *Carbonita* was better adapted than *Geisina* to different sedimentary niches, and it was more taxonomically diverse (Bless & Pollard, 1973). It has been proposed that *Carbonita* may have been a deposit feeder like the Recent *Cypridopsis*, and was perhaps therefore more adaptable than *Geisina*, which may have been a filter feeder like modern platycopes (Neale, 1984; Pollard, 1966). In terms of locomotion, some have argued the adaptation to a swimming mode of life was a key part to the success of the cypridoideans in colonizing non-marine environments in the mid-Mesozoic (along with the adaptation of desiccation-resistant eggs and parthenogenesis: Whatley, 1990*a,b*, 1992), and it is possible that this was also adopted by Carboniferous Carbonitidae.

6.b. Mechanisms for non-marine radiation

Like many aquatic animals, ostracods appear to have made the transition from marine to non-marine waters in a coastal setting. For example, early Mississippian *Carbonita* is associated with near-shore marine to low-salinity coastal ponds (Tibert & Scott, 1999).

SE 8699. (c–f) Images of the Randerston limestone 9, Anstruther Formation. (c) Vertically stacked hemispheroids and oncooids, field photograph. (d) Size-separated layers of oncooids and pisoliths, field photograph. (e) Abundant ooliths; the concentric laminae are a few microns in thickness, MPK 14004, PTS. (f) Abundant ostracod carapaces, single valves and fish teeth, MPK 14000, PTS, BSEM image. (g, h) Pisolithic plant-rich limestone, Kingsbarns section. (g) Top surface of the limestone bed with numerous log traces (see arrow), field photograph. (h) Cut section through the limestone bed, field sample 19. Scale bars 5 mm (a), 2 cm (b–d), 500 µm (e, f) and 10 mm (h).

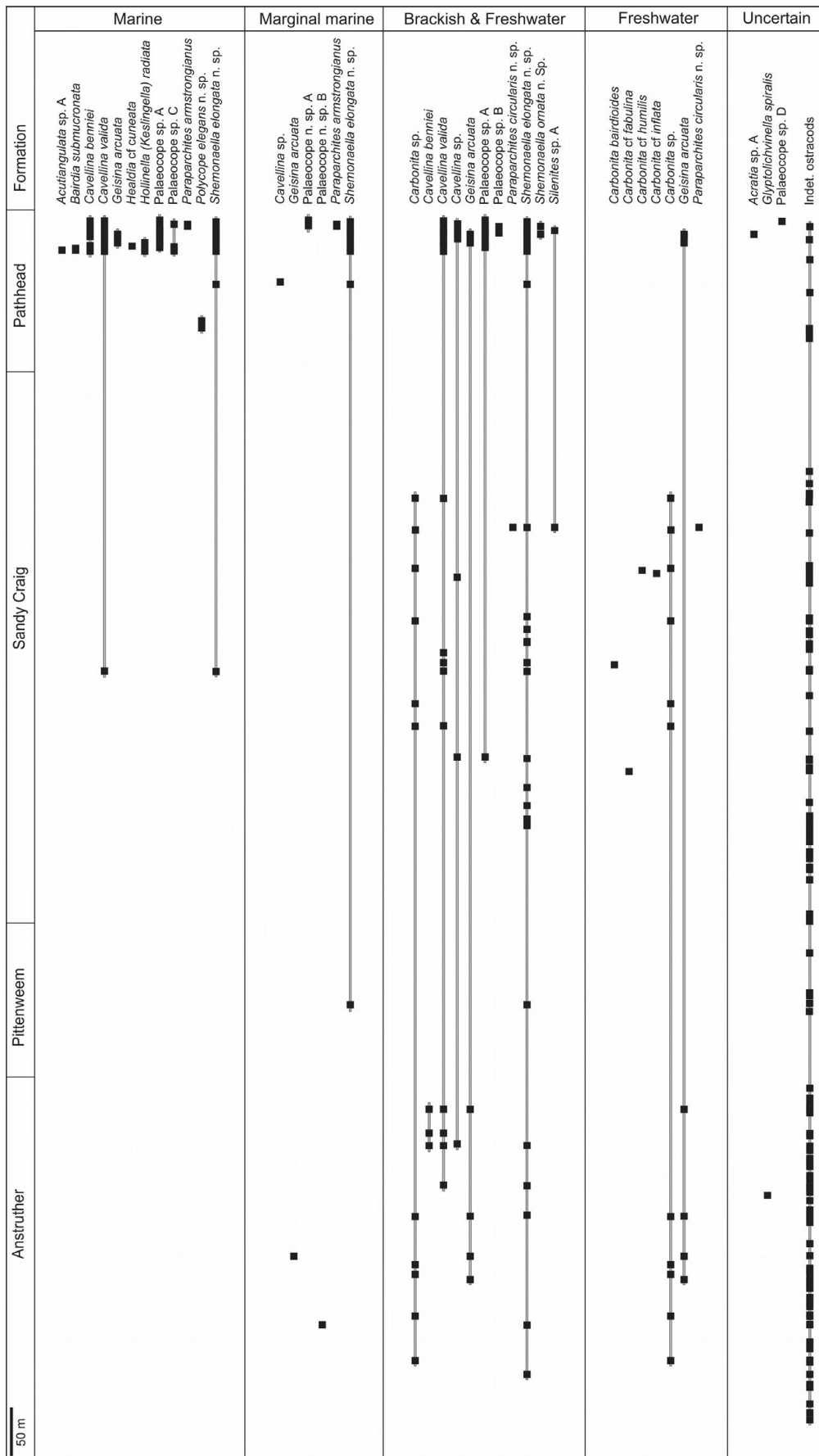


Figure 7. Stratigraphic range and palaeoenvironments of the Strathclyde Group ostracods. *Cavellina valida*, *Geisina arcuata*, *palaeocope* sp. A and *Shemonaella elongata* n. sp. are the most long ranging.

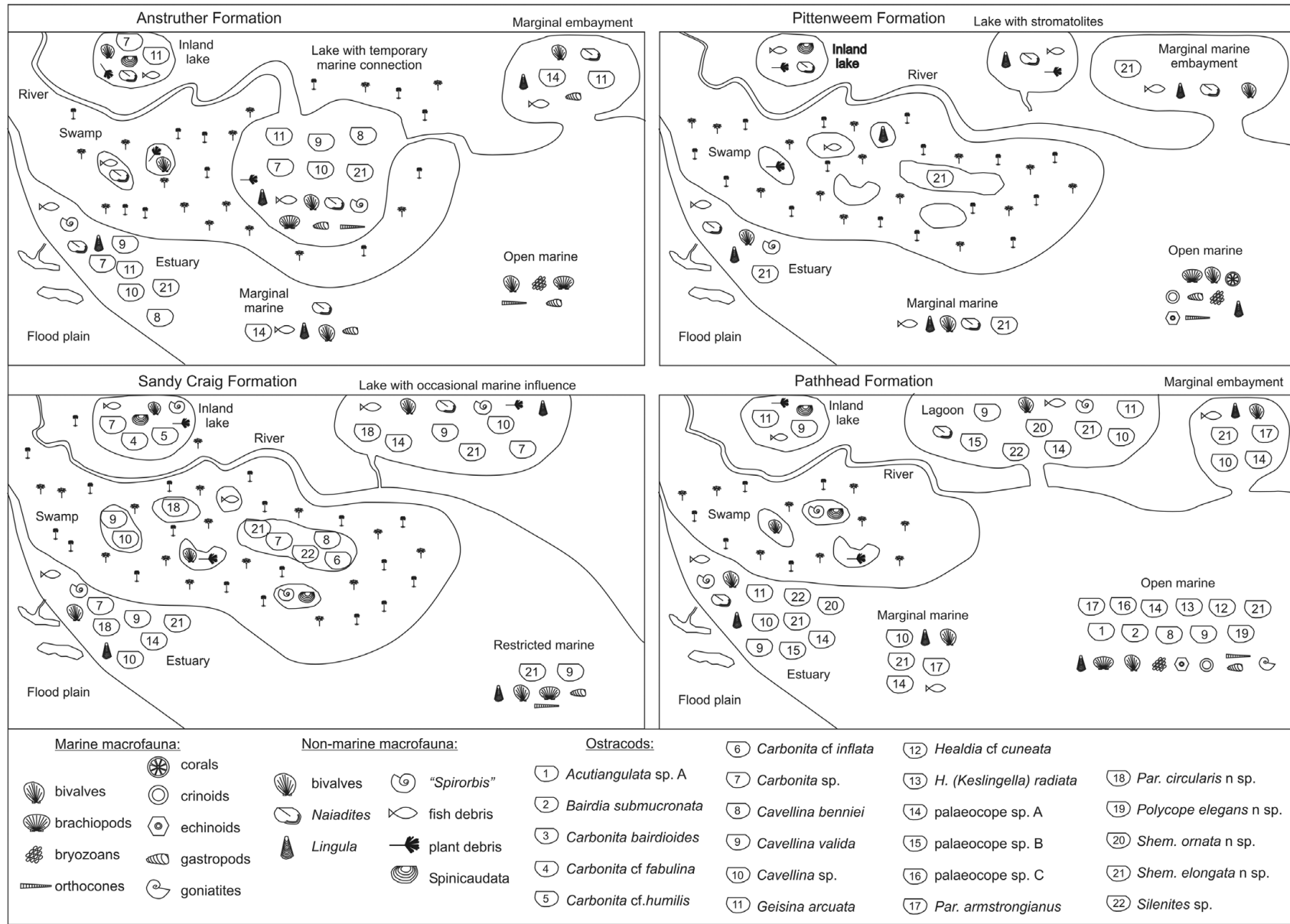


Figure 8. Palaeoenvironmental model of the ecological range of ostracods for the Anstruther to Pathhead formations. The environmental range of each ostracod species is plotted using the data from Tables 2 and 4, and does not include ostracods that have an indeterminate taxonomy or ecology. Plants are representations of a Carboniferous lycopsid and of *Valmeyerodendron*. Abbreviations used for ostracod species in the key: *H.* – *Hollinella*; *Par.* – *Paraparchites*; *Shem.* – *Shemonaella*. In the Anstruther Formation blackband ironstones are not present and coals are uncommon, so swampy conditions are minimized in the model. The presence of only *Shemonaella elongata* n. sp. ostracods in the Pittenweem Formation is due to poor preservation. The Sandy Craig Formation is dominated by non-marine conditions. Stromatolitic limestones are absent in the Pathhead Formation, so a near-shore lake is excluded from the model.

In the Pennsylvanian, *Carbonita* is also found in coastal environments, such as brackish waters and poorly drained coastal plain sediments (Falcon-Lang *et al.* 2006; Tibert & Dewey, 2006). This 'estuary effect' of non-marine colonization (Gray, 1988; Park & Gierlowski-Kordesch, 2007) is important as it allowed invertebrates to exploit marine transgressions and varying salinity to inhabit otherwise insupportable non-marine environments. In the Carboniferous of the MVS, the stratigraphical pattern of marine bands shows that there were fairly frequent but mostly short-lived marine transgressions and glacio-eustatic cycles from the late Viséan onwards (Kassi *et al.* 2004).

Following this estuarine or marine transgression pathway, it is possible that ostracods undertook 'active' and 'passive' (see Gray, 1988) non-marine colonization. Active invasion from the sea by euryhaline ostracods may have occurred at times of high sea-level. Marine species may have developed an osmoregulatory adaptation, to allow them to survive in rapidly changing salinities such as in an estuary. The 'incentive' for this costly physiological adaptation would have been access to a rich food source and relatively sparsely populated new habitat. Over time such ostracod species would become more tolerant of freshwater conditions and able to survive in freshwater bodies such as lakes. Evidence for this long-term ecological adaptation is suggested in the fossil record, with the first cases of ostracod-like animals close to land at delta-front settings in the early Cambrian (Loughlin & Hillier, 2010; Siveter & Williams, 1995), putative marginal marine to brackish ostracods from the Silurian (for example Floyd & Williams, 2003), brackish ostracods in the Devonian (for example Bless, 1983) and finally successful freshwater colonization in the Carboniferous (for example Vannier, Thiery & Racheboeuf, 2003).

Passive invasion may have occurred owing to fluctuating sea-levels and the restriction of ostracods to isolated habitats, for example in subtidal areas that were isolated and freshened when sea-level fell. As mentioned previously, reproductive adaptations such as resting eggs may also have enabled ostracods to exploit temporary coastal plain water bodies. However, the fairly rapid salinity change that would occur in this scenario means that only species that were already pre-adapted to euryhaline conditions would survive, owing to the pressures of osmoregulation. The 'patchy' fossil record of non-marine ostracods in the Devonian and earlier may be explained by a series of passive invasion events and 'failed' non-marine colonizations. Non-aquatic means of passive invasion have been proposed, such as the transport of ostracods or desiccation-resistant ostracod eggs on the body of tetrapods, or blown by humid winds (Lethiers & Damotte, 1993).

Whether adaptation was active or passive, there may have been evolutionary advantages in moving out of the marine realm. For example, the Late Devonian ocean anoxia (Algeo *et al.* 1995) may have driven adaptation into new environments. The onset

of the Carboniferous glaciation in the Mississippian (Fielding, Frank & Isbell, 2008; Mii, Grossman & Yancey, 1999) would have dramatically affected sea-level and destabilized the shallow marine shelf environment. There is evidence in marine invertebrate populations of low levels of origination, extinction and diversity, from the Mississippian/Pennsylvanian boundary (where there was a second order extinction) for the following 50 Ma (into the Permian; Stanley & Powell, 2003). Changes in the marine environment and ostracod populations may thus have driven some species to invest in non-marine adaptations.

6.c. Early non-marine environments

The earliest known record of freshwater ostracods is preserved in lacustrine algal limestones in the Anstruther Formation of the MVS, which were colonized by *Carbonita* sp. Ostracods may have initially colonized this environment owing to passive transport during marine transgression over the lake and remained there as the water freshened. The algae would have provided a suitable food source; a similar adaptation has been proposed for certain leperditicopids associated with stromatolites (see Siveter, 1984; Vannier, Wang & Coen, 2001; Warshauer & Smosna, 1977).

Coal seams and blackband ironstones are common in the Strathclyde Group, and are interpreted as wetland swamp deposits. No terrestrial macrofauna were observed (such as the Pennsylvanian land snail *Archandon*; Hebert & Calder, 2004), but these wetland freshwater environments are important for ostracods. *Carbonita* is recorded from blackband ironstones in this study and is even more common in the Pennsylvanian Coal Measures (see, for example, Sohn, 1985). Ostracods may have been fostered in these environments by exploiting the rich plant detritus coming from the land; the increase in the diversity of detritus-feeding epifauna can be linked to the increased abundance of Carboniferous land plants (Buatois *et al.* 1998).

Were the ostracods associated with coal deposits terrestrial? Genetic studies estimate that terrestrial ostracods may have been present as early as the Ordovician (Newman, 2005). The ostracods in organic-rich sediments in the present study are assumed to be fully aquatic, but it is possible that the absence of a fossil record of terrestrial ostracods may be a preservational rather than ecological issue (Horne, 2003), as carapaces are unlikely to be preserved in the acid peat-bog environment of coal deposits. Further studies on coal seams are needed to confirm an ostracod presence in coal deposits and a possible semi-terrestrial lifestyle for Mississippian ostracods.

6.d. Timing and duration of non-marine colonization

Of the most successful Carboniferous freshwater ostracods, *Geisina* became extinct by the mid-Permian, *Carbonita* at the end-Permian, while *Darwinula* survived but with a much reduced diversity (Horne, 2003).

Only darwinulids and limnocytherids survived the end-Permian extinction and are found in freshwaters today. This study supports the notion of brackish ostracods in the Mississippian (Tibert & Scott, 1999; Williams *et al.* 2006). Previous studies have recorded freshwater *Carbonita* from the late Mississippian (Pendleian; Sohn, 1985), while this study records them from the mid-Mississippian (Arundian). The colonization of non-marine environments by ostracods is evident from the Carboniferous until the end-Permian, but it was only one of a series of such ostracod radiations, to be repeated many times. For example, the Cytheroidea are thought to have undertaken seven distinct non-marine invasions from the Late Carboniferous to the present, the most active of which was during the Early Cretaceous (Horne, 2003; Tibert *et al.* 2003).

7. Ostracod taxonomic notes

Four new ostracod species are described in the Systematic Palaeontology Section 8 (authored by Bennett). Here, taxonomic notes are provided for the other species (Table 2, Figs 9–11), noting in some instances their first occurrence in the Mississippian sections studied. The familial and suprafamilial classification of ostracods from this study follows Whatley *et al.* (1993), supplemented by consideration of Sohn (1985) for the Superfamily Carbonitoidea, and Dewey & Fåhræus (1987) for the Family Geisinidae (Table 1).

7.a. Order Podocopida Müller, 1894

7.a.1. Suborder Podocopina Sars, 1866

Nine species from the families Bairdiidae (genera *Acratia*, *Acutiangulata*, *Bairdia*), Bairdiocyprididae (*Silenites*) and Carbonitidae (*Carbonita*) are recognized. *Acratia* sp. A is identified by its lateral valve outline (Fig. 11q), which most closely resembles *Acratia acuta* (Jones & Kirkby, 1895). *Acutiangulata* sp. A has a distinctly sub-quadrate lateral outline of the ventroposterior margin (Fig. 9a, d). *Bairdia submucronata* Jones & Kirkby (1879a) (topotypes designated herein as NHM specimens In 42133, OS 7457 and OS 7458, the latter two figured by Jones & Kirkby, 1879a and Robinson, 1978) possesses a postero-dorsal margin inclined at 10° to the horizontal in lateral view (Fig. 9b). This species is similar to *Bairdia altaica* Buschmina & Kononova, 1981 and *B. beedei* Ulrich & Bassler, 1906, but with more central inflation to the carapace. *Silenites* sp. A is identified by its sub-ovate lateral carapace outline and external surface ornament of 20 µm diameter reticulæ (Fig. 11o). The posterior end of the carapace is higher and more inflated than the anterior, which may indicate sexual dimorphism.

Carbonita has a long history of taxonomic revision (see Pollard, 1966; Anderson, 1970; Sohn, 1977; Horne, 2003 and Tibert & Dewey, 2006 for a

summary). The Scottish specimens lack details of the muscle scar, and their assignment to *Carbonita* is tentative. *Carbonita bairdioides* (Jones & Kirkby, 1879b) (lectotype designated here as NHM I 2566, fig. d in Athersuch *et al.* 2009) is distinguished by its sub-triangular, asymmetrical, lateral carapace outline and arched dorsal margin (Fig. 11g). *Carbonita cf. fabulina* (Jones & Kirkby, 1879b) has a more strongly arched dorsal margin and greater valve height versus length than *C. bairdioides* (Fig. 11a). *Carbonita cf. humilis* (Jones & Kirkby, 1879b) is identified by its ovate, symmetrical, lateral carapace outline and external surface ornamentation of 20 µm diameter reticulæ (Fig. 11c). *C. humilis* is one of the most common non-marine ostracods in the Pennsylvanian of Britain (Pollard, 1966; Anderson, 1970; Athersuch *et al.* 2009) and exhibits sexual dimorphism (Bless & Pollard, 1975). *Carbonita cf. inflata* (Jones & Kirkby, 1879b) is sub-triangular to sub-rounded in lateral carapace outline (Fig. 11b), but lacks the punctate ornament of Pollard's (1966) material of *C. inflata*. Anderson (1970) regarded *Bythocypris tumidus*, *Cypridopsis fabulina*, *Gutschickia ovata* and *Whipplella cuneiformis* to be junior synonyms of *C. inflata*.

Our material extends the range of certain genera in the Mississippian of Britain: *Acutiangulata* from the Lower Asbian (Robinson, 1978) up to the Brigantian (this study); *Bairdia submucronata* from the Asbian (Robinson 1978; Turner, Dewey & Fordham, 1997) to the Brigantian, and *Carbonita* from the Pennsylvanian (Athersuch *et al.* 2009) downwards to the Mississippian.

7.a.2. Suborder Metacopina Sylvester-Bradley, 1961

Healdia cf. cuneata Robinson, 1978 (from the family Healdiidae) is identified by its 85° lateral angle of the posterior margin (Fig. 9g), and the presence of small posterior and postero-ventral spines (between 7–10 µm in length). While *H. cuneata* lacks spines (Robinson, 1978), other species have much larger spines, such as *Healdia cornigera* (Jones & Kirkby, 1867).

7.a.3. Suborder Platycopina Sars, 1866

Four species from the families Cavellinidae (*Cavellina*), Geisinidae (*Geisina*) and *Glyptolichvinella* (family uncertain) are recognized. Owing to a lack of soft-part evidence, the relationship between Recent and Carboniferous platycopes is poorly understood (Horne, 2003). *Cavellina benniei* (Jones, Kirkby & Brady, 1884) (topotypes designated here as NHM OS 7339, OS 7340 and specimens from slide I. 1725, the former two figured in Jones, Kirkby & Brady, 1884 and Robinson, 1978) has a sub-quadrate lateral carapace outline (Fig. 10a). *Cavellina valida* (topotypes designated herein as NHM OS 7346 and OS 7347, fig. d in Jones, Kirkby & Brady, 1884 and Robinson, 1978) is defined by the 85° lateral angle of the posterior margin, lack of spines and right-over-left valve overreach

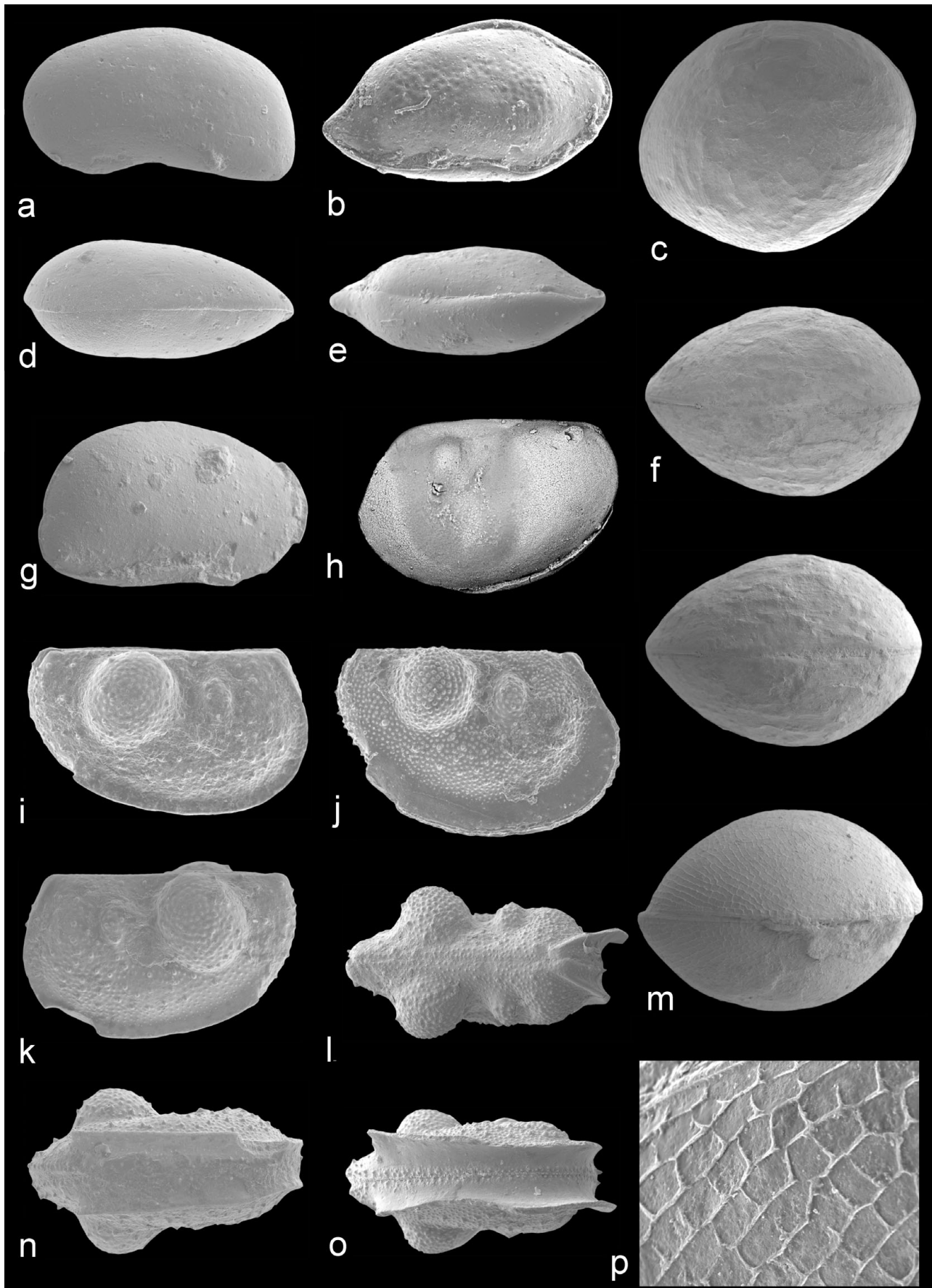


Figure 9. Marine ostracods. Specimen numbers are from the palaeontology collections of the BGS, Keyworth. All images are scanning electron micrographs. *Acutiangulata* sp. A: (a, d) carapace (MPK 13938; length 440 μm), left lateral and dorsal views, $\times 100$. *Bairdia submucronata* Jones & Kirkby, 1879a: (b, e) carapace (MPK 13939; length 830 μm), right lateral and dorsal views, $\times 60$. *Healdia* cf. *cuneata* Robinson, 1978: (g) carapace (MPK 13941; length 420 μm), right lateral view, $\times 110$. *Palaeocope* sp. C: (h) carapace

(Fig. 10e). Varying posterior inflation in adults indicates possible domiciliar sexual dimorphism, while the lack of inflation in *C. benniei* may reflect the small number of specimens identified (Table 2). *Geisina arcuata* Bean (1836) is identified by a shallow adductor sulcus and a strong right-over-left valve overlap (Fig. 11i). A surface ornament of polygonal pitted reticulation (Pollard, 1966) is absent. *Glyptolichvinella spiralis* Jones & Kirkby, 1880 (lectotype assigned here as NHM OS 7384, fig. d in Jones & Kirkby, 1885 and Robinson, 1978) has an external ornamentation of costae in an open spiral pattern (Fig. 10g). The carapace size is larger than other species with similar costal patterns, such as *Glyptolichvinella annularis* (Kummerow, 1939).

7.b. Order Leiocopida Schallreuter, 1973

Four species from the family Paraparchitidae (*Paraparchites armstrongianus* (Jones & Kirkby, 1886), *Paraparchites circularis* n. sp., *Shemonaella ornata* n. sp. and *Shemonaella elongata* n. sp.) are recognized. The new species are described in the Systematic Palaeontology (Section 8). *Paraparchites armstrongianus* (Jones & Kirkby, 1886) (lectotype assigned here as NHM I. 1756, fig. d in Jones & Kirkby, 1886) has a distinct antero-cardinal spine (Fig. 10h), larger than that of other paraparchitids (such as species of *Shishaella* and *Shivaella* (Robinson, 1978; Sohn, 1972)).

7.c. Order Palaeocopida Henningsmoen, 1953

Five species from the family Hollinellidae (*Hollinella* (*Keslingella*)) and palaeocopes of uncertain affinity are identified. *Hollinella* (*Keslingella*) *radiata* (topotype assigned herein as NHM OS 7331, fig. d in Jones & Kirkby, 1886 and Robinson, 1978) is distinguished by a small antero-dorsal node, a large postero-dorsal bulb, and an external ornament of tubercles and spines. The histium is twice as wide and the carapace is wider in some specimens (Fig. 9j), which are identified as heteromorphs (Kellett, 1936). Two adventral spines are present in juveniles, typical of the subgenus (Bless & Jordan, 1970).

Palaeocopes spp. are classified into four species (A–D), but are left in open nomenclature owing to the small number of specimens identified (Table 2) and their differences to known palaeocope genera. All have a straight dorsal margin, preplete carapace and lobate ornamentation. A large posterior lobe or inflated posterior end in some specimens indicates sexual dimorphism. Species A–D are distinguished

by differences in ornamentation. Palaeocope sp. A is quadrilobate (Fig. 10j), palaeocope sp. B trilobate, with spines on the anterior or anterior and posterior free margins (Fig. 10m, p). The spines are 20 µm in length and vary in shape (triangular, clavellate (widens distally) or needle like) and position (closely or distally spaced) between specimens, indicative of intra-species variation. *Jonesina fastigiata* (Jones & Kirkby, 1867) (fig. d in Robinson, 1978, pl. 4, figs 2a–b) resembles palaeocope sp. B, but has more spherical lobes. Palaeocope sp. C is trilobate, distinguished by a postero-cardinal spine (30 µm in length) on the posterior lobe (Fig. 9h). Palaeocope sp. D is trilobate, with flattened valve free margins, reticulate external ornament and no spines (Fig. 11p).

7.d. Order Myodocopida Sars, 1866

Polycope elegans n. sp. is the only representative of the family Polycopidae and is described in the following section.

8. Systematic palaeontology (C. Bennett)

Four new species are described from the Strathclyde Group. A differential diagnosis is given owing to the problems of otherwise distinguishing between species that have no or little carapace ornamentation.

Order LEIOCOPIDA Schallreuter, 1973
Suborder PARAPARCHITICOPINA Gramm & Ivanov,
1975
Superfamily PARAPARCHITOIDEA Scott, 1959
Family PARAPARCHITIDAE Scott, 1959
Genus *Paraparchites* Ulrich & Bassler, 1906

Type species. By original designation *Paraparchites humerosus* Ulrich & Bassler, 1906.

Diagnosis. See Dewey & Fähræus (1987), p. 108.

Paraparchites circularis n. sp.
Figure 11h, j–n

Holotype. MPK 13960, a left valve; length 800 µm; Fig. 11j.

Derivation of name. Latin *circularis*, ‘circular’, referring to the lateral valve shape.

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

Material. See Table 2. The average (mean) size of adult carapaces is length 840 µm, height 740 µm, width 420 µm.

(juvenile; MPK 13989; length 350 µm), left lateral view, × 129. *Polycope elegans* n. sp. (c, f) carapace (holotype; MPK 13942; length 1800 µm), right lateral and dorsal view (stereo pair), × 26; (m, p) carapace (MPK 13943; length 1550 µm), subdorsal view (× 33), and rectangular reticulation (image 230 µm wide; × 187). *Hollinella* (*Keslingella*) *radiata* (Jones & Kirkby, 1886): (i, k, n) carapace, heteromorph (MPK 13973; length 875 µm), right lateral, left lateral and right ventral views, × 54; (j, l, o) carapace, heteromorph, (MPK 13977; length 1000 µm), right lateral, dorsal and ventral views, × 48.

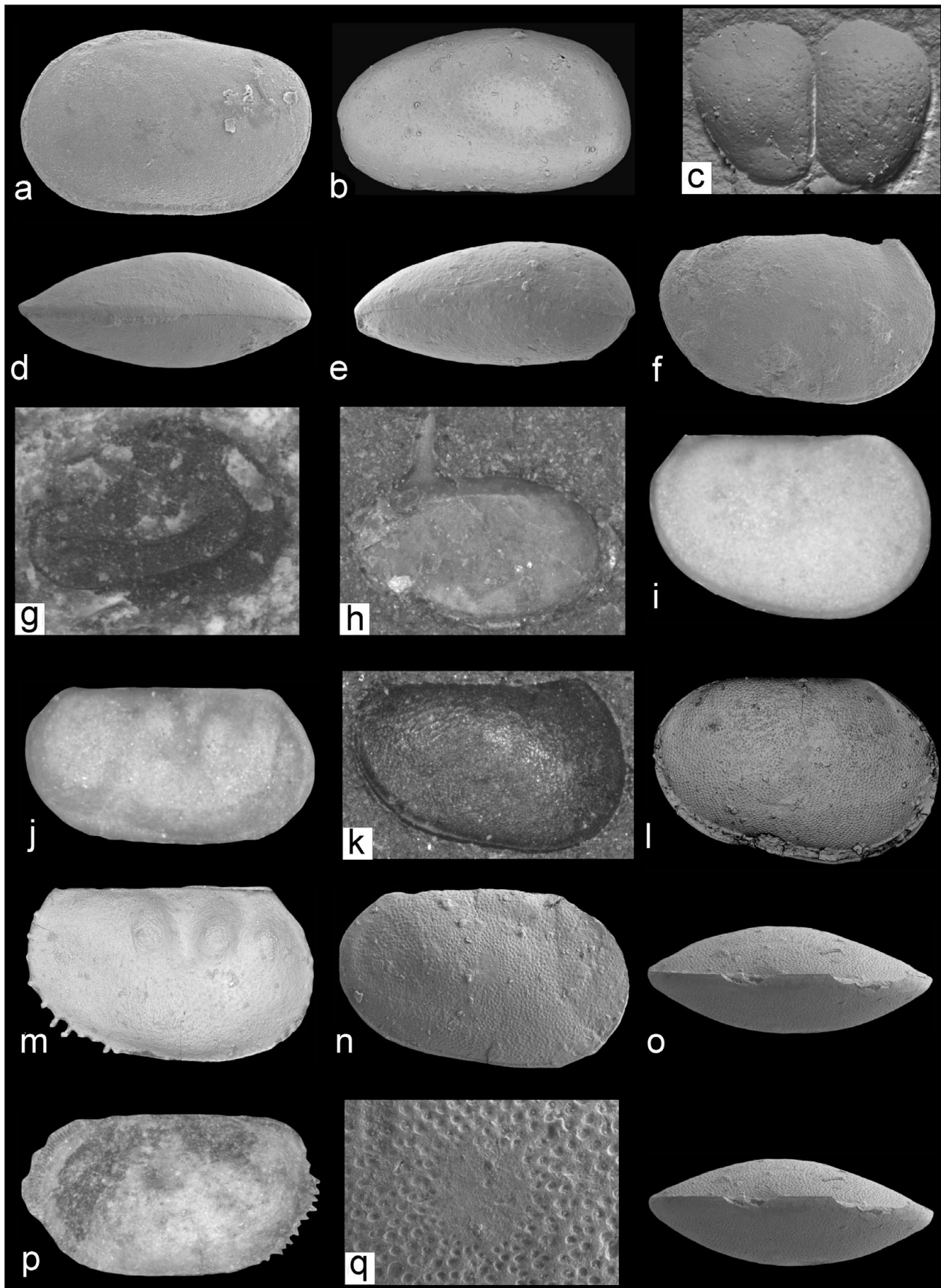


Figure 10. Eurytopic ostracods. Specimen numbers are from the palaeontology collections of the BGS, Keyworth. Images are scanning electron micrographs (a–f, l–o, q) or light photographs (g–k, p). *Cavellina benniei* (Jones, Kirkby & Brady, 1884): (a, d) carapace (large juvenile; MPK 13944; length 540 μm) left lateral and dorsal views, $\times 91$. *Cavellina valida* (Jones, Kirkby & Brady, 1884): (b, e) carapace (MPK 13945; length 570 μm), left lateral and dorsal views, $\times 84$. *Glyptolichvinella spiralis* (Jones & Kirkby, 1880)

Differential diagnosis. Species of *Paraparchites* with a sub-circular carapace outline in lateral view, except for a straight dorsal margin. The carapace has a high height:length ratio of 1:1.1. External surface of the valves have shallow circular punctae, each approximately 12 µm in diameter, and a smooth sub-circular central muscle scar spot approximately 60 µm in diameter. *Paraparchites circularis* n. sp. has a valve height:length that is greater than other large Mississippian paraparchitoideans which also have a similar outline shape, such as *Chamishaella suborbiculata* (Münster, 1830), *Paraparchites carbonaria* (Hall), *Paraparchites scotoburdigalensis* (Hibbert, 1836) and *Shemonaella scotoburdigalensis* (Hibbert, 1836). *Paraparchites discus* Williams *et al.* 2005, has an incised dorsum and smaller height:length ratio than this species.

Description. Carapace sub-circular in lateral outline, amplete, symmetrical. Dorsal margin straight, two-thirds the total carapace length, ventral, anterior and posterior margins rounded. Height slightly less than length, valves are centrally inflated. Internal moulds have anastomosing structures radiating from a central muscle spot. Right-over-left valve overlap to give a ridge around the valve free margins.

Discussion. The anastomosing structures on the internal surface of valves may reflect part of the circulatory system, as has been proposed for leperditid arthropods (Vannier, Wang & Coen, 2001). This species commonly occurs in monospecific assemblages or associated with rare *Carbonita* cf. *inflata* and *Silenites* sp. A. The genus is recorded from the Mississippian of Scotland (Latham, 1932; Williams *et al.* 2005), Canada (Dewey, 1988) and the USA (Benson, 1955; Sohn, 1971).

Genus *Shemonaella* Sohn, 1971

Type species. By original designation *Shemonaella dutroi* Sohn, 1971.

Diagnosis. See Dewey & Fåhraeus (1987), p. 109.

Shemonaella elongata n. sp. Figure 10c, f, i, k

Holotype. MPK 13964, a left valve; length 1200 µm; Fig. 10i.

Derivation of name. The Latin *elongata*, 'long, or elongate', referring to the unusual length to height carapace proportions.

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

Material. See Table 2. Average dimensions: length 1200 µm, height 760 µm.

Differential diagnosis. Species of *Shemonaella* with a long dorsal margin (80% of the carapace length), shallow carapace inflation and an unusually high height:length ratio for this genus of 1:1.6. Many paraparchitoideans have the same carapace size, shape and lack of external ornamentation as this species. These include the postplete *Shemonaella* sp. A of Williams *et al.* 2005, *Paraparchites inornatus* McCoy, 1844, *Paraparchites superbus* (Jones & Kirkby, 1886) and *Shishaella sohnella* Crasquin, 1985, and the preplete *Leperditia okeni* Münster (Jones & Kirkby, 1865), *Paraparchites nicklesi* (Ulrich, 1891), *Paraparchites okeni* Münster, 1830 and *Shishaella nanaformis* Crasquin, 1985. However, these species are all more centrally inflated, with a shorter carapace height and a shorter dorsal margin to carapace length.

Description. Carapace semicircular in lateral outline, subamplete to postplete. Dorsal margin straight, 80% the total carapace length. 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. This is one of the most common species in the Strathclyde Group, often present in abundance, in all formations and in a range of ecological settings (Tables 2, 3, 5, Figs 7, 8). The genus is recorded from the Mississippian of Britain (Robinson, 1978), Germany (Coen, 1990) and Canada (Crasquin, 1985; Dewey, 1993; Dewey & Fåhraeus, 1987).

Shemonaella ornata n. sp. Figure 10l, n, o, q

Holotype. MPK 13966, a carapace; length 1600 µm; Fig. 10l, o.

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 [National grid reference NO 4518 1419].

– environment uncertain: (g) left valve (MPK 13949; length 1000 µm), lateral view, specimen partly obscured by dolomite crystals, × 46. *Paraparchites armstrongianus* (Jones & Kirkby, 1886): (h) left valve of a disarticulated carapace (MPK 13950; length 1600 µm), lateral view, × 29. *Shemonaella elongata* n. sp.: (c) carapace (juvenile; MPK 13968; height of valve 385 µm), silicon rubber cast, × 73; (f) left valve (MPK 13965; length 1220 µm), lateral view, specimen broken at dorsal margin, × 41; (i) left valve (MPK 13964; holotype; CEB7; length 1200 µm), lateral view, × 39; (k) right valve (MPK 13967; length 1000 µm), internal mould, with anastomosing structures, × 48. *Shemonaella ornata* n. sp.: (l, o) carapace (MPK 13966; holotype; CEB6; length 1600 µm), left lateral and ventral (stereo pair) views, × 30; (n, q) left valve (MPK 13969; length 1400 µm), lateral view (× 34), and external view of the adductor muscle scar (120 µm diameter, × 131). Palaeocope sp. A: (j) right valve (MPK 13980; length 850 µm), lateral view, × 58. Palaeocope sp. B: (m) carapace (MPK 13984; length 630 µm), right lateral view, × 75; (p) left valve (MPK 13986; length 700 µm), lateral view, flattened specimen, × 70.

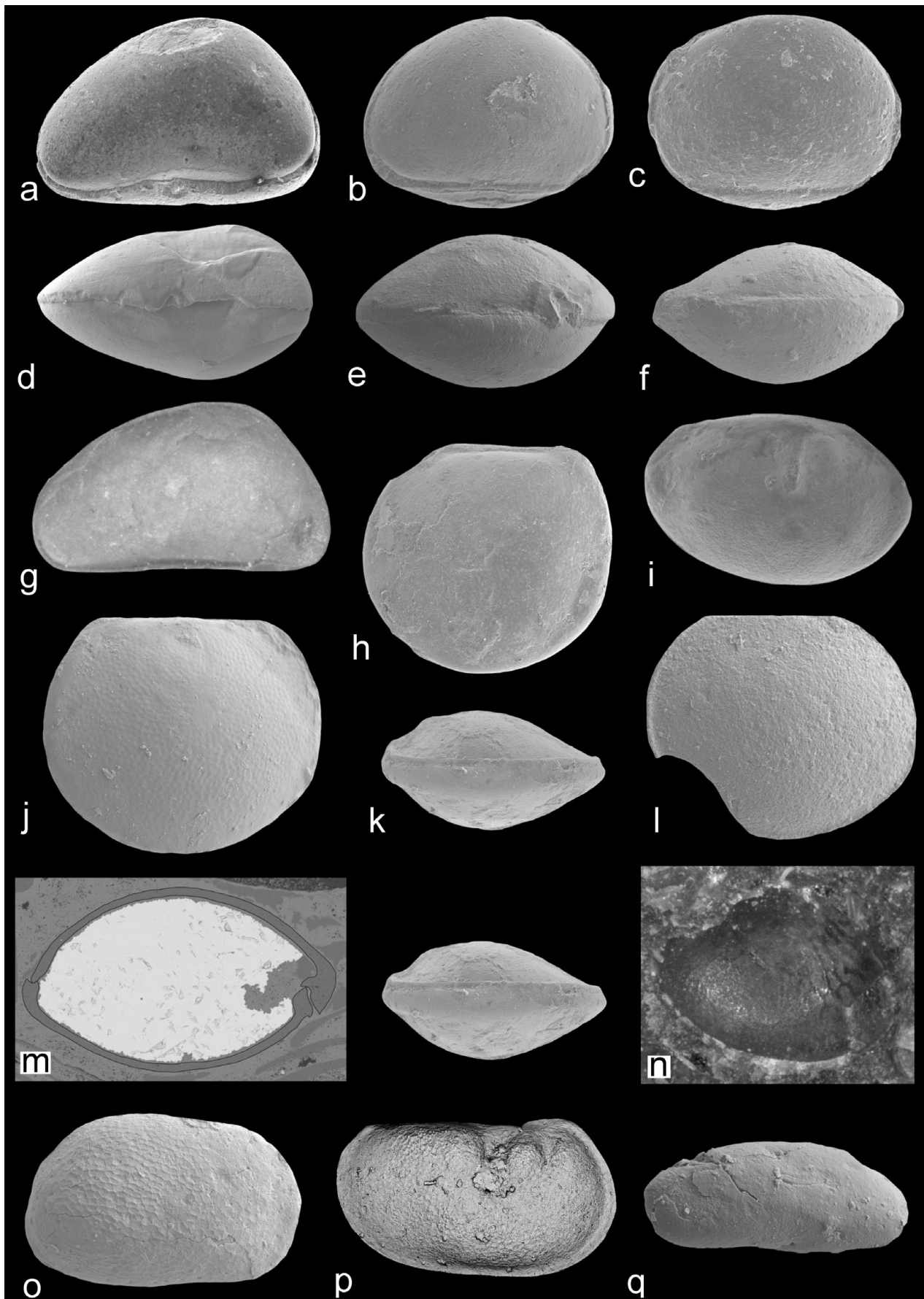


Figure 11. Freshwater (a–g), freshwater-brackish (h–o) and ‘ecology uncertain’ (p, q) ostracods. Specimen numbers are from the palaeontology collections of the BGS, Keyworth. Images are scanning electron micrographs (a–f, h–m, o–q) or light photographs (g, n). *Carbonita* cf. *fabulina* (Jones & Kirkby, 1879b): (a, d) carapace (MPK 13955; length 940 μm), left lateral and ventral views, $\times 51$. *Carbonita* cf. *inflata* (Jones & Kirkby, 1879b): (b, e) carapace (MPK 13953; length 875 μm), left lateral and dorsal views, $\times 48$.

Material. See Table 2. Average dimensions: length 1450 μm , height 920 μm , width 500 μm .

Differential diagnosis. Species of *Shemonaella* with an ornament of 10 μm diameter circular pits and a circular, smooth muscle scar spot (120 μm diameter) situated at the midpoint. This species has a larger carapace size and a unique ornament for *Shemonaella*, compared to other species of the genus. The dorsal margin is comparatively shorter than that of *Shemonaella elongata* n. sp. Specimens of *Leperditia youngiana* Jones & Kirkby, 1867 from the NHM 'Jones collection' has a similar carapace size, but an ornament of 5 μm diameter pits, not the 10 μm diameter pits of this new species.

Description. Carapace sub-ovate in lateral outline, postplete. Dorsal margin straight, two-thirds the total carapace length. 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, centrally inflated. Right-over-left valve overlap around all free margins excluding the dorsal margin.

Discussion. This species is limited in number of specimens and restricted in distribution compared to *Shemonaella elongata* n. sp. (Table 2, 3, Figs 7, 8).

Order MYODOCOPIDA Sars, 1866
Suborder CLADOCOPINA Sars, 1866
Superfamily POLYCOPOIDEA Sars, 1866
Family POLYCOPIDAE Sars, 1866
Genus *Polycope* Sars, 1866

Type species. By original designation *Polycope orbicularis* Sars, 1866.

Diagnosis. See Sars (1928), pp. 29–30.

Polycope elegans n. sp.
Figure 9c, f, m, p

Holotype. MPK 13942, a carapace; length 1800 μm ; Fig. 9c, f.

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 [National grid reference NO 4540 1409].

Material. See Table 2. Dimensions: length 1800 μm , height 1580 μm , width 1250 μm : MPK 13942.

Differential diagnosis. *Polycope* with a large carapace size and a unique radial pattern of hexagonal (at the valve centre) to rectangular (at the valve edge) reticulation. The reticulae are 40 μm in diameter. Other Mississippian *Polycope* mostly have a smaller carapace size, for example *Polycope sphaerula* (Gründel, 1961) and *Polycope spinula* Dewey & Fähræus, 1987. *Polycope youngiana* Jones, Kirkby & Brady, 1874 resembles the new species in size and shape, but it has an ornament of concentrically ringed grooves rather than reticulae, that is distinctly different.

Description. Carapace sub-circular in lateral outline, sub-spherical in shape, postplete. Dorsal margin straight, one-third the total carapace length, all other margins rounded. Carapace large, thick shelled, tumid. External surface ornament of reticulae arranged in a radial pattern from the midpoint. Reticulae change shape from hexagonal or polygonal in the valve centre, to rectangular or square at the edges of the valve. No valve overlap.

Discussion. This species is only found in the Denork core of the Pathhead Formation. The four samples that contain *Polycope elegans* n. sp. are each spaced at least a metre apart, suggesting that this species was present for a significant time interval. Other species of *Polycope* have been described from the Devonian/Carboniferous of Germany (Becker, Claus-Dieter & Klaus, 1993), the Mississippian of Northumberland (Dewey, 1993) and the Maritimes Basin of Canada (Dewey, 1988; Dewey & Fähræus, 1987).

9. Conclusions

(1) The Strathclyde Group of Fife, Scotland, represents a range of different depositional settings and environments, from fully marine conditions to deltaic sediments, marginal marine estuaries and lagoons, and brackish to freshwater lakes, swamps and fluvial systems. Ostracods and other fossils inhabited marine, brackish and freshwater environments. These deposits contain 25 ostracod species, including 4 that are new species.

(2) Macrofossil indicators of freshwater are the bivalves *Anthraconaia*, *Carbonicola* and *Cardiopteridium*, Spinicaudata, fish and plant debris.

(3) The Mississippian of the MVS contains some of the earliest freshwater ostracods globally. Freshwater *Carbonita* is described from the Arundian, middle Mississippian, in organic-rich mudstones and stromatolitic limestones. This study places the first freshwater ostracods approximately 15 Ma earlier than previously documented at 325 Ma.

(4) Brackish to freshwater macrofauna includes *Naiadites*, *Curvirimula* and '*Spirorbis*'. Brackish water

Carbonita cf. *humilis* (Jones & Kirkby, 1879b): (c, f) carapace (MPK 13956; length 840 μm), left lateral and ventral views, $\times 50$. *Carbonita bairdioides* (Jones & Kirkby, 1879b): (g) carapace (MPK 13957; length 800 μm), left lateral view, $\times 63$. *Geisina arcuata* (Bean, 1836): (i) carapace (MPK 13959; length 610 μm), right lateral view, $\times 74$. *Paraparchites circularis* n. sp.: (h, k) carapace (juvenile; MPK 13958; length 850 μm), left lateral and ventral (stereo pair) views, $\times 49$; (j) left valve (holotype; MPK 13960; length 800 μm), lateral view, $\times 58$; (l) right valve (MPK 13961; length 720 μm), lateral view, $\times 64$; (m) carapace (juvenile; MPK 13962; thin-section; length 600 μm), the valves are outlined in black, the hinge is to the left, $\times 87$; (n) carapace (MPK 13963; image 800 μm wide), oblique view of an internal skeinern, central muscle spot and anastomosing structures, $\times 54$. *Silenites* sp. A: (o) right valve (MPK 13971; length 680 μm), lateral view, $\times 68$. Palaeocope sp. D: (p) carapace (MPK 13991; length 700 μm), right lateral view, $\times 71$. *Acratia* sp. A: (q) single valve (MPK 13951; length 324 μm), lateral view, $\times 133$.

ostracods are *Geisina arcuata*, *Paraparchites circularis* n. sp., *Shemonaella ornata* n. sp. and *Silenites* sp. A.

(5) 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*, palaeocope species A and B, *Paraparchites armstrongianus* and *Shemonaella elongata* n. sp.

(6) Marine ostracods are *Acutiangulata* sp. A, *Bairdia submucronata*, *Healdia* cf. *cuneata*, *Hollinella* (*Keslingella*) *radiata*, palaeocope sp. C and *Polycope elegans* n. sp. They occur with a high diversity of marine macrofauna such as brachiopods, bryozoans, echinoderms and gastropods.

(7) The drivers of non-marine colonization by ostracods in the Mississippian can only be speculated upon, but may involve environmental (sea-level) change due to glaciation. The mechanisms to adapt to lower salinity such as osmoregulation and changes in reproduction are not fully known owing to a lack of knowledge of relevant soft parts. For example, there is insufficient evidence to suggest that desiccation-resistant eggs had developed during the Carboniferous, but links can be made to contemporaneous arthropods and living freshwater ostracods.

(8) Despite the success of the non-marine platycopes, podocopes and leiocopes, the majority did not survive the end-Permian extinction. Instead ostracods underwent a further series of terrestrial aquatic colonization events in the Mesozoic.

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References

- ALADIN, N. V. & POTTS, W. T. W. 1996. The osmoregulatory capacity of the Ostracoda. *Journal of Comparative Physiology B* **166**, 215–22.
- ALGEO, T. J., BERNER, R. A., MAYNARD, J. B. & SCHECKLER, S. E. 1995. Late Devonian ocean anoxic events and biotic crises: “rooted” in the evolution of vascular land plants? *GSA Today* **5**, 46–66.
- ANDERSON, F. W. 1970. Carboniferous ostracoda of 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**, 321–29.

- ATHERSUCH, J., GOODAY, A. J., POLLARD, J. E. & RILEY, N. J. 2009. Carboniferous. In *Ostracods in British Stratigraphy* (eds J. E. Whittaker & M. B. Hart), pp. 111–53. London: The Micropalaeontological Society Special Publications.
- BALLÈVRE, M. & LARDEUX, H. 2005. Signification paléocéologique et paléogéographique des bivalves du Carbonifère inférieur du bassin d’Ancenis (Massif armoricain). *Paléontologie Systématique* **4**, 109–21.
- 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**, 263–92.
- 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**, 376–7.
- 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**, 137–52.
- BENNISON, G. M. 1961. Small *Naiadites obesus* from the Calcareous Sandstone Series (Lower Carboniferous) of Fife. *Palaeontology* **4**, 300–11.
- BENSON, R. H. 1955. Ostracodes from the type section of the Fern Glen Formation. *Journal of Paleontology* **29**, 1030–9.
- 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. 1971. The new genus *Copelandella* from the Carboniferous – the youngest known beyrichioidean ostracodes. *Lethaia* **4**, 185–90.
- BLESS, M. J. M. & POLLARD, J. E. 1973. Paleocology 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**, 109–27.
- BLESS, M. J. M., STREEL, M. & BECKER, G. 1988. Distribution and palaeoenvironment of Devonian to Permian ostracod 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**, 347–62.
- BOARDMAN, E. L. 1989. Coal measures (Namurian and Westphalian) Blackband Iron Formations: fossil bog iron ores. *Sedimentology* **36**, 621–33.
- 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? In *Bridging the Gap: Trends in the ostracode biological and geological*

- sciences* (eds L. E. Park & A. J. Smith), pp. 153–79. The Paleontological Society Papers, vol. 9.
- 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**, 307–21.
- BRAND, P. J. 1996. Taxonomy and distribution of the Upper Carboniferous non-marine bivalve *Carbonicola aldammii*. *Palaeontology* **39**, 407–11.
- 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., 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**, 321–47.
- 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**, 217–40.
- BURCHETTE, T. P. & RIDING, R. 1977. Attached vermiform gastropods in Carboniferous marginal marine stromatolites and biostromes. *Lethaia* **10**, 17–28.
- BUSCHMINA, L. S. 1968. *Early Carboniferous Ostracoda of the Kuznetsk Basin*. Moscow: Izdatelstvo nauka, 128 pp.
- BUSCHMINA, L. S. & KONONOVA, L. I. 1981. Microfauna and biostratigraphy of the Devonian-Carboniferous Beds of the south of the western Siberia. *Academy of Sciences of the USSR, Siberian Branch, Institute of Geology and Geophysics, Transaction* **459**, 1–121.
- CARBONEL, P., COLIN, J.-P., DANIELOPOL, D., LÖFFLER, H. & NEUSTRUEVA, I. 1988. Paleocology of limnic ostracodes: a review of some major topics. *Palaeogeography, Palaeoclimatology, Palaeoecology* **62**, 413–6.
- 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.
- COEN, M. 1990. Revision of Münster's Carboniferous ostracode species. *Courier Forschungsinstitut Senckenberg* **123**, 265–73.
- COEN, M., MICHIELS, D. & PARISSÉ, E. 1988. Ostracodes dinantiens de l'Ardenne. *Mémoires de l'Institut Géologique de l'Université de Louvain* **34**, 1–42.
- 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**, 258–79.
- CRASQUIN, S. 1985. Zonation par les ostracodes dans le Mississippien de l'ouest Canadien. *Revue de Paléobiologie* **4**, 43–52.
- 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**, 181–92.
- DAVAUD, E. & GIRARD-CLOS, S. 2001. Recent freshwater ooids and oncoids from western Lake Geneva (Switzerland): indications of a common organically mediated origin. *Journal of Sedimentary Research* **71**, 423–9.
- DELO, D. M. 1930. Some Upper Carboniferous Ostracoda from the shale basin of western Texas. *Journal of Paleontology* **4**, 152–78.
- DEWEY, C. P. 1983. Ostracode palaeoecology of the Lower Carboniferous of Western Newfoundland. In *Applications of Ostracoda* (ed. R. F. Maddocks), pp. 104–15. University of Houston Geosciences.
- 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. 1993. Palaeoecology of ostracodes from a Lower Carboniferous chemosynthetic community. In *Ostracoda in the Earth and Life Sciences* (eds K. G. McKenzie & P. J. Jones), pp. 77–89. Proceedings of the 11th International Symposium on Ostracoda, Warrnambool, Victoria, Australia, 1991.
- DEWEY, C. P. & FÄHRAEUS, L. E. 1987. Taxonomy of Ostracoda (Crustacea) from Mississippian strata of maritime Canada. *Geologica et Palaeontologica* **21**, 93–135.
- DINELEY, D. L. & METCALF, S. J. 1999. British Carboniferous fossil fishes sites. In *Fossil Fishes of Great Britain* (ed. D. Palmer), pp. 265–312. Peterborough, UK: The Geological Conservation Review Series, Joint Nature Conservation Committee.
- 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**, 109–43.
- 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., BRADY, 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**, 1090–107.
- FERGUSON, L. 1963. The paleoecology of *Lingula squamiformis* Phillips during a Scottish Mississippian marine transgression. *Journal of Paleontology* **37**, 669–81.
- 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. *Geological Society of America Special Paper* **441**, 343–54.
- 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**, 383–92.
- FREYTTET, 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 Paléontologie* **86**, 195–241.
- FREYTTET, P. & VERRECCHIA, E. P. 1998. Freshwater organisms that build stromatolites: a synopsis of biocrystallization by prokaryotic and eukaryotic algae. *Sedimentology* **45**, 535–63.
- FRIEDMAN, G. M. & LUNDIN, R. F. 1998. Freshwater ostracodes from Upper Middle Devonian fluvial facies, Catskill Mountains, New York. *Journal of Paleontology* **72**, 485–90.

- FRIEND, P. F. & MOODY-STUART, M. 1970. Carbonate deposition on the river floodplains of the Wood Bay Formation (Devonian) of Spitzbergen. *Geological Magazine* **107**, 181–95.
- GRAMM, M. N. & IVANOV, V. K. 1975. The ostracod *Paraparchites minax ivanov* sp. nov. from the Permian of the U.S.S.R. and its muscle-scar field. *Palaeontology* **18**, 551–61.
- GRAY, J. 1988. Evolution of the freshwater ecosystem: the fossil record. *Palaeogeography, Palaeoclimatology, Palaeoecology* **62**, 1–214.
- GRÜNDEL, J. 1961. Zur biostratigraphie und fazies der Gattendorfia-Stufe in Mitteldeutschland und besonderer berücksichtigung der Ostracoden. *Freiberger Forschungshefte C* **111**, 53–173.
- 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**, 151–68.
- 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**, 1121–36.
- 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**, 247–54.
- HECKEL, P. H. & CLAYTON, G. 2006. The Carboniferous System. Use of the new official names for the subsystems, series, and stages. *Geological Acta* **4**, 403–7.
- HENNINGSMOEN, G. 1953. Classification of Paleozoic straight-hinged ostracods. *Norsk Geologisk Tidsskrift* **31**, 185–288.
- HIBBERT, S. 1836. 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 *Non-marine Permian Biostratigraphy and Biochronology* (eds S. G. Lucas, G. Cassinis & J. W. Schneider), pp. 297–324. Geological Society of London, Special Publication no. 265.
- HORNE, D. J. 2003. Key events in the ecological radiation of the Ostracoda. In *Bridging the Gap: Trends in the ostracode biological and geological sciences* (eds L. E. Park & A. J. Smith), pp. 181–201. The Paleontological Society Papers, vol. 9.
- JENKINS, T. B. H. 1960. Non-marine lamellibranch assemblages from the Coal Measures (Upper Carboniferous) of Pembrokeshire West Wales. *Palaeontology* **3**, 104–23.
- JOHNSON, W. R. 1936. The ostracods of the Missouri series in Nebraska. *Nebraska Geological Survey Paper* **11**, 1–52.
- JONES, P. J. & CHEN, P. J. 2000. Carboniferous and Permian Leaioida (Branchiopoda: Conchostraca) from Australia: taxonomic revision and biostratigraphic implications. *Records of the Australian Museum* **52**, 223–44.
- 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**, 404–10.
- JONES, T. R. & KIRKBY, J. W. 1867. On the Entomostraca of the Carboniferous rocks of Scotland. *Transactions of the Geological Society of Glasgow* **2**, 213–28.
- JONES, T. R. & KIRKBY, J. W. 1879a. 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**, 565–81.
- JONES, T. R. & KIRKBY, J. W. 1879b. 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**, 559–90.
- JONES, T. R. & KIRKBY, J. W. 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**, 174–90.
- JONES, T. R. & KIRKBY, J. W. 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**, 249–69.
- 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**, 452–60.
- JONES, T. R., KIRKBY, J. W. & BRADY, G. S. 1874. A monograph of the British fossil bivalved Entomostraca from the Carboniferous Formations. Part 1, number 1. The Cypridinidae and their allies. *Monograph of the Palaeontographical Society, London* 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. *Monograph of the Palaeontographical Society, London* 57–99.
- 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.
- KELLETT, B. 1936. Carboniferous ostracods. *Journal of Paleontology* **10**, 769–84.
- 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.
- KEYSER, D. 2005. Histological peculiarities of the nodding process in *Cyprideis torosa* (Jones) (Crustacea, Ostracoda). *Hydrobiologia* **538**, 95–106.
- KUMMEROW, E. H. E. 1939. Die Ostrakoden und phyllopoden des deutschen unterkarbons. *Abhandlungen der Preussischen Geologischen Landesanstalt, Berlin. Neue Folge, Heft 194*, **4**, 1–107.
- 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. Scottish Carboniferous Ostracoda. *Transactions of the Royal Society of Edinburgh* **LVII**, 351–95.
- 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**, 427–33.
- LOGAN, B. W., REZAK, R. & GINSBURG, R. N. 1964. Classification and environmental significance of algal stromatolites. *Journal of Geology* **72**, 68–83.
- LOUGHLIN, N. J. D. & HILLIER, R. D. 2010. Early Cambrian *Teichmus*-dominated ichnofabrics and palaeoenvironmental analysis of the Caerfai Group, Southwest Wales, UK. *Palaeogeography, Palaeoclimatology, Palaeoecology* **297**, 239–51.
- 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.
- MCCOY, F. 1844. *A synopsis of the characters of the Carboniferous Limestone fossils of Ireland*. Dublin: Dublin University Press, 207 pp.
- MIL, H.-S., GROSSMAN, E. L. & YANCEY, T. E. 1999. Carboniferous isotope stratigraphies of North America: implications for Carboniferous paleoceanography and Mississippian glaciation. *Geological Society of America Bulletin* **111**, 960–73.
- MONAGHAN, A. A. & PARRISH, R. R. 2005. Geochronology of Carboniferous-Permian magmatism in the Midland Valley of Scotland: implications for regional tectono-magmatic evolution and the numerical time scale. *Journal of the Geological Society, London* **162**, 1–15.
- MOORE, R. C. 1961. *Treatise on Invertebrate Paleontology, Pt. Q, Arthropoda 3*. Lawrence, Kansas, USA: Geological Society of America and University of Kansas Press, 442 pp.
- MÜLLER, G. W. 1894. Die ostracoden des Golfs von Neapel und der angrenzenden Meeres-abschitte. *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**, 60–7.
- NEALE, J. 1984. The Ostracoda and uniformitarianism: II. The earlier record: Cretaceous to Cambrian. *Proceedings of the Yorkshire Geological Society* **44**, 443–78.
- NEWMAN, W. A. 2005. Origin of the Ostracoda and their maxillopodan and hexapodan affinities. *Hydrobiologia* **538**, 1–21.
- OLEMPKA, E. 1993. An ostracod assemblage from late Viséan 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**, 160–79.
- PERYT, T. M. 1983. Classification of coated grains. In *Coated Grains* (ed. T. M. Peryt), pp. 3–6. Berlin: Springer-Verlag.
- POLLARD, J. E. 1966. A non-marine ostracod fauna from the coal measures of Durham and Northumberland. *Palaeontology* **9**, 667–97.
- POLLARD, J. E. 1969. Three ostracod-mussel bands in the Coal Measures (Westphalian) of Northumberland and Durham. *Proceedings of the Yorkshire Geological Society* **37**, 239–76.
- 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, V. M. 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 *Iskopaemye Ostrakody* (ed. K. Y. Gurevitsch), pp. 34–49. Kiev.
- PRIBYL, A. 1960. New information on the Upper Carboniferous freshwater and continental fauna from the Ostrava-Karviná Coal District. *Rozprawy Československé akademie věd* **70**, 3–71.
- RETALLACK, G. J. 2001. *Soils of the Past: An introduction to paleopedology*, 2nd ed. Oxford: Blackwell Science, 404 pp.
- RETRUM, J. B. & KAESLER, R. L. 2005. Early Permian Carbonitidae (Ostracoda): ontogeny, affinity, environment and systematics. *Journal of Micropalaeontology* **24**, 179–90.
- ROBINSON, E. 1978. The Carboniferous. In *A Stratigraphical Index of British Ostracoda* (eds R. H. Bate & E. Robinson), pp. 121–66. Liverpool, UK: Geological Journal Special Issue, No. 8.
- ROUNDY, P. V. 1926. Mississippian formations of San Saba County, Texas. *United States Geological Survey Professional Paper* **146**, 5–8.
- SALAS, M. J., VANNIER, J. & WILLIAMS, M. 2007. Early Ordovician ostracods from Argentina: their bearing on the origin of binodicope and palaeocope clades. *Journal of Paleontology* **81**, 1384–95.
- SARS, G. O. 1866. *Oversigt af Norges marine ostracoder*. Forhandler i Videnskabs-Selskabet i Christiania, 130 pp.
- SARS, G. O. 1887. Nye bidrag til kundskaben om middelhavets invertebrafauna. *Archiv for Mathematik og Naturvidenskab* **12**, 173–324.
- SARS, G. O. 1928. *An account of the crustacea of Norway with short descriptions and figures of all the specimens, vol. 9, Ostracoda*. Bergen: Bergen Museum, 241–77.
- SCHÄFER, P. 2007. Muschelkrebe (Ostracoden) aus permokarbonischen Karbonatbänken im rheinland-pfälzischen Teil des Saar-Nahe-Beckens. In *Kohlesümpfe, Seen und Halbwüsten* (eds T. Schindler & U. H. J. Heidtke). Polllichia.
- SCHALLREUTER, R. E. L. 1973. Tvaerenellidae (Ostracoda Palaeocopina) aus Backsteinkalk-Geschieben (Mittelordoviz) Norddeutschlands. *Palaeontographica A* **144**, 55–111.
- 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**, 443–51.
- SCOTT, H. W. 1944. Permian and Pennsylvanian fresh-water ostracodes. *Journal of Paleontology* **18**, 141–7.
- SCOTT, H. W. 1959. Type species of *Paraparchites* Ulrich and Bassler. *Journal of Paleontology* **33**, 670–4.
- SEARL, A. 1991. Early Dinantian dolomites from East Fife: hydrothermal overprinting of early diagenetic fabrics? *Journal of the Geological Society, London* **148**, 737–47.

- 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. & WILLIAMS, M. 1995. An early Cambrian assignment for the Caerfai Group of South Wales. *Journal of the Geological Society, London* **152**, 221–4.
- SOHN, I. G. 1961. Family Kloedenellidae Ulrich & Bassler, 1908. In *Treatise on Invertebrate Paleontology (Q) Arthropoda 3* (ed. R. C. Moore), pp. 181–7. Lawrence, Kansas, USA: Geological Society of America and University of Kansas Press.
- SOHN, I. G. 1969. Revision of some of Girty's invertebrate fossils from the Fayetteville Shale (Mississippian) of Arkansas and Oklahoma – Ostracodes. *United States 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**, 135–41.
- SOHN, I. G. 1985. Latest Mississippian (Namurian A) nonmarine ostracodes from West Virginia and Virginia. *Journal of Paleontology* **59**, 446–60.
- STANLEY, S. M. & POWELL, M. G. 2003. Depressed rates of origination and extinction during the late Paleozoic ice age: a new state for the global marine ecosystem. *Geology* **31**, 877–80.
- STEPHENSON, M. H., WILLIAMS, M., LENG, M. J. & MONAGHAN, A. A. 2004a. Aquatic plant microfossils of probable non-vascular origin from the Ballagan Formation (Lower Carboniferous), Midland Valley, Scotland. *Proceedings of the Yorkshire Geological Society* **55**, 145–58.
- STEPHENSON, M. H., WILLIAMS, M., MONAGHAN, A. A., ARKLEY, S., SMITH, R. A., DEAN, M., BROWNE, M. A. E. & LENG, M. J. 2004b. 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**, 131–43.
- STRAND, E. 1928. Miscellanea nomenclatoria zoologica et palaeontologica. *Archiv für Naturgeschichte* **92**, 40–1.
- SWAIN, F. M. 1976. Evolutionary development of cypriid ostracoda. *Abhandlungen und Verhandlungen des naturwissenschaftlichen Vereins in Hamburg, Neue Folge* **18/19** (Supplement), 103–19.
- SWARTZ, F. M. 1936. Revision of the Primitiidae and Beyrichiidae with new Ostracoda from the Lower Devonian of Pennsylvania. *Journal of Paleontology* **10**, 541–86.
- SYLVESTER-BRADLEY, P. C. 1961. Suborder Metacopina. In *Treatise on Invertebrate Paleontology, part Q, Arthropoda 3* (ed. R. C. Moore), p. Q358. Lawrence, Kansas, USA: Geological Society of America and University of Kansas Press.
- TAYLOR, P. D. & VINN, O. 2006. Convergent morphology in small spiral worm tubes ('*Spirorbis*') and its palaeoenvironmental implications. *Journal of the Geological Society, London* **163**, 225–8.
- TIBERT, N. E., COLIN, J.-P., LECKIE, R. M., BABINOT, J.-F. 2003. Revision of the ostracode genus *Fossocytheridea* Swain and Brown 1964: Mesozoic ancestral root for the modern eurytopic *Cyprideis* Jones. *Micropaleontology* **49**, 205–30.
- 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**, 246–60.
- 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**, 233–46.
- 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**, 177–83.
- ULRICH, E. O. 1891. New and little known American Paleozoic Ostracoda, Pt. 3, Carboniferous species. *Cincinnati Society of Natural History, Journal* **13**, 200–11.
- ULRICH, E. O. & BASSLER, R. S. 1906. New American Paleozoic Ostracoda. Notes and descriptions of Upper Carboniferous genera and species. *Proceedings of the United States National Museum* **30**, 149–64.
- ULRICH, E. O. & BASSLER, R. S. 1908. New American Paleozoic Ostracoda. Preliminary revision of the Beyrichiidae, with descriptions of new genera. *Proceedings of the United States National Museum* **35**, 277–340.
- VAN HARTEN, D. 2000. Variable nodding in *Cyprideis torosa* (Ostracoda, Crustacea): an overview, experimental results and a model from Catastrophe Theory. *Hydrobiologia* **419**, 131–9.
- VANNIER, J. & ABE, K. 1995. Size, body plan and respiration in the ostracoda. *Palaeontology* **38**, 843–73.
- VANNIER, J., THIERY, A. & RACHEBOEUF, P. R. 2003. Spinicaudatans and ostracods (Crustacea) from the Montceau Lagerstätte (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.
- WAKEFIELD, M. I. 1995. Ostracoda and palaeosalinity fluctuations in the Middle Jurassic Lealt Shale Formation, Inner Hebrides, Scotland. *Palaeontology* **38**, 583–617.
- WARSHAUER, S. M. & SMOSNA, R. 1977. Paleocologic controls of the ostracode communities in the Tonoloway limestone (Silurian; Pridoli) of the Central Appalachians. In *Aspects of Ecology and Zoogeography of Recent and Fossil Ostracoda* (eds H. Löffler & D. Danielopol), pp. 475–85. The Hague: Junk Publishers.
- WEBB, J. A. 1979. A reappraisal of the palaeoecology of conchostracans (Crustacea: Branchiopoda). *Neues Jahrbuch für Geologie und Palaeontologie, Abhandlungen* **158**, 259–75.

- WHATLEY, R. 1990a. The relationship between extrinsic and intrinsic events in the evolution of Mesozoic non-marine Ostracoda. *Extinction Events in Earth's History* **30**, 253–63.
- WHATLEY, R. 1990b. Ostracoda and global events. In *Ostracoda and Global Events* (eds R. Whatley & C. Maybury), pp. 3–24. Cambridge: Chapman and Hall.
- WHATLEY, R. 1992. The reproductive and dispersal strategies of Cretaceous non-marine Ostracoda: the key to pandemism. In *Aspects of Non-Marine Cretaceous Geology* (eds N. J. Mateer & P. J. Chen), pp. 177–92. Beijing: China Ocean Press.
- 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**, 111–8.
- WHATLEY, R. C., SIVETER, D. J. & BOOMER, I. 1993. Arthropoda (Crustacea: Ostracoda). In *The Fossil Record 2* (ed. M. J. Benton), pp. 343–56. London: Chapman and Hall.
- WILLIAMS, M., FLOYD, D. J., SALAS, M. J., SIVETER, D. J., STONE, P. & VANNIER, J. M. C. 2003. Patterns of ostracod migration for the 'North Atlantic' region during the Ordovician. *Palaeogeography, Palaeoclimatology, Palaeoecology* **195**, 193–228.
- 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., STEPHENSON, M. H., WILKINSON, I. P., LENG, M. L. & MILLER, C. G. 2005. Early Carboniferous (Late Tournaisian–Early Viséan) ostracods from the Ballagan Formation, central Scotland, UK. *Journal of Micropalaeontology* **24**, 77–94.
- 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.