Senckenbergiana lethaea	**88**	(1)	37–46	4 text-figs, 2 tabs	Frankfurt am Main, 30.06.2008

A review of the Carboniferous colonisation of non-marine environments by ostracods

With 4 Text-figures and 2 Tables

Carys Bennett

Abstract

This review examines the nature and chronology of the transition of ostracods from marine to non-marine aquatic environments in the Devonian and Carboniferous. There is putative evidence of ostracods in brackish waters from the middle Silurian, but more robust evidence from the Devonian. The first putative freshwater ostracods are species of the genera *Carbonita* and *Geisina* which are found in the early to middle Carboniferous Coal Measures. Freshwater ostracods are common in the middle Pennsylvanian Coal Measures of late Carboniferous age, with species of genera such as *Darwinula, Carbonita, Candona* and *Cypridopsis*. The Lower Carboniferous Viséan succession from the Midland Valley of Scotland provides a unique range of sedimentary environments from marine to non-marine, and a diverse range of ostracods and macrofauna. It is an ideal sequence to study the radiation of the Ostracoda from marine to non-marine realms. Non-marine species of *Carbonita* are found in the lower Viséan, associated with spirorbids, *Naiadites*, *Estheria*, plant and fish fragments. Marginal marine species include the genera *Geisina, Paraparchites*, *Shemonaella* and *Cavellina*, all of which are eurytopic. The first non-marine environments occupied by ostracods were near the shoreline, and influenced by marine transgressions. The adaptations needed to survive in freshwater or low salinities would have included changes in osmoregulation, feeding, and reproductive strategies such as parthenogenesis, to enable opportunistic colonisation of temporary freshwater habitats such as seasonal pools.

Key words: Ostracoda, non-marine, colonisation, Carboniferous, palaeoenvironment

Introduction

Ostracods are found today in a very wide range of aquatic environments, from freshwater aquifers to deep marine waters, ephemeral pools and damp terrestrial habitats (Horne 2003). A stratigraphical history of the different environments occupied by ostracods and traditionally presumed related taxa in the Palaeozoic is shown in Table 1. The first true ostracods occurred in the early Ordovician, and lived in shallow marine environments (Tinn & Meidla 2004, Williams et al. this volume), radiating into pelagic environments by the middle Silurian (Siveter 1984, Siveter et al. 1991, Vannier & Abe 1992). Carboniferous ostracods occupied a wide range of environments, from non-marine and near-shore facies to deep marine (Bless 1983); the most common genera are shown in Ostracods that inhabit terrestrial and freshwaters today are entirely Podocopida, belonging to the superfamilies Darwinuloidea, Cypridoidea and Cytheroidea (Horne 2003). The Cypridoidea are the dominant freshwater ostracods today, and it is possible that they had a late Palaeozoic origin, as has been suggested for the Terrestricytheroidea (Horne et al. 2004). Evolutionary studies show that in theory ostracods could have first inhabited terrestrial environments in the early Ordovician (Newman 2005), but there is no fossil evidence for this.

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

Carys Bennett, Department of Geology, University of Leicester, University Road, Leicester, LE1 7RH, UK, <ceb28@le.ac.uk>

Table 1. The ecological radiation of Palaeozoic Ostracoda and presumed related taxa. Key references for the different environments and events are: 1: Tinn & Meidla 2004; 2: Berdan 1984; 3: Siveter et al. 1991; 4: Clarkson et al. 1998; 5: Bless 1983; 6: Friedman & Lundin 1998; 7: Bless 1983; 8: Bless & Pollard 1973, Schäfer 2007; 9: Horne 2003.

Permian	Carbonitoidea and most Palaeocopida extinct end Permian (9)
Carboniferous	Freshwater ostracods common in Carboniferous Coal Measures e.g. *Carbonita* and *Dawinula* (8) Putative freshwater and common brackish water ostracods in the Mississipian e.g. *Geisina* (7)
Devonian	Leperditicopids in brackish water, extinct end Devonian (6) Marginal marine ostracods e. g. *Sansabella, Cavellina* (5)
Silurian	Putative evidence for brackish ostracods (4) Myodocopes colonise the pelagic realm (3)
Ordovician	Leperditicopids in shallow marine and hypersaline waters (2) Palaeocopes characterise shallow marie benthic environments (1)

This study reviews the evidence for the timing and nature of the colonisation of non-marine environments by ostracods. Here, non-marine refers to the complete range of salinities lower than that of 'normal marine', down to freshwater. The different proxies used to interpret a non-marine palaeoenvironment are critically assessed. The strongest evidence of ostracods adapting to reduced salinities is from the late Devonian and early Carboniferous. A multi-proxy approach is highlighted by a case study of marginal marine ostracods from the Midland Valley of Scotland. The physiological adaptations needed by the first non-marine ostracods are also discussed.

Determining palaeoenvironments containing ostracods

Criteria used to distinguish a non-marine environment include information from morphological and taxonomic comparisons with modern non-marine ostracods, sedimentology, associated flora and fauna, and geochemistry. The most comprehensive studies of palaeoenvironment use a multiproxy approach (for example Schultze et al. 1994, Tibert & Scott 1999, Williams et al. 2006).

Taxonomic uniformitarianism: Some Carboniferous freshwater ostracods such as *Darwinula, Candona* and *Cypridopsis* are comparable with their living freshwater podocopid relatives based on carapace characteristics only. *Carbonita* has been compared to Recent podocopes such as *Cypridopsis* (Neale 1984), but this is unconfirmed by soft part evidence, and the Carbonitoidea may be polyphyletic (Horne et al. 2002). The principle of taxonomic and hence ecological uniformitarianism can be applied within the Palaeozoic; for example, *Carbonita* from the middle Carboniferous Coal Measures (Pollard 1966, 1969) is considered indicative of freshwater when occurring in early Carboniferous age sediments (Pollard 1985). However, it must be noted that *Carbonita* was probably euryhaline, as it is also found in marginal marine sediments of the early Carboniferous (Tibert & Scott 1999).

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

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

Sedimentology: Hypersaline environments can be identified by the presence of evaporites, which commonly occur with desiccation cracks. Supratidal limestones are often deposited in hypersaline environments, as in, for example, those of the Dimock and Phillips limestones of Nova Scotia (Dewey 1987), where the limestones containing ostracods are associated with thick units of anhydrite and gypsum evaporites. A combination of detailed sedimentology and fossil evidence is the most common means for determining palaeoenvironment, as in the Hamilton Konservat-Lagerstätte of Kansas (Schultze et al. 1994), and the Joggins Formation of Nova Scotia, Canada (Falcon-Lang et al. 2006). In the former example, freshwater conditions were deduced by the presence of a fluvial palaeochannel containing sediment with a terrestrial flora, and a fauna of *Anthraconaia, Carbonita* and *Darwinula*.

A multi-proxy approach: Lower Carboniferous (Tournaisian) sediments from the Ballagan Formation, Midland Valley of Scotland provide multiple lines of evidence to deduce palaeoenvironment. These include sedimentology, palynology, ostracod palaeoecology, and geochemical analysis of ostracod shells (Stephenson et al. 2002, Williams et al. 2005, 2006). Both the carbonate and clastic sediments of the Ballagan Formation contain desiccation cracks and evaporites, suggesting conditions of fluctuating salinity and sea level. Certain algal palynomorphs such as *Botryococcus* ssp. are known from brackish to freshwater conditions (Stephenson et al. 2004). Ostracods form low diversity assemblages, and lack typical marine species. Ostracod and mollusc shells gave a range of -3‰ to

-11‰ $\delta^{18}O$, which was interpreted as marine and more freshwater end members respectively, including a significant diagenetic overprint (Williams et al. 2006). This is a rare example of geochemical work on Palaeozoic ostracods (the other case being from the Ordovician: Brenchley et al. 2003).

The timing of non-marine colonisation by ostracods

Hypersaline waters

The Leperditicopida, a putative ostracod group (Whatley et al. 1993), occur from the Ordovician to Devonian (Berdan 1984, Vannier et al. 2001). They are significantly larger than nearly all other ostracods, and are found in hypersaline waters in the Ordovician (Berdan 1984, Williams & Siveter 1996), and brackish to supposed fresh waters in the Devonian (Friedman & Lundin 1998, Knox & Gordon 1999). They commonly occur in low diversity communities, frequently associated with stromatolitic limestones (see Siveter 1984, Vannier et al. 2001, Warshauer & Smosna 1977). Although the Leperditicopida were seemingly adapted to a range of non-marine environments, their status as ostracods is uncertain as no soft parts are known.

Paraparchitacean ostracods are common in Carboniferous marine environments, and they dominate in early Carboniferous hypersaline sediments, as seen in examples from Canada (Dewey 1983, 1987, 1989) and Scotland (Williams et al. 2006). They commonly occur as low diversity, high abundance assemblages, with evidence of opportunistic reproduction strategies such as supposed progenesis and parthenogenesis (Dewey 1987).

Brackish waters

The middle Silurian Straiton Grits Formation of south west Scotland, contains beyrichiacean palaeocopes thought to be deposited in a brackish, coastal lagoon (Clarkson et al. 1998, Floyd & Williams 2003). This is the oldest known occurrence of beyrichiaceans in reduced salinities, although there is a lack of supporting evidence such as geochemical data, to endorse a low salinity signal.

The early Devonian and middle Carboniferous (Westphalian) of the Brabant Basin in Belgium contains some possible brackish water ostracod assemblages (Bless 1983, Bless et al. 1988). The early Devonian sediments in question are interpreted as a deltaic, brackish environment based on the sediments and fauna, and is another early record of brackish water ostracods (Rebske et al. 1985). The ostracods *Euprimites*? *koeppeni* (a palaeocope) and *Rebskeella waxweilerensis* (affinity unknown), are associated with abundant plant fragments, miospores, *Modiolopsis ekpempusa* and the leperditicope *Herrmannina*.

Leperditicopes from the middle Devonian of the Catskill Mountains, New York State, were interpreted as living in a freshwater environment (Friedman & Lundin 1998). They occur in fluvial sandstones, with abundant plant fragments, fish scales, and the bivalve *Archandon catskillensis*. A study of the overlying succession indicated brackish conditions, and the presence of the palaeocope *Welleria*, a genus unknown from non-marine deposits (Knox & Gordon 1999).

Carbonita is first recorded from the middle Devonian Dushan Formation of Kweichow, China (Shi 1964). This is questionable as *Carbonita* is figured poorly and listed with commonly marine ostracods, and there are no details on the sediments, associated macrofossils or an environmental interpretation. This is also the case for some early Carboniferous records which include species of *Carbonita* with a large list of marine ostracods, but there is no information on the sedimentology or associated fauna to allow an environmental reconstruction (for example Buschmina 1965, Samoilova & Smirnova 1960). The earliest record of *Carbonita* with details of macrofossils and sediments that indicate a brackish setting is from the early Carboniferous (Tournaisian) of Nova Scotia (Tibert & Scott 1999). It occurs with the ostracods *Bairdiacypris, Shemonaella* and *Copelandella* in a range of environments from near-shore marine to low salinity coastal ponds. Tournaisian ostracods from the Midland Valley of Scotland (Ballagan Formation) include numerous taxa that are interpreted as living in a marginal marine and brackish water environment, such as species of *Sansabella, Sulcella, Glyptolichvinella, Bythocypris* and *Cavellina* (Williams et al. 2005, 2006). The middle Carboniferous of Great Britain contains *Shemonaella scotoburdigalensis*, *Cavellina* and possibly *Carbonita*, interpreted to be from a brackish setting (Pollard 1985). The earliest documentation of freshwater ostracods (*Shemonaella scotoburdigalensis*) is from the Lower Carboniferous Burdiehouse Limestone of Scotland (Hibbert 1834). However, that claim is disputed, as *Shemonaella* and the associated fauna of spirorbids, coprolites, fish and plant fragments are commonly also found in brackish waters in the Carboniferous. Paraparchitacean, platycope and bairdioidean ostracods occur in reportedly brackish settings from the Mississippian of the Maritimes Basin of Canada (Dewey 1983, 1989). However, supporting evidence for brackish conditions from the macrofauna and sediments is somewhat limited.

Freshwaters

Deposits adjacent to the Devonian – Carboniferous boundary in South China have the earliest record of putative freshwater ostracods; *Leperditia* and *Gutschickia*? were used to signal a lagoonal and a freshwater environment respectively (Coen 1989). However, elsewhere *Leperditia* is also found in marine conditions, and *Gutschickia*? may have been misidentified (evidently on the muscle scar pattern). The ostracods in question co-occur with typically stenohaline, and marginal marine ostracod species. Thus, it is considered that in this case, there is not enough data to verify a freshwater setting, and a marine-influenced setting is more likely.

Supposed freshwater ostracods including the genera *Carbonita, Darwinula, Gutschickia, Pruvostina* and *Whipplella* are described from middle Carboniferous sediments of Virginia (Sohn 1985), in carbonaceous shales above a rooted clay, at the base of a marine transgression. Again more sedimentological and macrofossil data are needed to confirm a fully freshwater setting. The lower Pennsylvanian Joggins Formation of Nova Scotia contains ostracods including *Carbonita*, and is interpreted from the sediments and the macrofauna as repre-

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

Deep marine	**Shallow marine**	**Marginal & Brackish**	**Freshwater**	**Hypersaline**
Bairdiaceans	*Acratia*	*Beyrichiopsis*	Mississippian:	*Beyrichiopsis*
Tricornids	*Amphissites*	*Bythocypris*	*Carbonita*	*Paraparchites*
Entomozoaceans	*Bairdia*	*Cavellina*	*Geisina*	*Shemonaella*
	Bairdiacyprsis	*Chamishaella*	*Velatomorpha*	
	Basslerella	*Geisina*		
	Coryellina	*Glyptolichvinella*	Pennsylvanian:	
	Cribroconcha	*Glyptopleura*	*Candona*	
	Geffenina	*Knoxiella*	*Carbonita*	
	Healdia	*Paraparchites*	*Cypridina*	
	Hollinella	*Sansabella*	*Cypridopsis*	
	Jonesina	*Shemonaella*	*Darwinula*	
	Kirkbya	*Silenites*	*Gutschickia*	
	Monoceratina	*Sulcella*	*Hilboldtina*	
	Polycope		*Pruvostina*	
	Shishaella		*Suchonella*	
	Shivaella		*Whipplella*	
	Youngiella			

senting a fresh to brackish water palaeoenvironment (Falcon-Lang et al. 2006, Tibert & Dewey 2006).

The Pennsylvanian Coal Measures contain the majority of the Carboniferous freshwater ostracods, and were a key environment for non-marine colonisation. The Coal Measures of Northern England contain *Geisina arcuata* and species of *Carbonita* (Pollard 1966, 1969, Anderson 1970, Bless & Pollard 1973). *Carbonita* is numerically dominant over *Geisina* from the Lower to Upper Coal Measures, and this reflects an increasing freshwater influence through time. Ostracods that occur in the Coal Measures of North America, Europe and Russia include species of *Candona, Carbonita, Cypridina, Cypridopsis, Darwinula, Gutschickia*, *Hilboldtina, Pruvostina, Whipplella* and *Suchonella* (Scott & Summerson 1943, Scott 1944, Cooper 1946, Kummerow 1949, Buschmina 1959, Přibyl 1960, Sohn 1977, Schäfer 2007; see Table 2).

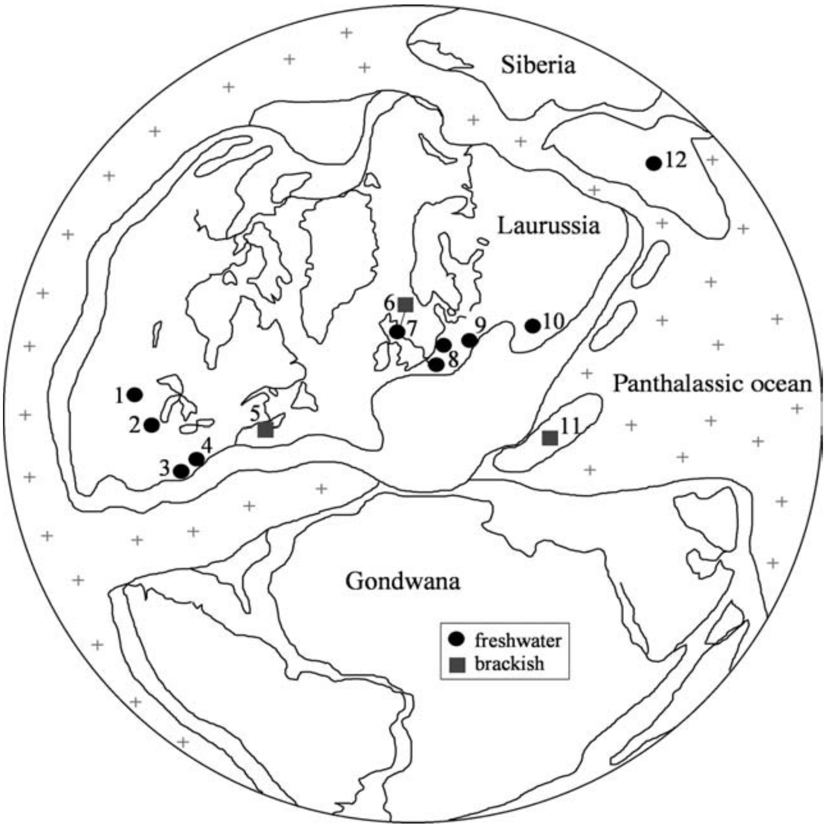
The first record of ostracods from an unequivocally freshwater setting is the occurrence of *Carbonita* in the Monteceau Lagerstätte, from the late Carboniferous of France (Vannier et al. 2003). The ostracods are associated with spinicaudant arthropods (for example *Euestheria*), which are known from the Recent and fossil record as a freshwater group. The Monteceau ostracods were thought to have lived in an ephemeral freshwater pond in an intramountain basin. There is no record of any marine influence to the sedimentation, as opposed to the Coal Measures described above, which are sometimes associated with marine incursions.

Integrity of the fossil record of non-marine ostracods

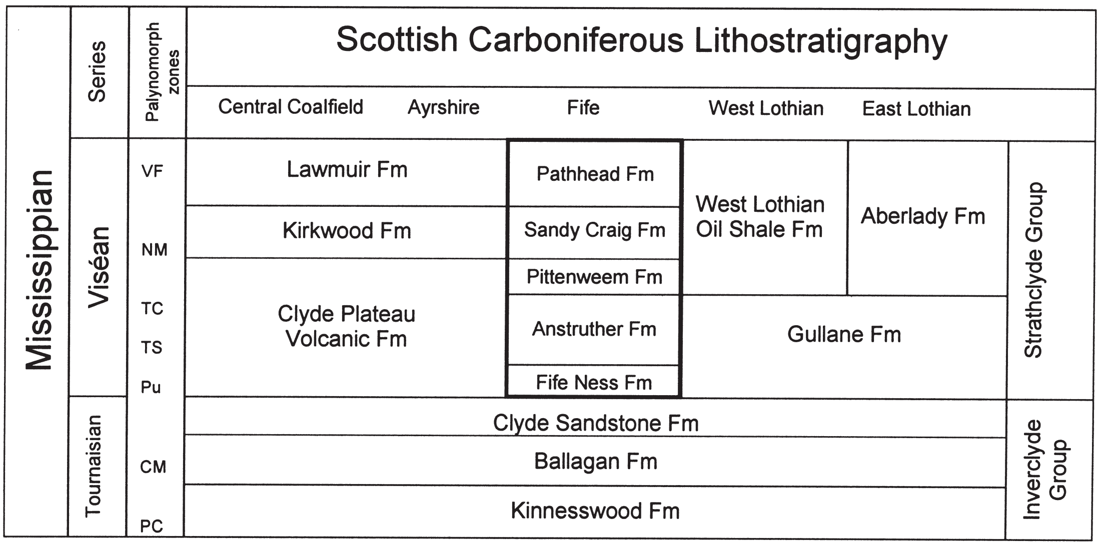
The majority of the published fossil evidence for Carboniferous non-marine ostracods comes from North America, Canada and Western Europe, with fewer records of non-marine taxa from China and Russia (Text-fig. 1). Although most of the occurrences are from Laurussia, the data reflect 'collection bias' rather than an original palaeontological signal. This can be verified by the fact that similar marginal marine assemblages are found from Europe, Russia, North America, Canada and Africa (Bless 1983, Bless & Massa 1982). More fossil discoveries could probably provide evidence for the origin of fully freshwater ostracods back to the early Carboniferous, and possibly the late Devonian.

Lower Carboniferous of Scotland: a multi-proxy case study

The Lower Carboniferous (Viséan) Strathclyde Group of the Midland Valley of Scotland shows some of the earliest evidence of ostracods from reduced and low salinity environments. The palaeogeography is that of a restricted marine seaway, giving a wide range of environments, while contemporaneous volcanism and abundant palynomorphs provide robust dating (Monaghan & Parrish 2005, Stephenson et al. 2004). The



Text-fig. 1. Distribution of Carboniferous non-marine ostracods referred to in this article. The palaeogeographic map is a reconstruction of the Lower Carboniferous at 335Ma, modified from Ziegler (1989). Literature that includes non-marine species, for example *Darwinula*, but which does not give an environmental interpretation is not included. Numbers next to freshwater and brackish water occurrences indicate where the information is published in the literature. 1: Kansas, USA: Schultze et al. 1994. 2: Illinois, USA: Cooper 1946. 3: Virginia, USA: Sohn 1985. 4: Southern Appalacian Coal Field, USA: Scott & Summerson 1943. 5: Nova Scotia, Canada: Tibert & Scott 1999, Dewey 1987, 1989. 6: Midland Valley of Scotland: this study, Williams et al. 2006. Berwickshire, Scotland: Pollard 1985. 7: Northern England: Bless & Pollard 1973, Pollard 1966, 1969. 8: Limburg, The Netherlands: Bless & Pollard 1973. Brabant Massif, Belgium: Bless 1983, Bless et al. 1988. Central France: Vannier et al. 2003. 9: South West Germany: Schäfer 2007, Ruhr region, Germany: Kummerow 1949. 10: Czech Republic: Přibyl 1960. 11: South China: Coen 1989. 12: central Kazakhstan: Buschmina 1959.



Text-fig. 2. Mississippian stratigraphy of the Midland Valley of Scotland (modified from Browne et al. 1999). The formations studied from Fife are indicated within the black box.

Text-fig. 3. Selected non-marine and marginal marine ostracods from the Strathclyde Group, Midland Valley of Scotland. 1 – 4 are non-marine species, 5 – 8 are marginal marine species. Sample numbers relate to British Geological Survey borehole samples. Images 2, 5 and 6 are light photographs, the others are scanning electron micrographs.
1: *Geisina* cf. *arcuata* (Bean, 1836) Kellett, 1936, carapace, right lateral view, 610µm length, × 66, EN 4872.
2: *Carbonita bairdioides* (Jones & Kirkby, 1879), carapace, left lateral view, 800µm length, × 46, 6E 6562.
3: *Carbonita* cf. *inflata* (Jones & Kirkby, 1879), carapace, left lateral view, 875µm length, × 39, SE 8413.
4: *Carbonita* cf. *humilis* (Jones & Kirkby, 1879), carapace, right lateral view, 840µm length, × 40, SE 8476.
5: Palaeocope, right valve, 850µm length, × 46, EN 4805.
6: *Shemonaella* sp., left valve, 1200µm length, × 31, EN 4805.
7: *Cavellina benniei* Jones, Kirkby & Brady, 1874, juvenile, carapace, left lateral view, 540µm length, × 65, 6E 9601.
8: *Cavellina taidonensis* Bushmina, 1968, juvenile, carapace, left lateral view, 500µm length, × 68, EN 4859.

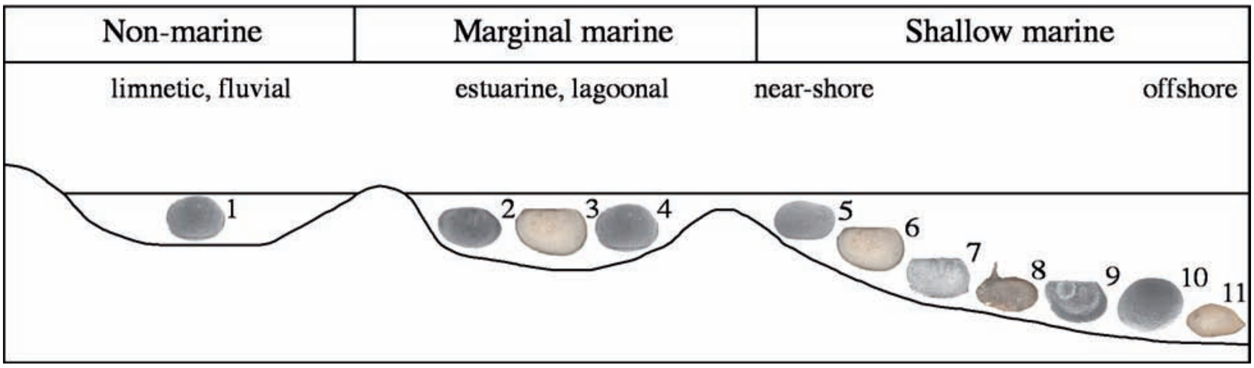
Strathclyde Group (Text-fig. 2) is characterised by a range of sediments, from marine successions deposited in a shallow seaway, through deltaic and marginal marine, to fluvial and lacustrine deposits. Most of the succession is marginal marine and fluvially dominated. The stratigraphy has been recently revised, and marine transgressions can be correlated regionally (Browne et al. 1999). A multi-proxy analysis of the Ballagan Formation from the Midland Valley of Scotland gave evidence for hypersaline and brackish water ostracods (Williams et al. 2006).

The Strathclyde Group contains podocope, platycope and palaeocope ostracods, mainly occurring in mudstones and siltstones. Marine and non-marine environments are distinguished on the basis of macrofauna and sedimentology. A fairly low diversity marine ostracod fauna comprises of *Bairdia submucronata, Hollinella radiata, Hollinella longispina* and *Polycope* sp. The taxa are associated with typically stenohaline marine macrofauna such as bryozoans, goniatite fragments and brachiopods. There are a wide variety of eurytopic ostracods, found in marine and non-marine sediments, including species of *Cavellina*, *Shemonaella* and *Paraparchites*.

Ostracods interpreted as non-marine are *Geisina* cf. *arcuata* and species of *Carbonita* (Text-fig. 3), of which the oldest specimens are from the lower Viséan. These ostracods are associated with fish and plant debris, *Naiadites* and *Curvirimula* bivalves, *Estheria* spinicaudants and spirorbids. They are found in silts and mudstones between sandy units, and in microbial limestones such as stromatolites. The sediments and macrofauna are indicative of low salinity conditions. However, the palaeosalinity cannot be accurately determined from the sediments and macrofossils alone, as the macrofauna associated with these ostracods is typically found in a range of brackish and freshwater salinities. Petrological and geochemical studies of algal limestones from the Strathclyde Group indicated a lacustrine origin (Guirdham et al. 2003). There is no evidence of hypersalinity in the form of evaporites, but there are seat earths and palaeosols which indicate subaerial exposure. Text-fig. 4 provides a schematic diagram of the possible environments occupied by the ostracods from the Strathclyde Group, from non-marine to shallow marine settings.

Adaptations for life in non-marine environments

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



Text-fig. 4. The possible range of environments and associated ostracods from the Midland Valley of Scotland, Strathclyde Group. The ostracod images are: 1: *Carbonita,* 2: *Geisina,* 3: *Shemonaella,* 4: *Carbonita,* 5: *Cavellina,* 6: *Shemonaella,* 7: a palaeocope, 8: *Paraparchites,* 9: *Hollinella,* 10: *Polycope* and 11: *Bairdia*.

lar morphology to the Leperditicopida, their thick shells and relatively large size thus aiding in osmoregulation.

The survival of *Carbonita* species over *Geisina* species into the Permian may have been dictated by their feeding strategies. In the Pennsylvanian Coal Measures of northern England, *Geisina* and *Carbonita* occur in different facies (Pollard 1966). *Geisina* has been interpreted as a filter feeder, while *Carbonita* may have been a deposit feeder like the Recent *Cypridopsis*, mainly crawling on the bottom (Neale 1984, Pollard 1966). It is clear that *Carbonita* was better adapted to freshwaters than *Geisina*, as it has a greater diversity of species and adapted to a wider range of sedimentary niches (Bless & Pollard 1973). The strategy of producing resting eggs resistant to desiccation and transport, as seen in the spinicaudant arthropods, may also have been used by the first freshwater ostracods, due to their co-occurrence in the temporary pond environment of the Monteceau Lagerstätte (Vannier et al. 2003). The Cretaceous of Brazil has produced possible ostracod eggs (Smith 1999), but the only confirmed fossil ostracod eggs are from the Silurian (Siveter et al. 2007). The occurrence of desiccation-resistant eggs would enable the survival of ostracods that lived in ephemeral water bodies such as seasonal freshwater lakes.

There are two possible environmental pathways that ostracods could take in order to colonise freshwaters: 1. Active invasion from the sea by euryhaline ostracods. 2. Passive invasion from the sea by the restriction of ostracods to isolated habitats (see Gray 1988). A driving force for active invasion may have been the abundance of land plants, which exploded in their diversity and abundance in the Carboniferous (Bateman et al. 1998). This is a unique feature of the late Devonian and early Carboniferous, and provided a nutrient-rich terrestrial habitat in non-marine waters. Mississippian sediments across the globe show fluctuating sea levels, which could result in environmental scenarios which would aid freshwater colonisation. For example, passive invasion could occur in coastal areas that were first subtidal, then rapidly exposed by falling sea levels, creating stranded saline water bodies that would freshen over time. Active invasion may have occurred if ostracods migrated up estuaries and into coastal lakes or rivers at times of high sea level. Modern estuaries have predominantly freshwater ostracod species that are widely distributed (see, for example Yozzo & Steineck 1994).

Conclusions

- Ostracods were adapted to brackish conditions from the Devonian, and the leperditicopid arthropods (putative ostracods) were adapted to a wide range of non-marine environments, including hypersaline, from the Ordovician onwards.
- The first putative freshwater ostracods occurred in the early to middle Carbonifeous, and consist solely of species of *Carbonita* and *Geisina*. A more diverse freshwater fauna including *Darwinula* occurs in the middle Pennsylvanian Coal Measures.
- The recognition of palaeoenvironments of a non-marine nature requires a multi-proxy approach, incorporating data from ostracod and associated faunas, sedimentology, geochemistry and palynology.
- There is a large gap in the data on Carboniferous non-marine ostracods, geochemically and geographically, with most of the records occurring in Western Europe, North America and Canada.
- The range of environments, abundance of macrofossils, palynomorphs, the record of well-dated sequences and the potential for geochemical studies render the Lower Carboniferous of the Midland Valley of Scotland a good sequence in which to investigate the marine to non-marine transition of the Ostracoda. Non-marine ostracods include *Geisina* and *Carbonita* and euryhaline ostracods are dominantly paraparchitaceans and kloedenellaceans.
- The first non-marine environments were probably influenced by marine waters, thus leading to variable salinity values. Ostracods may have become adapted to euryhaline conditions through changes in osmoregulation, which would allow them to live in a range of salinities. They may also have used reproductive strategies such as parthenogenesis in order to survive when other groups could not.

Acknowledgements

Thanks go to the British Geological Survey for funding the project, and access to boreholes from the Scottish Carboniferous. Scientific discussions were carried out with David Siveter, Mark Williams and Sarah Davies at the University of Leicester, Ian Wilkinson at the British Geological Survey, and Giles Miller at the Natural History Museum. Alan Lord kindly provided access to the Senckenberg ostracod collections and library in Frankfurt am Main.

References

Aladin, N.V. & Potts, W.T.W. (1996): The osmoregulatory capacity of the Ostracoda. – Journal of Comparative Physiology, B, **166**: 215 – 222.

Anderson, F.W. (1970): Carboniferous ostracoda: the genus *Carbonita* Strand. – Bulletin of the Geological Survey of Great Britain, **32**: 69 – 121.

Bateman, R.M., Crane, P.R., DiMichele, W.A., Kendrick, P.R., Rowe, N.P. & Speck, T. (1998): Early evolution of land plants: Phylogeny, Physiology, and Ecology of the Primary Terrestrial Radiation. – Annual Review of Ecological Systems, **29**: 263 – 292.

Bean, W. (1836): Description and figures of *Unio distortus* Bean, and *Cypris concentrica* Bean, from the Upper Sandstone and shale of Scarborough, and *Cypris arcuata* Bean, from the coal formation of Newcastle. – Magazine of Natural History, **9**: 376 – 377.

Becker, G., Coen, M., Lord, A.R & Malz, H. (1990): In the footsteps of Griffith and M'Coy or, Lower Carboniferous Ostracods from Ireland and the definition of the genus *Bairdia* M'Coy 1844 (Part 2). – Courier Forschungsinstitut Senckenberg, **123**: 275 – 290.

Benson, R.H. (1955): Ostracodes from the type section of the Fern Glen Formation. – Journal of Paleontology, **29**: 1030 – 1039.

Berdan, J. (1984): Leperditicopid Ostracodes from Ordovician rocks of Kentucky and nearby States and characteristic features of the Order Leperditicopida. – United States Geological Survey Professional Paper, **1066-J**: 1 – 37.

Bless, M.J.M. (1983): Late Devonian and Carboniferous ostracode assemblages and their relationship to the depositional environment. – Bulletin de la Société belge de Géologie, **92**: 31 – 53.

Bless, M.J.M. & Massa, D. (1982): Carboniferous Ostracodes in the Rhadames Basin of Western Libya: Palaeoecological implications and comparison with North America, Europe and the USSR. – Revue de l'Institut Français du Pétrole, **37**: 19 – 61.

Bless, M.J.M. & Pollard, J.E. (1973): Paleoecology and Ostracode Faunas of Westphalian Ostracode Bands from Limburg, The Netherlands and Lancashire, Great Britain. – Mededelingen Rijks Geologische Dienst, Nieuwe Serie, **24**: 21 – 53.

Bless, M.J.M., 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 – 362.

Brand, P.J. (1996): Taxonomy and distribution of the Upper Carboniferous non-marine bivalve *Carbonicola aldamii*. – Palaeontology, **39**: 407 – 411.

Brenchley, P.J., Carden, G.A., Hints, L., Kaljo, D., Marshall, J.D., Martma, T., Meidla, T. & Nolvak, J. (2003): High-resolution stable isotope stratigraphy of Upper Ordovician sequences: Constraints on the timing of bioevents and environmental changes associated with mass extinction and glaciation. – Geological Society of America Bulletin, **115**: 89 – 104.

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. British Geological Survey research report RR/99/07.

Buschmina, L.S. (1959): Carboniferous ostracods from the Coal Measures of Central Kazakhstan. – Trudy Laboratorii Geologii Uglya Akademii Nauk SSSR, **9**, 174 – 252.

Buschmina, L.S. (1965): Ostracoda from the Abyshev horizon (Lower Carboniferous) of the Kuznetsk Coal Basin. – Stratigrafiya i paleontologiya Paleozoya aziatskoy chasti SSSR, 64 – 98.

Buschmina, L.S. (1968): Early Carboniferous ostracoda of the Kuznetsk Basin. Izdatelstvo nauka: 1 – 28.

Carbonel, P., Colin, J-P., Danielopol, D., Loffler, H. & Neustrueva, I. (1988): Paleoecology of limnic ostracodes: a review of some major topics. – Palaeogeography, Palaeoclimatology, Palaeoecology, **62**: 413 – 416.

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.

Clift, S.G. & Trueman, A.E. (1929): The sequence of non-marine lamellibranchs in the Coal Measures of Nottinghamshire and Derbyshire. – Quarterly Journal of the Geological Society, **1xxxv**, part 1: 77 – 109.

Coen, M. (1989): Ostracodes of the Devonian-Carboniferous transition beds of South China. – Bulletin de la Société Belge de Géologie, **98**: 311 – 317.

Cooper, C.L. (1946): Pennsylvanian ostracodes of Illinois. – Bulletin of the Illinois State Geological Survey, **70**: 1 – 177.

Crasquin, S. (1985): Zonation par les ostracodes dans le Mississippian de l'ouest Canadien. – Revue de Paléobiologie, **4**: 43 – 52.

Dewey, C.P. (1983): Ostracode palaeoecology of the Lower Carboniferous of Western Newfoundland. – In: Maddocks, R.F. (Ed.): Applications of Ostracoda: 104 – 115; University of Houston Geosciences.

Dewey, C.P. (1987): Palaeoecology of a hypersaline Carboniferous ostracod fauna. – Journal of Micropalaeontology, **6**: 29 – 33.

Dewey, C.P. (1989): Lower Carboniferous ostracodes from the Maritimes Basin of eastern Canada: A review. – Atlantic Geology, **25**: 63 – 71.

Dewey, C.P. (1992): A revision of "some ostracodes from the Pennington Formation of Alabama" (Ehrlich, 1964). – Geological Society of Alabama, **163**: 1 – 15.

Dewey, C.P., Puckett, T.M. & Devery, H.B. (1990): Palaeogeographical significance of ostracod biofacies from Mississippian strata of the Black Warrior Basin, northwestern Alabama: a preliminary report. – In: Whatley, R. & Maybury, C. (Eds): Ostracoda and Global Events: 527 – 540; Chapman and Hall.

Dewey, C.P. & Puckett, T.M. (1993): Ostracodes as a tool for understanding the distribution of shelf-related environments in the Chesterian strata of the Black Warrior Basin in Alabama. In: Pashin, J.C. (Ed.): New Perspectives on the Mississippian System of Alabama: A guidebook for the 30th annual field trip of the Alabama Geological Society: 61 – 68.

Falcon-Lang, H.J., Benton, M.J., Braddy, S.J. & Davies, S.J. (2006): The Pennsylvanian tropical biome reconstructed from the Joggins Formation of Nova Scotia, Canada. – Journal of the Geological Society, London, **163**: 1 – 16.

Floyd, J.D. & Williams, M. (2003): A revised correlation of Silurian rocks in the Girvan district, SW Scotland. – Transactions of the Royal Society of Edinburgh: Earth Sciences, **93**: 383 – 392.

Friedman, G.M. & Lundin, R.F. (1998): Freshwater Ostracodes from Upper Middle Devonian fluvial facies, Catskill Mountains, New York. – Journal of Palaeontology, **72**: 485 – 490.

Gray, J. (1988): Evolution of the freshwater ecosystem: the fossil record. – Palaeogeography, Palaeoclimatology, Palaeoecology, **62**: 1 – 214.

Guirdham, C., Andrews, JE., Browne, M.A.E. & Dean, M.T. (2003): Stratigraphic and palaeoenvironmental significance of microbial carbonates in the Asbian Sandy Craig Formation of Fife. – Scottish Journal of Geology, **39**: 151 – 168.

Hibbert, S. (1834): On the freshwater limestones of Burdiehouse in the neighbourhood of Edinburgh, belonging to the Carboniferous Group of rocks. With supplementary notes on freshwater limestones. – Transactions of the Royal Society of Edinburgh, **13**: 169 – 241.

Horne, D.J. (2003): Key Events in the Ecological Radiation of the Ostracoda. – Palaeontological Society Papers, **9**: 181 – 201.

Horne, D.J., Cohen, A. & Martens, K. (2002): Taxonomy, Morphology and Biology of Quaternary and Living Ostracoda. – The Ostracoda: Applications in Quaternary Research. – Geophysical Monograph, **131**: 5 – 36.

Horne, D.J., Smith, R.J., Whittaker, J.E. & Murray, J.W. (2004): The first British record and a new species of the superfamily Terrestricytheroidea (Crustacea, Ostracoda): morphology, ontogeny, lifestyle and phylogeny. – Zoological Journal of the Linnean Society, **142**: 253 – 288.

Jones, T.R. & Kirkby, J.W. (1879): 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**, number **4**: 28 – 40.

Jones, T.R., Kirkby, J.W. & Brady, G.S. (1874): A Monograph of the British Fossil Bivalved Entomostraca from the Carboniferous Formations. Part 1, No. 1. The Cypridinadae and their allies. – Monograph of the Palaeontographical Society, 28: 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, No. 2. The Cypridinadae and their allies. – Monograph of the Palaeontographical Society, 38: 57 – 92.

Keen, M.C. (1977): Ostracod assemblages and the depositional environments of the Headon, Osborne, and Bembridge Beds (Upper Eocene) of the Hampshire Basin. – Palaeontology, **20**: 405 – 445.

Kellett, B. (1936): Carboniferous ostracods. – Journal of Paleontology, **10**, 769 – 784.

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.

Kummerow, E. (1949): Über einige Süßwasser-Ostracoden des Ruhrkohlengebietes. – Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Monatshefte, **B**, **1949**: 45 – 59.

Lethiers, F. (1981): Ostracodes du Dévonien terminal de l'Ouest du Canada: systématique, biostratigraphie et paléoécologie. – Geobios mémoire spécial, **5**: 1 – 234.

Monaghan, A.A. & Parrish, R.R. (2005): Geochronology of Carboniferous-Permian magmatism in the Midland Valley of Scotland: implications for regional tectonomagmatic evolution and the numerical time scale. – Journal of the Geological Society, London, **162**: 1 – 15.

Neale, J. (1984): The Ostracoda and uniformitarianism: II. The earlier record: Cretaceous to Cambrian. – Proceedings of the Yorkshire Geological Society, **44**: 443 – 478.

Newman, W.A. (2005). Origin of the Ostracoda and their maxillopodan and hexapodan affinities. – Hydrobiologia, **538**: 1 – 21.

Pollard, J.E. (1966): A non-marine ostracod fauna from the Coal Measures of Durham and Northumberland. – Palaeontology, **9**: 667 – 697.

Pollard, J.E. (1969): Three ostracod-mussel bands in the Coal Measures (Westphalian) of Northumberland and Durham. – Proceedings of the Yorkshire Geological Society, **37**: 239 – 276.

Pollard, J.E. (1985): Coprolites and ostracods from the Dinantian of Foulden, Berwickshire, Scotland. – Transactions of the Royal Society of Edinburgh: Earth Sciences, **76**: 49 – 51.

Přibyl, A. (1960): New information on the Upper Carboniferous freshwater and continental fauna from the Ostrava-Karviná Coal District. – Rozpravy Československé akademie věd, **70**: 3 – 71.

Rebske, W.C. Bless, M.J.M., Paproth, E. & Steemans, E.P. (1985): Over enkele fossielen uit de klerf-schichten (Onder-Emsien) bij Waxweiler (Eifel, BRD) en hun leefmilieu. – Grondboor en Hamer, **5**: 142 – 155.

Samoilova, R.B. & Smirnova, R.F. (1960): On new ostracode genera and species from the Palaeozoic of the southern part of the Moscow area basin. – Meterialy po geologii i poleznym isokpaemyn tsentralnykh rayonov europeyskoy chasti SSSR, **3**: 64 – 111.

Schäfer, P. (2007): Muschelkrebse (Ostracoden) aus permokarbonischen Karbonatbänken im rheinland-pfälzischen Teil des Saar-Nahe-Beckens. In: Schindler, T., Heidtke, U.H.J. (Eds): Kohlesümpfe, Seen und Halbwüsten: 156 – 163; Pollichia.

Schultze, H.P., Maples, C.G. & Cunningham, C.R. (1994): The Hamilton Konservat-Lagerstatte: Stephanian terrestrial biota in a marginal-marine setting. – Transactions of the Royal Society of Edinburgh, Earth Sciences, **84**: 443 – 451.

Scott, H.W. (1944): Permian and Pennsylvanian fresh-water ostracodes. – Journal of Paleontology, **18**: 141 – 147.

Scott, H. W. & Summerson, C.H. (1943): Non-marine Ostracoda from the Lower Pennsylvanian in the Southern Appalachians, and their bearing on inter-continental correlation. – American Journal of Science, **241**: 653 – 675.

Shi, C.-G. (1964): The Middle and Upper Devonian ostracoda from Dushan and Douyun, S. Kueichow. – Acta Palaeontologica Sinica, **12**: 50 – 65.

Siveter, D.J. (1984): Ecology of Silurian Ostracods. . – Special Papers in Palaeontology, **32**: 71 – 85.

Siveter, D.J., Vannier, J.M.C. & Palmer, D. (1991): Silurian Myodocopes: Pioneer pelagic ostracods and the chronology of an ecological shift. – Journal of Micropalaeontology, **10**: 151 – 173.

Siveter, D.J., Siveter, Derek, J., Sutton, M.D. & Briggs, D.E.G. (2007): Brood care in a Silurian ostracod. – Proceedings of the Royal Society, **B274**: 465 – 469.

Smith, R.J. (1999): Possible fossil ostracod (Crustacea) eggs from the Cretaceous of Brazil. – Journal of Micropalaeontology, **18**: 81 – 87.

Sohn, I.G. (1977): Muscle scars of Late Palaeozoic freshwater ostracodes from West Virginia. – Journal of Research, US Geological Survey, **5**: 135 – 141.

Sohn, I.G. (1985): Latest Mississippian (Namurian A) non marine ostracodes from West Virginia and Virginia. – Journal of Paleontology, **59**: 446 – 460.

Stephenson, M.H., Williams, M., Monaghan, A., Arkley, S. & Smith, R. (2002): Biostratigraphy and palaeoenvironments of the Ballagan Formation (lower Carboniferous) in Ayrshire. – Scottish Journal of Geology, **38**: 93 – 111.

Stephenson, M.H., Williams, M., Leng, M.J. & Monaghan, A.A. (2004): Aquatic plant microfossils of probable non-vascular origin from the Ballagan Formation (Lower Carboniferous), Midland Valley, Scotland. – Proceedings of the Yorkshire Geological Society, **55**: 145 – 158.

Taylor, P.D. & Vinn, O. (2006): Convergent morphology in small spiral worm tubes ("Spirorbis") and its palaeoenvironmental implications. – Journal of the Geological Society of London, **163**: 225 – 228.

Tibert, N.E. & Dewey, C.P. (2006): *Velatomorpha,* a new healdioidean ostracode genus from the early Pennsylvanian Joggins Formation, Nova Scotia, Canada. – Micropaleontology, **52**: 51 – 66.

Tibert, N.E. & Scott, D.B. (1999): Ostracodes and agglutinated foraminifera as indicators of palaeoenvironmental change in an Early Carboniferous brackish bay, Atlantic Canada. – Palaios, **14**: 246 – 260.

Tinn, O. & Meidla, T. (2004): Phylogenetic relationships of Early-Middle Ordovician ostracods of Baltoscandia. – Palaeontology, **47**: 199 – 221.

Vannier, J. & Abe, K. (1992): Recent and early Palaeozoic myodocope ostracods: functional morphology, phylogeny, distribution and lifestyles. – Palaeontology, **35**: 485 – 517.

Vannier, J. & Abe, K. (1995): Size, body plan and respiration in the Ostracoda. – Palaeontology, **38**: 843 – 873.

Vannier, J., Thiery, A. & Racheboeuf, P.R. (2003): Spinicaudatans and Ostracods (Crustacea) from the Montceau Lagerstatte (Late Carboniferous, France): Morphology and palaeoenvironmental significance. – Palaeontology, **46**: 999 – 1030.

Vannier, J., Wang, S.-Q. & Coen, M. (2001): Leperditicopid arthropods (Ordovician - Late Devonian): functional morphology and ecological range. – Journal of Paleontology, **75**: 75 – 95.

Warshauer, S. M. & Smosna, R. (1977): Paleoecologic controls of the ostracode communities in the tonoloway limestone (Silurian; Pridoli) of the Central Appalachians. – In: Löffler, H. & Danielopol, D. (Eds): Aspects of ecology and zoogeography of Recent and fossil ostracoda: 475 – 485; The Hague.

Whatley, R.C. (1983): The application of Ostracoda to palaeoenvironmental analysis. – In: Maddocks, R.F. (Ed.): Applications of Ostracoda: 51 – 77; University of Houston Geosciences.

Whatley, R.C., Siveter, D.J. & Boomer, I. (1993): Arthropoda (Crustacea: Ostracoda). – In: Benton, M. J. (Ed.): The Fossil Record 2: 343 – 356; London (Chapman and Hall).

Williams, M. & Siveter, D.J. (1996): Lithofacies-influenced ostracod associations in the middle Ordovician Bromide Formation, Oklahoma, USA. – Journal of Micropalaeontology, **15**: 69 – 81.

Williams, M., Stephenson, M.H., Wilkinson, I.P., Leng, M.L. & Miller, C.G. (2005): Early Carboniferous (Late Tournaisian-Early Visean) ostracods from the Ballagan Formation, central Scotland, UK. – Journal of Micropalaeontology, **24**: 77 – 94.

Williams, M., Leng, M.L., Stephenson, M.H., Andrews, J.E., Wilkinson, I.P., Siveter, D.J., Horne, D.J. & Vannier, J.M.C. (2006): Evidence that Early Carboniferous ostracods colonised coastal flood plain brackish water environments. – Palaeogeography, Palaeoclimatology, Palaeoecology, **230**: 299 – 318.

Williams, M., Siveter, D.J., Salas, M.J., Vannier, J., Popov, L.E. & Ghobadi Pour, M. (2008): The earliest ostracods: the geological evidence. – Senckenbergiana lethaea (this issue).

Yozzo, D.J. & Steinbeck, P.L. (1994): Ostracoda from tidal freshwater wetlands at Stockport, Hudson River estuary: abundance, distribution and composition. – Estuaries, **17**: 680 – 684.

Ziegler, P.A. (1989): Evolution of Laurussia, a study in late Palaeozoic plate tectonics. – Kluwer (Dordrecht, The Netherlands).

Manuscript received: 27 November 2007
Reviewed manuscript accepted: 21 February 2008