

THE TAXONOMIC, PALAEOECOLOGIC AND  
BIOGEOGRAPHIC IMPORTANCE OF THE LATE ORDOVICIAN  
LAURENTIAN OSTRACOD FAUNA OF THE GIRVAN DISTRICT,  
SW SCOTLAND

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by

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# THE TAXONOMIC, PALAEOECOLOGIC AND BIOGEOGRAPHIC IMPORTANCE OF THE LATE ORDOVICIAN LAURENTIAN OSTRACOD FAUNA OF THE GIRVAN DISTRICT, SW SCOTLAND

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## Abstract

Ostracods form a numerically important component of certain Late Ordovician faunas of the Girvan district, southwest Scotland. Fifty-two ostracod taxa are identified, including twenty-three discussed in open nomenclature, and seventeen species that are considered as nomen dubia. The fauna reveals new and important data bearing on the biostratigraphic, palaeogeographic and palaeoecologic significance of the Girvan Lower Palaeozoic succession. Much of the Ordovician ostracod fauna of the Girvan district preserved in clastic deposits represents transported material. However, those ostracods from the early Katian Craighead Limestone Formation define shallow marine and open marine faunas respectively. The Girvan ostracods include many short-ranging species which are useful for inter-regional correlation of the Late Ordovician succession of Scotland and North America; these include *Hippula ventrospinosa*, *Balticella deckeri*, *Eurychilina sunbloodensis* and *Baltonotella parsispinosa* which characterize Sandbian age strata, and *Kinnekullea comma* which is typical for the Katian (*anceps* graptolite Biozone). Biogeographically most of the Girvan fauna is typically of North American aspect at the species level but from the early Katian onwards shows generic links with Baltica and Avalonia.

The spatial and temporal distribution patterns of the Girvan Late Ordovician ostracod fauna are assessed in the context of the entire Late Ordovician Laurentian ostracod assemblage particularly for the Sandbian interval, where ostracod diversity was highest at species and genus level. Multivariate analysis demonstrates that geography had the strongest control on the global distribution of Ordovician benthic ostracods. Within Laurentia Sandbian ostracods show striking inter-basinal endemism at species level, ranging from 25% endemic in the Foxe Basin of the Franklin district, Canada to 75% in the Michigan basin. This pattern of endemism is common in other benthic groups such as brachiopods, and may indicate rapid speciation in microhabitats. Despite the strong overprint of local endemism, pan-continental faunal differences are noticed between the midcontinent and marginal Laurentian ostracod assemblages that are confirmed by multivariate analysis, and these allow the demarcation of a 'Midcontinent' and a southern 'Marginal' province for the Sandbian. Ostracod assemblages of the two provinces appear to have been controlled by physical parameters such as temperature and salinity which are related to water depth and latitude.

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## Chapter 1: Introduction

### Introduction

Ostracods are small (about one to two millimetres in length) crustaceans with a bivalved calcified carapace and an extensive fossil record extending back to the Cambrian (Harvey *et al.* 2012). Their Cambrian record is known from soft anatomy represented by appendages (Harvey *et al.* 2012); whereas the Ordovician ostracods are known from carapaces. Ostracods are a diverse class of living aquatic crustaceans, and are the most abundant among fossil arthropods (Schellenberg 2007; Pokorny 1978). Ostracods have undergone ecological radiations into a range of aquatic environments (Pokorny 1978). The earliest ostracods were predominantly benthic and occupied shallow marine habitats (Tinn & Meidla 2004; Salas *et al.* 2007; Williams *et al.* 2008; Ghobadi Pour *et al.* 2011); they radiated into pelagic environments during the Silurian (Siveter *et al.* 1991) and also colonised fresh water habitats by the Carboniferous (Bennett 2008; Bennett *et al.* 2011).

Ostracods are documented from all major palaeocontinental regions from the Early Ordovician onwards (Salas *et al.* 2007, 2011; Williams *et al.* 2003; Ghobadi Pour *et al.* 2011). The most diverse and abundant Ordovician ostracod fauna is recorded from the successions of North America and the Baltic region. Ordovician ostracods occupied benthic neritic habitats and apparently possessed limited trans-oceanic dispersal capability. They are therefore widely used to track the relative palaeogeographic position of Ordovician continents (Schallreuter & Siveter 1985); to demarcate biogeographical provinces (Williams *et al.* 2003; Vannier *et al.* 1989; Meidla *et al.* in press) and to demonstrate lithofacies distribution patterns (e.g. Vannier *et al.* 1989).

This study focuses on the Late Ordovician ostracod fauna of the Girvan district, southwest Scotland and also examines the broad distributional patterns of the Late Ordovician ostracods of palaeocontinental Laurentia. Though the earliest finds of Ordovician ostracods in the Girvan area extends back to the mid-nineteenth century (M'Coy 1851), they have been rarely studied (Anderson & Pringle 1946; Jones 1893; Siveter 1978). In contrast, the Ordovician ostracod faunas from other parts of Britain such as south Wales and northern England have been widely studied in the last thirty-five years (Siveter 1978, 1982, 1983, 1985, 2009; Jones 1986, 1987) after the initial reconnaissance studies of the mid-nineteenth century (Salter 1845, 1848, 1852, 1854). Most of these faunas have undergone extensive re-evaluation including description in monographs (Jones 1986, 1987). They have been shown to have local stratigraphic value and are have been widely used in palaeogeography (Schallreuter & Siveter 1985; Jones 1986, 1987; Siveter 2009). The neglect of Girvan ostracods might reflect their unattractive state of preservation and difficulty of recovery. Nonetheless, ostracods occur at a number of stratigraphic horizons in the Late Ordovician of Girvan (Fig. 1); they occur in both shallow marine carbonates and deep marine clastics (Williams *et al.* 2001a). They co-occur in association with other shelly faunas such as trilobites and brachiopods, and in some cases with graptolites and chitinozoans, making them useful tools for more precise inter-regional biostratigraphic correlation of Scotland with the Late Ordovician successions of North America (Floyd *et al.* 1999; Mohibullah *et al.* 2011). Some recent studies have attempted to evaluate their biostratigraphic, palaeogeographic and paleoecological significance and have highlighted their relative neglect (Floyd *et al.* 1999; Williams & Floyd 2000; Williams *et al.* 2001a).

The Girvan Ordovician faunas, including ostracods, have strong Laurentian affinities (Tripp 1980a, b; Williams *et al.* 2001a). Laurentia straddled the equator during the Ordovician with its northern and southern margins extending into the tropics and subtropics (Cocks & Torsvik 2005; Vandenbroucke *et al.* 2010a, b). Ostracods are extensively documented from the Late Ordovician successions of North America from peritidal to deep shelf facies (Williams & Siveter 1996; Kraft 1962; Kay 1934, 1940). Their wide spatial ranges may express broad latitudinal and depth-related changes, which have been evaluated from individual formations (Copeland 1982; Williams & Siveter 1996).

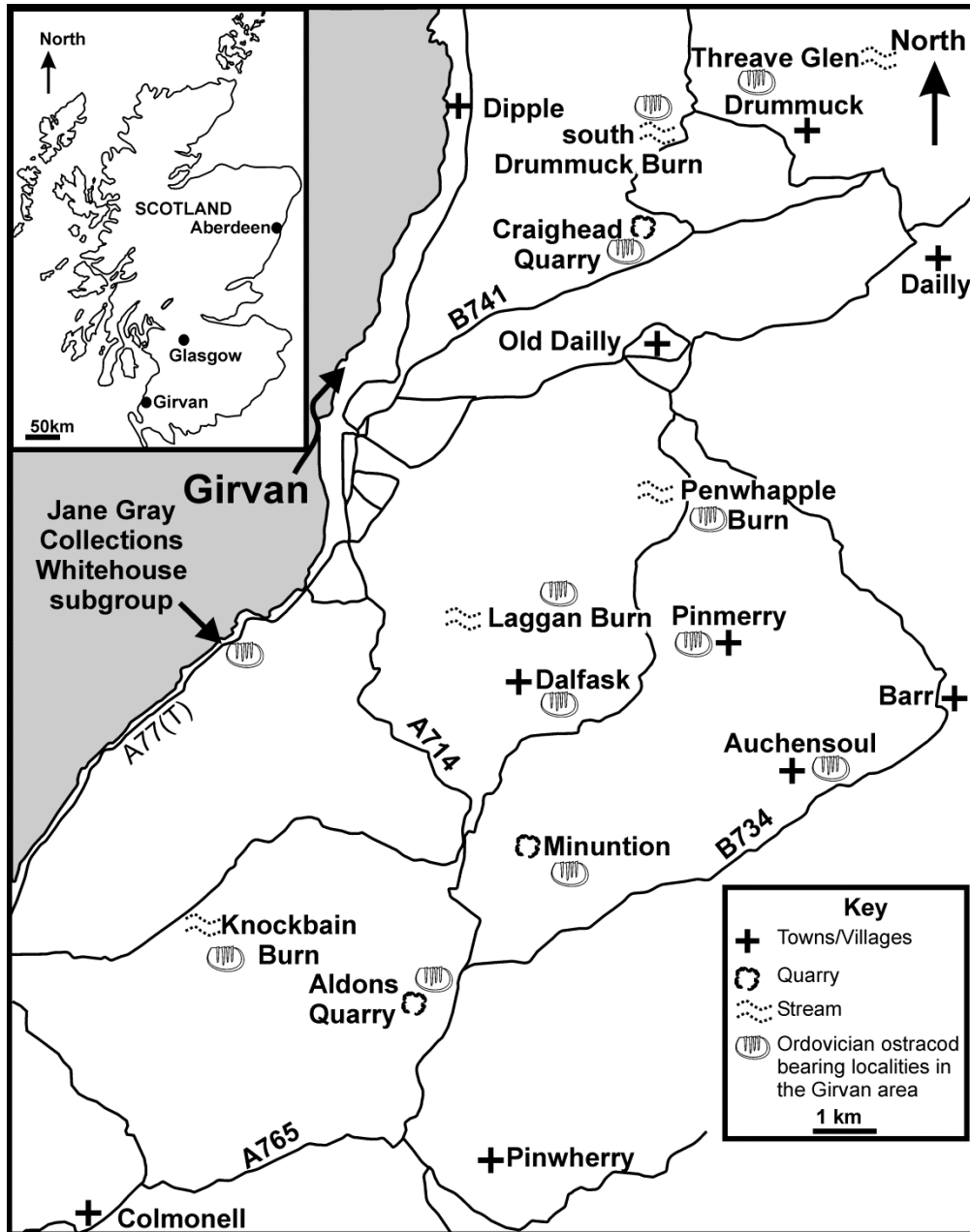


Figure 1. Distribution of ostracod-bearing localities in the Ordovician of the Girvan district, southwest Scotland.

The aims of this study are

- To determine the taxonomic affinities of the Late Ordovician ostracod fauna of Girvan, Scotland

- To study the biostratigraphic significance of the Late Ordovician ostracods of Girvan
- To determine the palaeoecology of different ostracod groups of Girvan
- To establish the biogeographical significance of the Girvan ostracod fauna
- To assess the Girvan fauna within the overall distributional patterns of the Late Ordovician ostracods of palaeocontinental Laurentia

### **Ordovician of Girvan**

Girvan lies within the Midland Valley Terrane which lay on the eastern margin of the Laurentian palaeocontinent (Cocks & Fortey 1982; McKerrow *et al.* 1991). The Ordovician sedimentary successions of Girvan rest unconformably on the ophiolitic Ballantrae complex (Fig. 2). The Ballantrae complex was obducted on to the south-eastern margin of the Midland Valley Terrane during the mid-Ordovician, and, later in the mid-Ordovician, deposition commenced in a proximal fore-arc setting (Owen & Rushton 1999). Sediments were deposited in a wide range of environments, from fluvio-deltaic to shallow marine carbonates and deep marine clastics, and thus represent conglomerate, sandstone, mudstone and carbonate lithologies (Bluck 1985; Ingham 2000). The sedimentation patterns in the Girvan district were controlled, in part, by a fault system that produced rapid changes in sedimentation during the Ordovician, with shallow and deep marine facies often juxtaposed with each other (Williams 1962; Harper & Stewart 2008). Abundant and diverse shelly fauna occur in shallow marine carbonates, sandstones and conglomerates, and graptolites in deep water mudstones. This interplay of facies and fauna provide excellent opportunities for inter-regional biostratigraphic correlation (Harper & Stewart 2008; Mohibullah *et al.* 2011; Chapter 3).

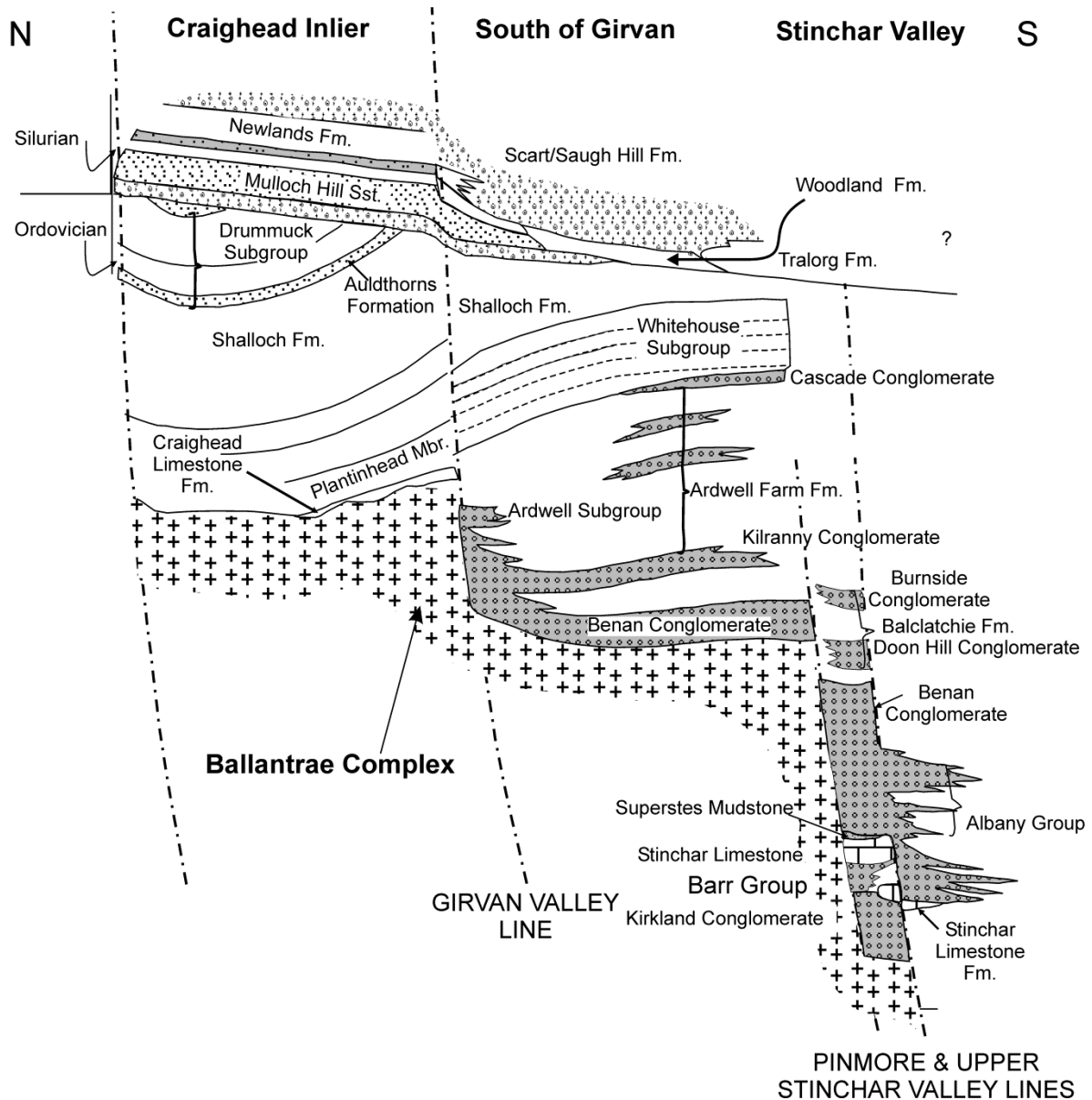


Figure 2. Schematic cross-section showing the lithostratigraphical and structural setting of the Ordovician and Lower Silurian strata of the Girvan district across major faults (modified from Ingham 1992a; and Harper & Stewart 2008).

The stratigraphical succession of Girvan comprises the Albany, Barr and Ardmillan groups in ascending order (Fig. 3; Owen & Rushton 1999; Ingham 2000), the latter containing most of horizons from which the Girvan ostracod fauna has been recovered (Williams *et al.* 2001a). The Ardmillan Group was entirely deposited

during the Late Ordovician and is further subdivided into Ardwell, Whitehouse and Drummuck subgroups, the former yielding the most diverse ostracod fauna of the Late Ordovician of Girvan (Ingham 2000). The Ardwell Subgroup has a complex lithostratigraphy and across the major regional faults shows temporal and lithofacies changes (Ingham 1992a; Owen & Rushton 1999). On the Girvan foreshore and in the Stinchar Valley it is represented by Sandbian to Katian age conglomerates, sandstones and mudstones of the Kilranny Conglomerate, Balclatchie and Ardwell Farm formations (Owen & Rushton 1999). North of the Girvan Valley, in the Craighead Inlier, it is represented by a thick succession of Craighead Limestone carbonates interdigitating with marine mudstones that yield graptolites of *clingani* Biozone age, indicating an interval equivalent to the upper Ardwell Farm Formation (Fig. 3). The Whitehouse Subgroup is also exposed on the Girvan foreshore and in the Girvan valley and is partly represented in the Craighead Inlier (Ingham 2000). Most of the Whitehouse Subgroup was deposited on the outer shelf and slope and yields diverse brachiopod and trilobite assemblages (Harper & Stewart 2008). Ostracods have rare occurrences and are mostly represented by indeterminate moulds (Williams *et al.* 2001a), which nonetheless were sometimes (over-) identified as discrete species by Jones (1893). The Drummuck Subgroup is exposed only within the Craighead Inlier and was deposited in outer shelf-slope settings, yielding graptolites, trilobites and ostracods of inter-regional biostratigraphical and biogeographical significance (Harper & Stewart 2008; Floyd *et al.* 1999; Williams *et al.* 2000).

Period	International standard stages	British graptolite biozones	Lithostratigraphy			
			Group/ Subgroup	Craighead Inlier	Girvan foreshore	Stinchar Valley
Ordovician	Hirnantian	<i>persculptus</i>	Drumuck Subgroup			
		<i>extraordinarius</i>		High Mains Fm		
	Katian	<i>anceps</i>	Drumuck Subgroup	South Threave Fm (Mbr)		
				Lady Burn Fm (Mbr)		
				Quarrel Hill Fm		
				Auldthorns Fm		
		<i>complanatus</i>	Ardmillan Group	Shalloch Fm	Shalloch Fm	Shalloch Fm
				[faulted junction]	Mill Fm (Mbr)	Mill Fm
					Myoch Fm (Mbr)	Myoch Fm
		<i>linearis</i>			Penwhapple Fm	Penwhapple Fm
					Three Mile Fm	
				South Shore Fm		
	clingani Biozone	<i>morrisi</i> Subzone	Ardwell Subgroup	Plantinhead Fm	Ardwell Farm Fm	Ardwell Farm Fm
		<i>caudatus</i> Subzone		Craighead Limestone Fm Kiln Mudst Mbr Sericoidae Mudst Mbr		
	Sandbian	<i>bicornis</i>	Ardwell Subgroup			
		<i>gracilis</i>			Kilranny Cong	Balclatchie Fm (Mbr)
	Darriwilian	<i>teretiusculus</i>	Barr Group		Benan Cong	Benan Cong
						Superstes Mudstone (Mbr)
						Stinchar Lst (Mbr)
						Confinis Flags
						Auchensoul Bridge Mudstones
						Auchensoul Lst
						Kirkland Cong
	Early Ordovician				Ballantrae complex	

Figure 3. Lithostratigraphical distribution of Ordovician ostracods of the Girvan district, southwest Scotland. Stratigraphy after Ingham 2000, Williams *et al.* 2001 British graptolite Biozones are after Williams *et al.* 2004; Zalasiewicz *et al.* 2010 and Loydell 2012. Symbols: Mbr, Member; Cong, conglomerate; Fm, Formation; Lst, Limestone.

## Material

The ostracod materials studied here are from the Craighead Limestone Formation, Balclatchie Formation, lower part of Ardwell Farm Formation, Mill Formation, Lady Burn Formation and South Threave Formation (Fig. 3). Most of the materials were

collected during a number of field trips to the area, supplemented by the examination of the Girvan ostracod collections in the British Geological Survey Keyworth Nottingham (BGS), The Natural History Museum, London (NHM UK) and the Hunterian Museum Glasgow.

Most of the Late Ordovician Girvan ostracods are preserved as internal and external moulds with the exception of the Craighead Limestone Formation, which represents well preserved calcitic 'crack-out' material from Limestones; and moderately preserved calcitic carapaces from the inter-bedded mudstones. The lower Ardwell Farm and Balclatchie formations also yield few 'crack-out' specimens. The mould faunas represent both well- and poorly preserved material; the mould fauna from the Ardwell Farm, Lady Burn and South Threave formations preserve fine details of the ostracod valves, whereas the fauna of the Mill Formation, Kiln and Sericoidea mudstone members of the Craighead Limestone Formation are indeterminate moulds which lack diagnostic morphology.

### **Methodology**

Various methods have been used in this study which are summarised here but described in detail in each relevant chapter.

- Ostracod calcitic valves from the limestones were excavated with needles whereas calcitic carapaces from mudstones have been recovered using 10% H<sub>2</sub>O<sub>2</sub> to dissociate the rock, wet sieved with 1mm, 500 and 250 micron sieves, and dried in the oven, the ostracods being collected with a fine brush under a binocular microscope.

- Mould fauna have been cast with silicon rubber compounds (see Siveter 1984a; Purnell 2003).
- All specimens, except those from the Mill Formation were gold coated with the sputter coater 'Emitech K500X' and imaged with the Scanning electron microscope Hitachi S-3600N at Leicester University. The specimens from the Mill Formation were coated with ammonium chloride sublimate and photographed with a digital (Canon Eos) camera.
- To evaluate the broad, continental-scale distribution pattern of Ordovician ostracods, data were compiled from the published literature and analysed with multivariate statistical techniques.

### **Chapters Summary**

Overview of chapter 2. This chapter describes the systematic palaeontology of the Late Ordovician ostracod fauna of Girvan. These results will be submitted as a Monograph to the Palaeontographical Society for which the title has been accepted (A monograph of the Late Ordovician ostracod fauna of the Girvan district, southwest Scotland).

Overview of chapter 3. This chapter documents the ostracod fauna from the Late Ordovician (Sandbian) Ardwell Farm Formation with their biogeographic and biostratigraphic significance. The fauna is transported, being represented by disarticulated ostracod valves. These results have been published in the Scottish Journal of Geology (Mohibullah, M., Vandenbroucke, T.R.A., Williams, M., Floyd, J., Meidla, T., Zalasiewicz, J.A., Siveter, D.J. 2011. Late Ordovician (Sandbian)

ostracods from the Ardwell Farm Formation, southwest Scotland. *Scottish Journal of Geology*, **47**, 57-66). See Appendix 4.

Overview of chapter 4. In this chapter the ostracod fauna from the Late Ordovician (early Katian) Craighead Limestone Formation is documented. Two different ostracod assemblages are recognized, and the biostratigraphic and biogeographic significance of the fauna is discussed. These results have been published in Geological Magazine (Mohibullah, M., Afzal, J., Williams, M., Meidla, T., Siveter, D.J., Zalasiewicz, J.A. 2010. Ostracods from Upper Ordovician (Katian) carbonate lithofacies in southwest Scotland. *Geological Magazine*, **147**, 919-939). See Appendix 5.

Overview of chapter 5. To give context to the Girvan fauna, in this chapter I have evaluated the distributional patterns of the entire Laurentian Ordovician ostracods, focussing particularly on the diverse faunas of Sandbian age (Copeland 1965, 1982; Williams & Siveter 1996; Harris 1957; Swain 1957, 1962; Kraft 1962). Inter-basinal endemism and faunal differences between the midcontinent and margins of Laurentia are described and two ostracod provinces are demarcated. These results form a research paper, submitted to Plos One (Mohibullah M., Williams M., Vandenbroucke, T.R.V., Sabbe, K., Zalasiewicz, J.A. 'Marine Ostracod Provinciality in the Ordovician of Palaeocontinental Laurentia and its Environmental and Geographical Expression') that is currently under review.

Each chapter of this thesis (apart from chapter 1 and Chapter 6) stand as a publication and is either published, in press or under peer-review).

## **Chapter 2: A monograph of the Late Ordovician ostracod faunas of the Girvan district, southwest Scotland**

### **Abstract**

The Late Ordovician ostracod fauna of the Girvan district, southwest Scotland comprises fifty-two species from twenty-six genera and fifteen families, including twenty-three species described in open nomenclature, and seventeen that are considered as nomina dubia. The ostracods include representatives of the Suborders Palaeocopa, Binodicopa, Leiocopa, Platycopa and Metacopa. The fauna includes several species that allow inter-continental correlation with the Late Ordovician succession of North America. These include the Sandbian species *Eurychilina sunbloodensis*, *Balticella deckeri*, *Baltonotella parsispinosa* and *Hippula ventrospinosa*, and the Katian species *Kinnekullea comma*. Biogeographically, the Girvan ostracod fauna of Sandbian age shows strong affinities at species-level with the fauna of palaeocontinental Laurentia, but from the early Katian onwards there are species level links with the Baltic region, and some common taxa at generic and species-level with palaeocontinental Avalonia.

### **Introduction**

Ostracods are small bivalved crustaceans (about one millimetre in length) with a fossil record extending back to the Cambrian (Harvey *et al.* 2012). Ordovician ostracods are recorded worldwide (e.g. Meidla 1996; Willams & Siveter 1996; Ghobadi Pour *et al.* 2006, 2011; Salas *et al.* 2007; Schallreuter *et al.* 2008), the richest and most abundant fauna being documented from the Baltic region and

North America (e.g. Vannier *et al.* 1989; Meidla 1996; Williams *et al.* 2003). Ostracods formed a numerically abundant component of marine benthic arthropod faunas and have been widely used in biostratigraphic, biogeographic and palaeoenvironmental analyses.

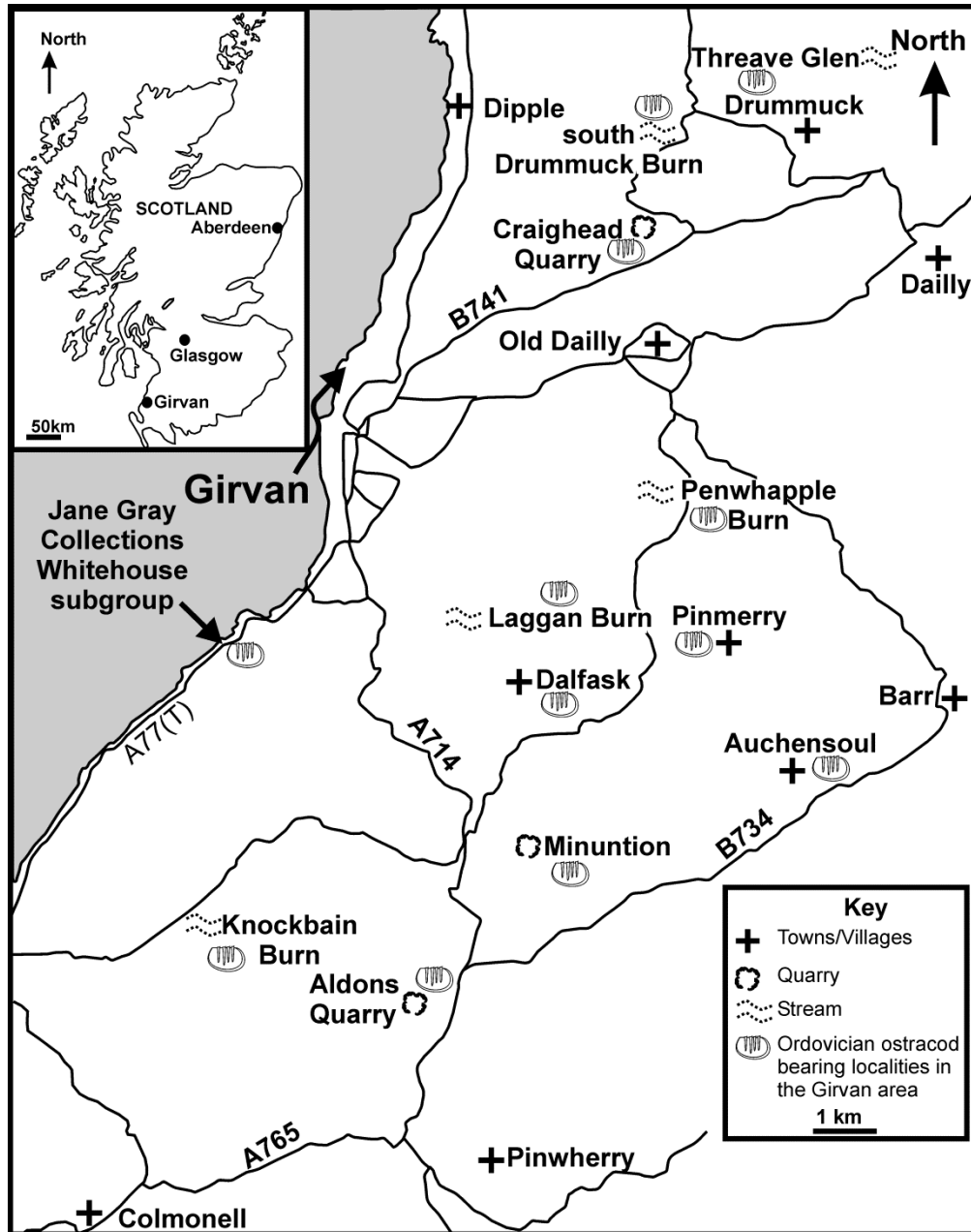


Figure 1. Map showing the distribution of ostracod-bearing localities in the Ordovician of the Girvan district, southwest Scotland.

The Girvan district of southwest Scotland is a classical area for the study of the British Ordovician succession (Fig. 1). It has yielded rich brachiopod (Williams 1962; Harper & Owen 1986; Harper & Stewart 2008), trilobite (Tripp 1980a, b, 1993) and graptolite faunas (Williams 1987), which have been instrumental for both local and interregional correlation of the Lower Palaeozoic succession (Harper & Stewart 2008; Rushton 2001, 2003). Ostracod faunas have also been documented from the Ordovician succession (e.g. Williams *et al.* 2001a; Mohibullah *et al.* 2010, 2011; Fig. 1; Chapter 3, 4) but there has been no systematic study of their taxonomic and biogeographic significance, largely because of their poor preservation and difficulty of extraction from the rock. Some 52 species are documented in this monograph, including 23 in open nomenclature, and 17 that are considered as nomina dubia.

### History of Research

The Ordovician of the Girvan district forms a thick succession of marine shelf carbonates and clastic sedimentary rocks. These successions yield rich fossil assemblages and represent all major Ordovician faunal groups such as graptolites, brachiopods, trilobites, chitinozoans, conodonts, gastropods and ostracods (Williams *et al.* 2001a; Williams 1962; Bergström 1990; Vandenbroucke *et al.* 2003; Harper & Stewart 2008; Bulman 1944-47; Bergström 1990; Tripp 1980a, b; Ingham & Tripp 1991; Ebbestad 2008; Stewart & Owen 2008). Most of these groups have been well documented for their biostratigraphic, palaeogeographic and palaeoenvironmental significance (Rushton *et al.* 1996; Rushton 2001, 2003; Bergström 1990; Harper 1979, 1981, 1982; Harper & Stewart 2008). Amongst these fossil groups, brachiopods

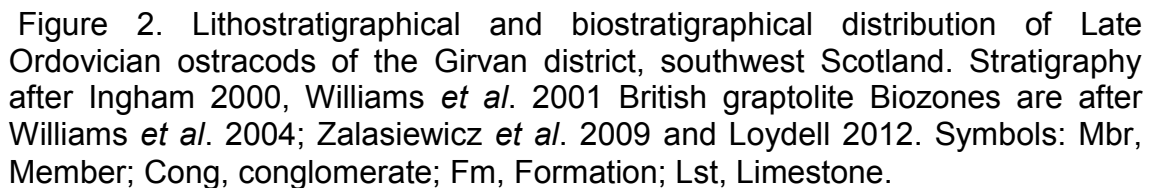
represent one of the most abundant and diverse faunas and occur throughout the Mid-Late Ordovician Barr and Ardmillan succession (Harper & Stewart 2008; herein see Fig. 2). The extensive collection of Girvan brachiopods during the last fifty years, quantified in a series of publications and monographs, has revealed the Laurentian affinities of the Girvan faunas, and the palaeogeographic and palaeoenvironmental evolution of the Girvan district during the Ordovician (Williams 1962; Harper 1979, 1981, 1982, 1984, 1988, 1989, 2001, 2006; Harper & Owen 1986; Harper & Stewart 2008). Similarly, much of the Ordovician succession also yields trilobites - in association with brachiopods - as in the Balclatchie and Ardwell Farm formations (Fig. 2), and these display similar North American affinities (Harper & Owen 1986; Williams 1962; Tripp 1980a, b; Rushton *et al.* 1996; Stewart & Owen 2008). Other faunal groups such as graptolites, conodonts and chitinozoans which have wider biostratigraphic significance are found at several stratigraphic levels in the Girvan district (e.g. Bulman 1944-47; Rushton 2001, 2003; Williams 1987; Williams *et al.* 2004; Bergström 1990; Vandenbroucke *et al.* 2003) and allow precise correlation of the Ordovician of the Girvan district to global standards (Webby *et al.* 2004, Finney 2005; Bergström *et al.* 2009).

Ostracods also form an important component of the Girvan Ordovician fauna and are documented from both the carbonate and clastic sedimentary rocks (Floyd *et al.* 1999; Williams *et al.* 2001a; Mohibullah *et al.* 2010, 2011; Chapter 3, 4). Ordovician ostracods from Girvan were first documented by M'Coy in 1851. A few decades later, Jones (1879, 1893) documented ostracods from Mid and Late Ordovician strata (Stinchar Limestone, Superstes Mudstone and Whitehouse Group, see figs 1, 2) but most of these are preserved as poor

moulds without diagnostic morphology. After Jones (1893), the study of Girvan ostracods received little attention, with scant references by Peach & Horne (1899), Anderson & Pringle (1946) and Siveter (1978). More recently, the Girvan ostracods have been documented from individual formations (e.g. Floyd *et al.* 1999; Williams & Floyd 2000; Mohibullah *et al.* 2010, 2011; Chapter 3, 4) but there has been no modern systematic treatment of the entire Late Ordovician fauna.

### **Stratigraphy**

In the Girvan district of Scotland much of the Late Ordovician succession has been biostratigraphically dated using graptolites (Bulman 1944-47; Rushton *et al.* 1996; Rushton 2001, 2003; Floyd *et al.* 1999; Williams 1987; Williams *et al.* 1972), and where graptolites are absent, the coeval conodont biozones have been recognised (Bergström 1990). In addition to graptolites and conodonts, chitinozoans and shelly fossils such as brachiopods and trilobites have also been used for biostratigraphic correlation (Tripp 1980a, b; Leslie & Bergström 1995; Vandenbroucke *et al.* 2003; Mohibullah *et al.* 2011; Chapter 3). The interplay of graptolite-bearing and shell-bearing horizons in the Girvan succession, for example at Craighead Quarry (Tripp 1980a; Mohibullah *et al.* 2010; Chapter 4) or in Lady Burn (e.g. Floyd *et al.* 1999), means that correlation between rocks deposited in shelf and pelagic facies can be achieved with a high degree of precision, and thus the Girvan succession can be readily tied to the evolving global chronostratigraphic scheme (Finney 2005; Webby *et al.* 2004; Fig. 2).



Ostracods in the Late Ordovician succession of Girvan occur in the Balclatchie, Ardwell Farm, Craighead Limestone, Mill, Myoch, Lady Burn and south Threave formations (Williams *et al.* 2001a; Floyd *et al.* 1999; Mohibullah *et al.* 2010, 2011; Chapter 3, 4 also see figs 1, 2). The Balclatchie Formation yields conodont fauna of the lower *Amorphognathus tvaerensis* (*Baltoniodus gerdae* Subzone) Biozone, which is coeval with the basal *bicornis* graptolite Biozone (Bergström 1990). The lower Ardwell Farm Formation is dated as Sandbian on the basis of chitinozoans (Mohibullah *et al.* 2011; Chapter 3) and is probably also of *bicornis* graptolite Biozone age. The Craighead Limestone Formation is dated as early Katian based on graptolites of the lower *clingani* Biozone (*caudatus* Subzone) in the Sericoidea Mudstone Member (Rickards in Tripp, 1980a), and the limestones yield a fauna of lower *Amorphognathus superbus* conodont Biozone age (Bergström 1990; Mohibullah *et al.* 2010). The Myoch Formation yields trilobites of late Sandbian and early Katian age (*linearis* graptolite Biozone; Owen & Rushton 1999). The Mill Formation yields graptolites of the *complanatus* Biozone (Williams 1987). The Lady Burn and South Threave formations are also dated with graptolites yielding an *anceps* Biozone age (Williams *et al.* 1972; Floyd *et al.* 1999).

### **Localities**

The localities from which fifty-two ostracods have been collected or recorded are listed below. National Grid references (NGR), lithostratigraphic units, biostratigraphic/chronostratigraphic horizons, relevant references, and ostracod taxa recorded are given for each locality.



Figure 3. Overview of Pinmerry and location of strata of the lower part of the Ardwell Farm Formation sampled for ostracods on the eastern (**A**) and western (**B**) bank of the stream at Pinmerry Farm.

1. Section exposed on the south bank of Penwhapple Burn, situated about 200 m WNW of Penwhapple Bridge, Penwhapple Burn, Girvan (NGR NX 255 969); see Williams 1962, p., 255; Tripp 1980b p. 124; Williams *et al.* 2001a. Calcitic 'crack-out' material and external moulds, from the Balclatchie Formation (lower *bicornis* graptolite Biozone).
2. Mudstones exposed on the north bank of a tributary to the Laggan Burn, situated about 550 m NW of Dalfask Farm, Girvan (NGR NX 206 946); see

Williams 1962, p., 255; Tripp 1980b p. 124; Williams *et al.* 2001a. Decalcified moulds, from the Balclatchie Formation (lower *bicornis* graptolite Biozone).

3. Calcareous blue-grey greywackes exposed on the south bank of Knockbain Burn, situated about 600 m SW of Millenderdale Farm, Knockbain Burn, Girvan (NGR NX 167 902); see Williams 1962, p. 255; Tripp 1980b p. 124; Williams *et al.* 2001a. Decalcified moulds from the Balclatchie Formation (lower *bicornis* graptolite Biozone).

4. Blue-grey mudstones exposed on Dalfask Hill, situated about 670 m ESE of Dalfask Farm, Dalfask, Girvan (NGR NX 213 946); see Williams 1962, p. 255; Tripp 1980b p. 123, 124; Williams *et al.* 2001a. Decalcified moulds, from the Balclatchie Formation (lower *bicornis* graptolite Biozone).

5. Eastern and western bank of the stream at Pinmerry Farm, Stinchar Valley, SE of Girvan (Fig. 3. NGR NX 240 948); see Williams *et al.* 2001a; Mohibullah *et al.* 2011. Abundant external moulds and a few calcitic specimens, from the late Sandbian (*bicornis* graptolite Biozone), lower Ardwell Farm Formation.

6a. A single horizon within a succession of irregularly bedded limestones at the southern end of the Craighead Quarry, Girvan (Fig. 4: sub-locality A; NGR NS 234 012); see Williams 1962, pl. 4; Williams & Floyd 2000, Fig. 2; Mohibullah *et al.* 2010). Hundreds of calcitic 'crack-out' specimens including the holotype *Oepikella tunnicliffi* Williams & Floyd, 2000 and *Leperditella girvanensis* n. sp. from the early Katian Craighead Limestone Formation (lower *clingani* Biozone).

6b. Breccia-calcarenite in the middle of the quarry at Craighead Quarry, Girvan (Fig. 4: sub-locality B; NGR NS 234 013); see Mohibullah *et al.* 2010. A single ostracod (indeterminate) from the early Katian Craighead Limestone Formation (lower *clingani* Biozone).

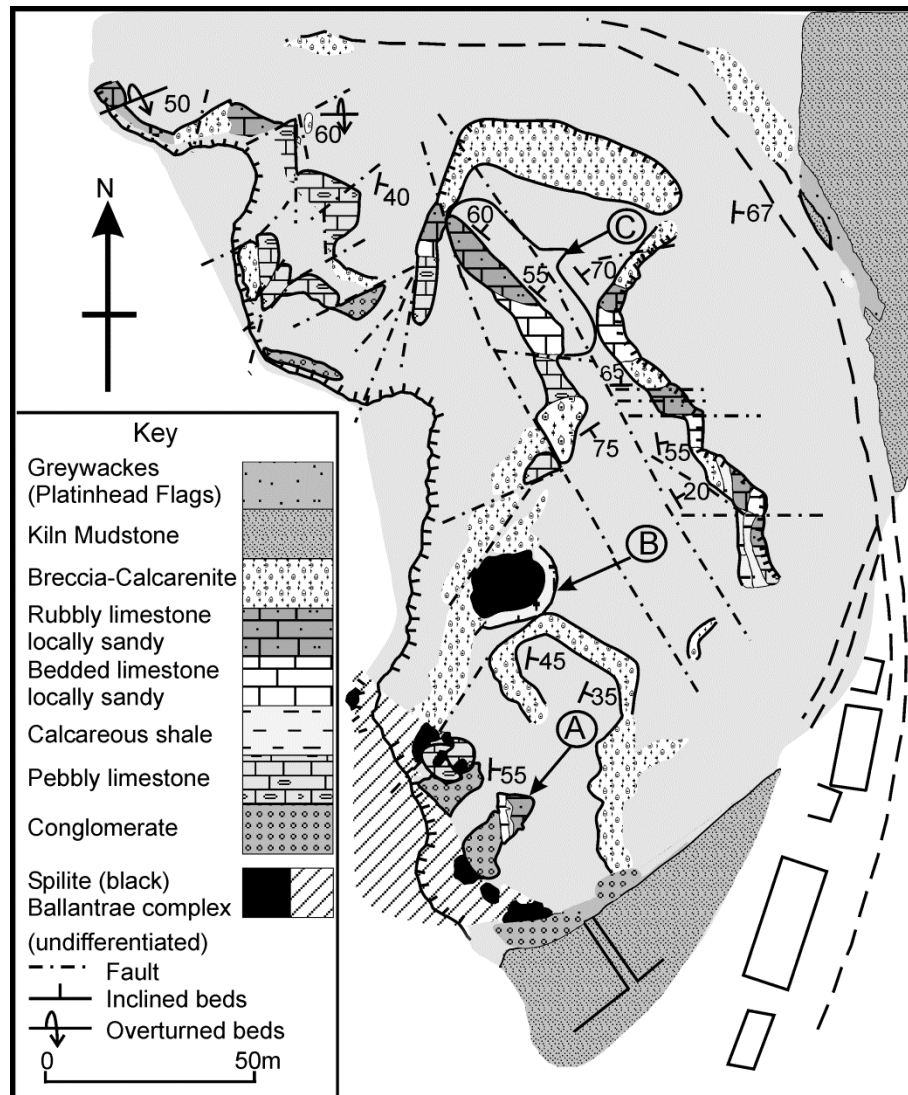


Figure 4. Geological map of Craighead Quarry (redrawn from Williams 1962): 'A', 'B' and 'C' are the ostracod-bearing localities. Grey shading represents the sub-crop of the Craighead Limestone Formation. Numbers next to inclined beds represent degree of inclination.

6c. Mudstones interbedded with thin-bedded limestones at the northern end of Craighead Quarry, Girvan (Fig. 4: sub-locality C; NGR NS 234 014); Mohibullah *et al.* 2010. Hundreds of calcitic specimens including the holotype *Duoarcus levigatus* Mohibullah *et al.* 2010, from fifteen mudstone samples (See Fig. 5)

spaced through ten metres of succession, from the early Katian Craighead Limestone Formation (lower *clingani* Biozone).



Figure 5. Craighead Quarry showing the inter-bedded limestone and shales (locality 6c) of the Craighead Limestone Formation. Sample horizons indicated by arrows.

7. Limestone exposed in Quarry 2 situated at about 150 m to the SE of the Main Quarries (A, B, C), Craighead Inlier, Girvan NGR (NS 233 011); see Williams & Floyd 2000; Williams 1962, pl. 4). Tens of calcitic ‘crack-out’ specimens from the Craighead Limestone Formation.

8. Mudstones of the Kiln Mudstone Member, Craighead Limestone Formation, exposed west of Craighead Farm, about 5.5 km NE of Girvan [NX 234 013]; see

Tripp 1980a Fig. 1; Williams & Floyd 2000, Fig 3. Tens of decalcified internal moulds.

9. Mudstones of the Sericoidea Mudstone Member, Craighead Limestone Formation, exposed west of Craighead Farm, about 5.5 km NE of Girvan [NX 234 013]; see Tripp 1980a Fig. 1; Williams & Floyd 2000, Fig 3. Tens of decalcified internal moulds.

10. Red mudstones at Girvan foreshore (NGR NS 250 037); (Keith Ingham and Neil Clark collection at GLAHM). A few decalcified internal moulds from the Red Mudstone Member, Myoch Formation (*linearis* graptolite Biozone).

11. Greenish-grey shales at Whitehouse foreshore (NGR NS 250 037); see Jones 1893; Williams *et al.* 2001a. Internal moulds from the Mill Formation (*complanatus* graptolite Biozone).

12. Brown-weathering, nodular silty mudstones, south Drummuck Burn situated about 650 m southwest of Drummuck Farm (NGR NS 236 031); (see Floyd *et al.* 1999). Decalcified external and internal moulds including the holotype *Euprimites limus* Floyd, Williams & Rushton, 1999, from the Lady Burn Formation (late Katian *anceps* graptolite Biozone).

13. Threave Glen, Girvan (NGR NS 250 037); see Floyd *et al.* (1999). Decalcified external and internal moulds from the Starfish Beds, South Threave Formation (the upper subzone of the *anceps* graptolite Biozone).

## Material and techniques

The Ordovician succession of the Girvan district has been subjected to tectonic deformation during the Caledonian orogeny and the ostracod material is therefore of variable preservation. The Ordovician ostracods are preserved as

calcitic 'crack-out' material, as calcitic valves and carapaces from processed mudstones, and as mould material in both limestones and mudstones (Floyd *et al.* 1999; Williams *et al.* 2001a; Mohibullah *et al.* 2010, 2011; chapters 3, 4). The best preserved faunas are 'crack-out' material from the limestones of the Craighead Limestone Formation which preserve fine details of the shell ornament (Williams & Floyd 2000; Mohibullah *et al.* 2010; Chapter 4). Calcitic specimens from the mudstones of the Craighead Limestone Formation have moderate preservation and in many cases valves are corroded or incomplete and the fine details are lost (Mohibullah *et al.* 2010; Chapter 4). The mould material from mudstones has a wide range of preservation from very poor, such as those from the Mill Formation that lack diagnostic morphology, to those of the Lady Burn, South Threave and lower Ardwell Farm formations that preserve detailed information about ornament and lobation. Many of the species that are known from mudstones are represented by only a few or even single valves.

A variety of techniques are used for examining material from different modes of preservation. The calcitic specimens from calcareous mudstones of the Craighead Limestone Formation were extracted using dilute hydrogen peroxide. Mudstone samples were left in a 10% H<sub>2</sub>O<sub>2</sub> solution for one day, wet sieved with 1 mm, 500 µm and 250 µm sieves, dried in an oven, and then picked for microfossils with a fine brush under a WILD M8 binocular microscope. The calcitic 'crack-out' ostracods were excavated from limestones with needles (see Williams & Floyd 2000; Mohibullah *et al.* 2010). Decalcified external moulds such as those from the lower Ardwell Farm, Lady Burn and South Threave formations have been cast using silicon rubber techniques (Floyds *et al.* 1999; Mohibullah *et al.* 2011; Chapter 3).

For scanning electron microscopy, specimens were mounted on aluminium stubs and coated with gold/aluminium alloy 'Emitech K500X'. Specimens were photographed with a HITACHI S-3600N scanning electron microscope at Leicester University. The internal moulds of the Mill Formation were coated with ammonium chloride sublimates and imaged with a digital (Canon Eos) camera.

### **Terminology**

The morphological terminology used here for Ordovician ostracod carapaces is that summarised in Vannier *et al.* (1989; see Fig. 6), itself building on the work of Henningsmoen (1953, 1954), Jaanusson (1957) and Schallreuter (1973, 1975, 1979, 1985). Vannier *et al.* (1989) summarised the major taxonomic groups of Ordovician ostracods, distinguishing them on the basis of key morphological features of the carapace such as lobes, sulci, presence of calcified inner lamella, dimorphic characters and valve overlap (see Fig. 6).

Ostracods have a calcified bivalved carapace with a dorsal hinge-line and possess carapace features such as lobes and sulci. L1 is the anterior lobe, L2 is the preadductorial lobe, L3 is the postadductorial lobe and L4 is the posterior lobe. S1 is the anterior sulcus; S2 is the adductorial sulcus, whereas S3 is the posterior sulcus. The ostracod carapace may also have a small circular or ovate smooth muscle spot situated centrally, and corresponding to the internal adductorial muscle attachment. The surface of an ostracod carapace may be smooth or have ornamentation consisting of pustules, punctae, reticulæ or granulae (see Fig. 6).

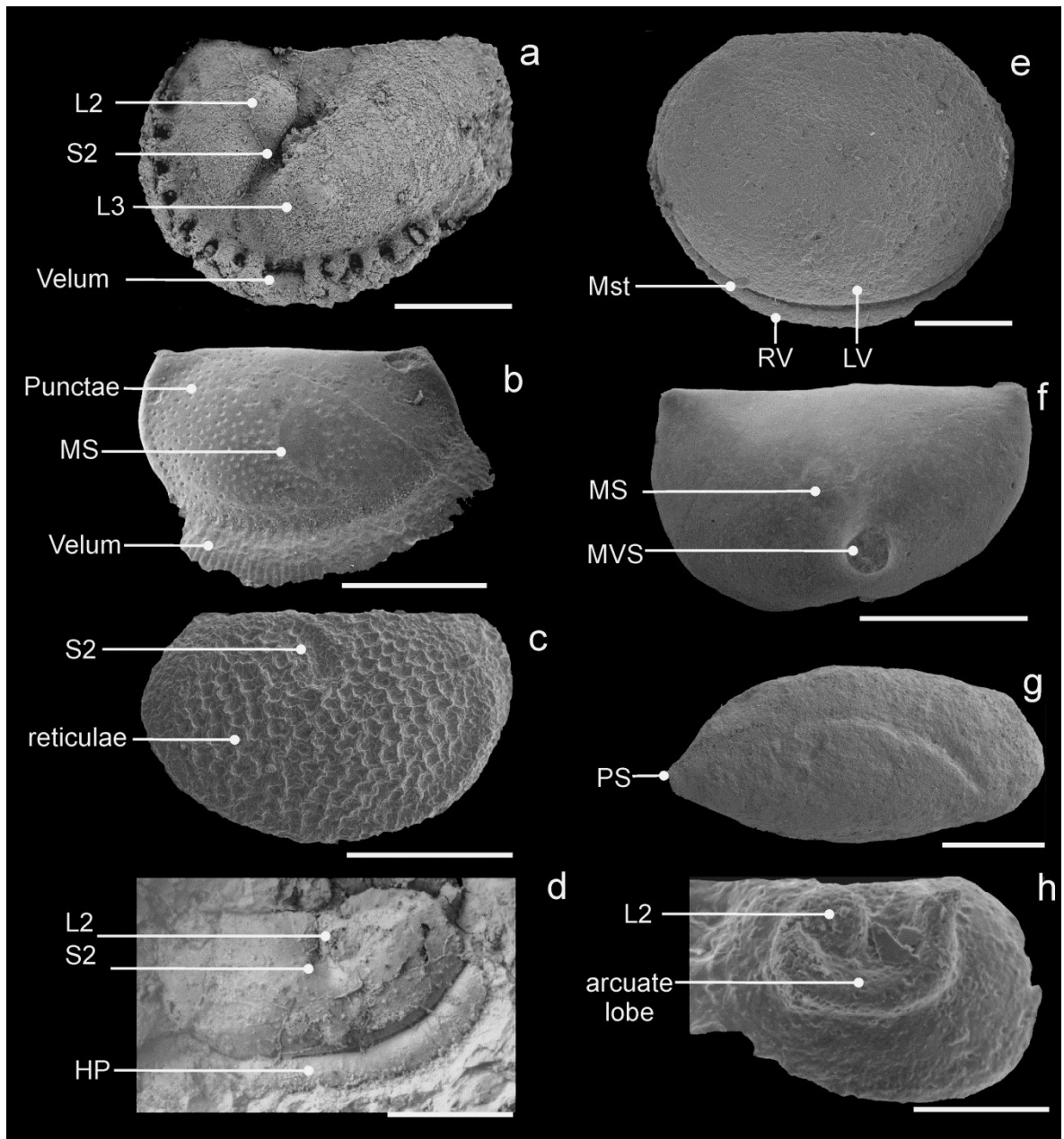


Figure 6. Terminology for the ostracod carapace. (a-d) are palaeocopes, (e) leiocope, (f, g) podocopes, (h) binodicope. Symbols: L2, pre-adductorial lobe; L3, posteroventral lobe; S2, adductor sulcus; Mst, Marginal structure; MS, muscle spot; HP, heteromorphous pouch; PS, posteroventral spine; MVS, midventral spine. (a, c, f, h) left valve, lateral view; (b, d, g) right valve lateral view; (e) left view of carapace. Scale bars (a, e, g) 0.5 mm; (b) 1.0 mm; (c) 0.3 mm; (d) 0.49 mm; (f) 0.75 mm; (h) 0.43 mm.

## Repositories

Ostracod material studied here is deposited in the following repositories. The British Geological Survey, Keyworth Nottingham (BGS) has the holotypes of

*Euprimites limus* Floyd, Williams & Rushton, 1999 from the Lady Burn Formation, *Oepikella tunnicliffi* Williams & Floyd, 2000, *Duoarcus levigatus* Mohibullah *et al.* 2010 and *Leperditella girvanensis* n. sp. from the early Katian Craighead Limestone Formation. It also houses other ostracod material from the Craighead Limestone Formation (Williams & Floyd 2000; Mohibullah *et al.* 2010; Chapter 4, the Kiln Mudstone Member of the Craighead Limestone Formation at Craighead Quarry (Williams & Floyd 2000); the ostracod material from the South Threave Formation (late Katian *pacificus* Subzone of the *anceps* Biozone) at Threave Glen (see Floyd *et al.* 1999; Williams *et al.* 2001a); material from the late Katian Lady Burn Formation (*anceps* graptolite Biozone; see Floyds *et al.* 1999); ostracods from the Sandbian lower Ardwell Farm Formation at Pinmerry (Williams *et al.* 2001a; Mohibullah *et al.* 2011; Chapter 3); and the Balclatchie Formation material from Laggan Burn (see Williams *et al.* 2001a).

The Hunterian Museum of Glasgow University (GLAHM): houses material from the Sandbian age Balclatchie Formation at Penwhapple Burn, Knockbain, Laggan Burn and Dalfask; material from the Sandbian lower Ardwell Farm Formation at Pinmerry (see Williams *et al.* 2001a); material from the Kiln and Sericoidea Mudstone Members of the Craighead Limestone Formation (see Williams & Floyd 2000); and some specimens from the limestones of the Craighead Limestone Formation at Craighead Quarry (see Williams & Floyd 2000) and a few internal moulds from the Myoch and Mill Formations at Whitehouse foreshore.

The Natural History Museum, London (NHM UK): houses the material from the Katian age Mill Formation (*complanatus* graptolite *Biozone*) at the Whitehouse foreshore (Jones 1893; also see Williams *et al.* 2001a); and the Lady Burn Formation at Drummuck Burn (Jones 1879; Floyd *et al.* 1999).

### **Systematic Descriptions**

We follow the taxonomic scheme of Vannier *et al.* (1999) itself based largely on the works of Henningsmoen (1953, 1954), Jaanusson (1957) and Schallreuter (1973, 1975, 1979, 1985).

Phylum ARTHROPODA Siebold & Stannius, 1845

Subphylum CRUSTACEA Pennant, 1777

Class OSTRACODA Latreille, 1802

Subclass PODOCOPA Sars, 1866

Order BEYRICHIOCOPA Pokorný, 1954

Suborder PALAEOCOPA Henningsmoen, 1953

Superfamily EURYCHILINACEA Ulrich & Bassler, 1923

Family OEPIKELLIDAE Jaanusson, 1957

Subfamily OEPIKELLINAE Jaanusson, 1957

Genus **OEPIKELLA** Thorslund, 1940

*Type species.* *Oepikella tvaerensis* Thorslund, 1940, by original designation.  
From the Ordovician Lower Chasmops Limestone, Tvären, Sweden.

*Occurrence.* From the Ordovician of Scotland (Williams & Floyd 2000; Williams *et al.* 2001a; Mohibullah *et al.* 2010), Kentucky (Warshauer & Berdan 1982), Ontario (Copeland 1965), district of Franklin and district of Mackenzie, Canada (Copeland 1977a, b), and the Baltic region (Jaansussón 1957; Öpik 1937; Schallreuter 1984).

**Oepikella tunnicliffi** Williams & Floyd, 2000 Pl. 1, figs 1-3

2000 *Oepikella tunnicliffi* sp. nov. Williams & Floyd, p. 58-59, figs 5a-e.

2001a *Oepikella tunnicliffi* Williams & Floyd, 2000; Williams *et al.*, fig. k.

2010 *Oepikella tunnicliffi* Williams & Floyd, 2000; Mohibullah *et al.*, figs 6h, i, m.

*Holotype.* A heteromorphic right valve, BGS 16E1961 (pl. 1, fig. 1), from the Craighead Limestone Formation, locality 6a.

*Material.* More than 25 valves (many incomplete): BGS JS15411, JS15468, JS15471, BGS (Keyworth) 16E952, 16E1886, 16E1929, 16E1938, 16E1961, 16E1962, 16E1965, 16E1966, 16E1967, 16E1982, 16E1987, 16E2036, 16E2835, 16E2847, 16E2851, 16E2852, MWL4126-4129, MWL2500-MWL2504 (topotypes), and GLAHM A1379, A1381, A1383.

*Measurements.* Complete specimens are 1.7-2.6 mm in length, probably representing at least two moult stages. Heteromorphs of *O. tunnicliffi* are rarer than adult tecomorphs.

*Diagnosis.* (After Williams & Floyd 2000) *Oepikella* with gently convex heteromorphic velum of even width throughout (c. 0.3 mm) which extends from

the mid-anterior to posteroventral region. Tecnomorph with very narrow velar ridge which is confined to the ventral margin and in ventral view is gently arched.

*Description.* (After Williams & Floyd 2000) Tecnomorphic valve amplete, its lateral valve outline sub-oval. Heteromorphic valve preplete, incorporating well-developed velum: for morphology of heteromorphic and tecnomorphic velum see diagnosis. Valves non-lobate, but with sub-circular to ovate, sub-centrally positioned smooth muscle spot whose diameter is 0.4-0.5 mm in larger specimens. From a ventral aspect the domiciliar part of the valves are evenly and gently convex for both the tecnomorph and heteromorph. Cardinal corners of valves laterally compressed. Larger valves (length greater than 2 mm) have densely packed punctae (10 - 12 punctae in a line per mm). Smaller valves have finer and less densely packed punctae. Punctae absent at valve margins.

*Discussion.* Species of *Oepikella* are widespread in the Baltic region (Öpik 1937; Thorslund 1940; Sarv 1959; Schallreuter 1984; Meidla 1996) and North America (Copeland 1965; Warshauer & Berdan 1982). The type-species *O. tvaerensis* has tecnomorphs much larger than heteromorphs (see Jaanusson 1957). Tecnomorphs of *O. tunnicliffi* also seem to be larger than the heteromorphs. *O. tunnicliffi* differs from *O. tvaerensis* in having: coarse punctae, a narrow tecnomorphic velar ridge, a heteromorphic velum less convex and extended more posteriorly, and weakly flattened cardinal corners. The coarse punctae and flattened cardinal corners of *O. tunnicliffi* differentiates it from *O. lumniosa* Sarv, 1959 which is finely punctate and lacks the flattened cardinal corners.

*Occurrence.* Only from the Late Ordovician (early Katian) Craighead Limestone Formation, Craighead Quarry, Girvan district, southwest Scotland (Williams & Floyd 2000; Mohibullah *et al.* 2010), locality 6a.

Subfamily AMPLETOCHILININAE Schallreuter, 1975

Genus **PLATYBOLBINA** Henningsmoen, 1953

*Type species.* By original designation; *Primitia distans* Krause, 1889 from a glacial drift boulder (of Upper Ordovician age), Germany.

*Diagnosis.* (Modified from Meidla 1996) Valves preplete, lateral outline sub-ovate to sub-quadrate. Non-sulcate or S2 developed as a weak sulcal depression, or with indistinct knob-like weakly elevated L2. Tecnomorphic velum developed along the entire free margin and may be shortened in some species, heteromorphs with a convex dolon anteroventrally. Surface reticulate or smooth. Muscle spot present; the size and shape varies in different species.

*Occurrence.* From the Ordovician of Scotland (Williams & Floyd 2000; Williams *et al.* 2001a; Mohibullah *et al.* 2010) Virginia (Kraft 1962), Michigan (Kesling 1960a), Baltoscandia (Henningsmoen 1954; Jannusson 1957; Meidla 1996), Britain (Vannier *et al.* 1989), the Czech Republic and Siberia (Meidla 1996).

**Platybolbina** cf. **punctata** (Kraft, 1962)      Pl. 1, fig. 11, Pl. 2, fig. 1

2000 *Platybolbina* cf. *punctata* (Kraft, 1962) Williams & Floyd, figs 5k, l, n.

2001a *Platybolbina* cf. *punctata* (Kraft, 1962) Williams *et al.*, fig. 5m.

2010 *Platybolbina* cf. *punctata* (Kraft, 1962) Mohibullah *et al.*, fig. 6d.

*Material.* Three valves BGS 16E1984, 16E1986 and GLAHM A1382.

*Measurement.* Based on specimen GLAHM A1382, length 1.9 mm, height 1.1 mm.

*Description.* Valves preplete, sub-ovate in lateral view. Surface finely reticulate with a well-developed smooth muscle spot. Velum entire along the ventral and anterior margins but abruptly terminated at mid-posterior. Dorsal margin straight or slightly sinuous.

*Discussion.* The velum is terminated at its ventral margin by a narrow convex rim, which differentiates it from Kraft's type material of *P. punctata* from Virginia.

*Occurrence.* Late Ordovician (early Katian) Craighead Limestone Formation of the Girvan district, southwest Scotland (Williams & Floyd 2000; Mohibullah *et al.* 2010), locality 6a.

Family EURYCHILINIDAE Ulrich & Bassler, 1923

Subfamily EURYCHILININAE Ulrich & Bassler, 1923

Genus **EURYCHILINA** Ulrich, 1889

*Type species.* By original designation; *Eurychilina reticulata*, Ulrich 1889 from the Guttenburg Member, Decorah Formation, Fountain, Minnesota.

*Occurrence.* Species of *Eurychilina* are widespread in the Ordovician of Scotland (Williams *et al.* 2001a), Oklahoma (Harris 1957; Williams & Siveter

1996), Virginia (Kraft 1962), New York (Swain 1962), Pennsylvania (Swain 1962), Iowa (Kay 1940), Minnesota (Kay 1934; Swain *et al.* 1961), Michigan (Kesling 1960b), Kentucky (Warshauer & Berdan 1982), District of Mackenzie (Copeland 1974, 1982), Ontario (Copeland 1965) and Baffin Island, Canada (Copeland 2000). Also from Late Ordovician strata of Altai, Russia (Melnikova 2010) and Himachal Pradesh, northern India (Schallreuter *et al.* 2008).

**Eurychilina sunbloodensis** Copeland, 1974                      Pl. 2, fig. 10

1974 *Eurychilina sunbloodensis* Copeland n. sp.; pl. 1, figs 1-11; text-figure 6.4.

2001a *Eurychilina* cf. *sunbloodensis* Copeland, 1974; Williams, fig. 5e.

*Material.* A right valve GLAHM 114089.

*Measurement.* Length 1.90 mm, height 1.33 mm.

*Description.* Valves postplete, hinge line nearly straight and long. S2 deep, L2 well defined and sub-circular in shape (about 200 µm in diameter). The anterior valve margin is more sharply rounded than the posterior. Heteromorphic brood pouch is narrow and 'sausage'-shaped and extends along the ventral margin.

*Discussion.* *Eurychilina sunbloodensis* has the well-defined preadductorial node, deep adductorial sulcus and narrow heteromorphic dolon extending along the ventral margin that characterises the Canadian material of this species.

*Occurrence.* Late Ordovician (Sandbian) Balclatchie Formation at Penwhapple Burn, Girvan district, southwest Scotland (Williams *et al.* 2001a), locality 1.

Superfamily HOLLINACEA Swartz, 1936

Family TETRADELLIDAE Swartz, 1936

Genus **KIESOWIA** Ulrich & Bassler, 1908

*Type species.* *Beyrichia dissecta* Krause, 1892; from a glacial drift boulder (of Late Ordovician age), Germany.

*Diagnosis.* (Slightly modified from Meidla 1996). Valves amplete to slightly preplete. Quadrilobate with L3 or all lobes having sub-horizontal partitions into broad nodes; L1 may have posteriorly directed spine at the dorsal margin. S2 strong, long and sigmoidal; S3 curved; S1 weak. Tecnomorphic velum may be complete or part developed.

*Discussion.* For further information see Meidla (1996, p. 56).

*Occurrence.* Late Ordovician strata of Scotland (Mohibullah *et al.* 2010) and Minnesota (Kay 1940), and Late Ordovician and Early Silurian(?) strata of Baltoscandia (Meidla 1996).

**Kiesowia** sp. Pl. 1, fig. 6

2010 *Kiesowia* sp. Mohibullah *et al.*, fig. 6g.

*Material.* A single carapace, GSE15344.

*Measurement.* Length 0.77 mm, height 0.62 mm.

*Description.* Quadrilobate, all lobes except L1 are partitioned into nodes. L1 is curved along the anterior margin; L2 is situated just below the anterodorsal region and narrows at its base where it connects with L1; L3 is node-like, positioned mid-ventrally; L4 is located in the posterodorsal part of the valve, curved posteriorly where it is divided by a furrow into two broad nodes. Hinge long and straight.

*Discussion.* *Kiesowia* sp. differs from the type species *Kiesowia dissecta* (Krause, 1892) by having L1 not subdivided into nodes, whereas in *Kiesowia dissecta* all lobes are completely partitioned into nodes.

*Occurrence.* Late Ordovician (Katian) Craighead Limestone Formation, Girvan district, Scotland (Mohibullah *et al.* 2010), locality 6c.

#### Genus **HIPPULA** Tromelin & Lebesconte, 1876

*Type species.* *Hippa latens* Barrande, 1872 from the Ordovician of Bohemia.

*Discussion.* Based on the number of toral ridges and cavities Schallreuter (1983, 1984) recognized four subgenera of *Hippula*: *H. (Cetona)*, *H. (Hippula)*, *H. (Kanyginia)* and *H. (Pseudocetona)*. But Meidla (1996) considered these subdivisions to be largely artificial. Similarly Orr (1987, unpublished PhD) found it difficult to apply these subdivisions to *Hippula* species from the Portrane Limestone of Ireland. We follow Meidla and Orr in not using the *Hippula* subgenus.

*Occurrence.* Late Ordovician strata of southwest Scotland (Williams *et al.* 2001a; Mohibullah *et al.* 2011), Oklahoma (Williams & Siveter 1996), Virginia (Kraft 1962), Mackenzie district, Canada (Copeland 1974; 1982), the Late Ordovician (Katian) strata of England (Jones 1987; Williams *et al.* 2001b), Ireland (Orr 1987), Bohemia (Vannier *et al.* 1989) and the Mid and Late Ordovician of the strata Baltic region (Schallreuter 1964, 1984; Vannier *et al.* 1989; Olempska 1994; Meidla 1996).

**Hippula ventrospinosa** (Kraft, 1962) Pl. 2, figs 2, 3

1962 *Ctenobolbina ventrospinosa* n. sp. Kraft, p. 146-147, pl. 11, figs 14-17, pl. 12, figs 1-8, text-figs 10n, 12a.

2001a '*Ctenobolbina*' *ventrospinosa* Kraft, 1962; Williams *et al.*, figs 5h, i.

2011 '*Ctenobolbina*' *ventrospinosa* Kraft, 1962; Mohibullah *et al.*, figs 4a, b, f.

*Holotype.* A heteromorphic right valve USNM 136614 from the Edinburg Formation at Strasburg Junction, Virginia (Kraft, 1962).

*Material.* About thirteen external moulds, BGS GSE 15383, GSE 15384, GSE 15388, MWL 3572, MWL 3573, MWL 3581 GLAHM 114370, 114371, 114365, 114367, 114086, 114088, A18512.

*Measurement.* Based on GSE 15383 and GSE 15384: Length 1.56-1.6 mm, height 1.16-1.25 mm.

*Diagnosis.* *Hippula* species with a well-defined L2, long, deep and sigmoidal S2 and a well developed S3; L3 bears a small spine. Velum entire along the anterior and ventral margin and is terminated at mid-posterior.

*Description.* Valves preplete, S2 long, deep and sigmoidal. L2 well defined, L3 well developed and bearing a small spine. Velum entire along the anterior and ventral margin and is terminated at mid-posterior. The anterior margin is more broadly convex than the anterior: lateral outline of dorsal margin straight.

*Occurrence.* From the Late Ordovician (late Sandbian) lower Ardwell Farm Formation of the Girvan district, southwest Scotland (Williams *et al.* 2001a; Mohibullah *et al.* 2011, locality 5) and the Edinburg Formation of Virginia, USA (Kraft, 1962).

Genus **VITTELLA** Schallreuter, 1964

*Type species.* By original designation *Vittella vittensis* Schallreuter, 1964 from a Late Ordovician Backsteinkalk erratic boulder, northern Germany.

*Occurrence.* Ordovician of ?Scotland, Baltoscandia (Jannusson 1957; Schallreuter 1964), Siberia (Meidla 1996), England and Wales (Jones 1986; Siveter 2009).

**Vittella** sp. Pl. 2, fig. 11

*Material.* Eleven internal moulds BGS 16E896, 16E905, 16E905, 16E906, 16E919, 16E920, 16E972/973, 16E998/99, 16E963.

*Measurement.* Based on 16E919 Length 0.61 mm, height 0.5 mm.

1999 *Vittella?* sp. Floyd, Williams & Rushton, 1999, fig. 4h.

2001a *Vittella?* sp. Floyd, Williams & Rushton, 1999; Williams *et al.*, fig. 5bb.

*Discussion.* *Vittella* sp. has preplete valves, an indistinct preadductorial node, and a long and sigmoidal adductorial sulcus and posteroventral lobe which is typical for species of *Vittella*. Due to poor preservation our assignment is confined to generic level.

*Occurrence.* From the Late Ordovician (late Katian, *anceps* graptolite Biozone) Lady Burn Formation, Girvan district, southwest Scotland (Floyd *et al.* 1999; Williams *et al.* 2001a), locality 12.

Family EUPRIMITIIDAE Hessland, 1949

Subfamily EUPRIMITIINAE Hessland, 1949

Genus **HALLATIA** Kay, 1934

*Type species.* *Hallatia labiosa* (Ulrich, 1894; *H. healyensis* Kay, 1934 is a junior synonym); designated Kay 1934, p. 334.

*Diagnosis.* Valves subamplete and unisulcate, S2 deep. Both the anterior and posterior lobes are gently convex, convexity increases towards the dorsal margin. Posterior lobe may have a dorsal cusp. Margin of valves laterally compressed; the posterior margin being broader than the anterior. Velum dimorphic in some species. Surface smooth, striate or reticulate.

*Discussion.* Some species of *Hallatia* have previously been assigned to *Halliella* Ulrich 1890 (see Kay 1940). The type species of *Halliella* (*H. retifera* Ulrich, 1892) differs from *Hallatia* by having a strongly concave ventral margin, a pronounced marginal ridge and different velar morphology. Some species of

*Hallatia* have also been assigned to *Euprimitia* (Kay 1940, p. 252; Kraft 1962, p. 26; Copeland 1965, p. 11). However, the type species of *Euprimitia* (*E. sanctpauli*) does not have a tecomorphic velum, whereas in *Hallatia* both dimorphs have the velum.

*Occurrence.* Ordovician of Scotland (Mohibullah *et al.* 2011), Oklahoma (Williams & Siveter 1996), Virginia (Kraft 1962), Iowa (Kay 1934, 1940), Minnesota (Kay 1940; Swain 1996) and Ontario (Kay 1934; Copeland 1965).

**Hallatia** cf. **labiosa** (Ulrich, 1894)      Pl. 1, fig. 5

2011 *Hallatia* cf. *labiosa* (Ulrich, 1894); Mohibullah *et al.*, fig. 4g.

*Material.* A single left valve (external mould).

*Measurement.* Length 0.7 mm, height 0.45 mm.

*Description.* Valves subamplete, unisulate, S2 deep. Both the anterior and posterior margins are gently convex from a lateral view. Cardinal angles obtuse. Dorsal margin straight, ventral margin convex. Surface punctate.

*Discussion.* *Hallatia* cf. *labiosa* closely resembles *H. labiosa* from the Bromide Formation of Oklahoma (Williams & Siveter 1996), the Edinburg Formation of Virginia (Kraft 1962) and the Decorah Formation of Iowa (Kay 1934) in shape, sulcation and morphology of the valve margins. The style of punctate ornament in the Girvan specimen is different from the variably reticulate to smooth ornament of the North American material. However, as the latter show wide

variability in ornament, this may not preclude the Girvan specimen from ultimately being assigned unequivocally to *H. labiosa*.

*Occurrence.* A single specimen from the Late Ordovician (Sandbian) lower Ardwell Farm Formation of the Girvan district, southwest Scotland (Mohibullah *et al.* 2011), locality 5.

Family TVAERENELLIDAE Jaanusson, 1957

Subfamily TVAERENELLINAE Jaanusson, 1957

Genus **LEVISULCULUS** Jaanusson, 1957

*Type species.* By original designation, *Levisulculus lineatus* Jaanusson, 1957.

*Diagnosis.* (After Jaanusson 1957) Valves strongly preplete and elongate. S2 developed as a narrow curved depression. Heteromorphic velum extending from mid-posterior and terminating slightly below the antero-cardinal corner, whereas in tecnomorphs have moderately broad to narrow velar flange. Hinge line long and straight. Surface may be smooth, granular or reticulate.

*Occurrence.* From the Late Ordovician strata of Scotland (Williams & Floyd 2000; Mohibullah *et al.* 2010), Michigan (Kesling 1960b), Pennsylvania (Swain 1962), Ontario Canada (Copeland 1965). Also from the Ordovician of Baltoscandia (Jaanusson 1957; Vannier *et al.* 1989) and Bohemia (Schallreuter & Krůta 1991).

**Levisulculus** cf. **michiganensis** Kesling, 1960b      Pl. 1, figs 7, 8

2000 *Levisulculus* cf. *michiganensis* Kesling, 1960; Williams & Floyd, 2000, figs 5q, t.

2001a *Levisulculus* cf. *michiganensis* Kesling, 1960; Williams *et al.*, fig. 5q.

2010 *Levisulculus* cf. *michiganensis* Kesling, 1960; Mohibullah *et al.*, fig. 6j.

*Material.* Two valves, BGS 16E2037, BGS 16E1960.

*Measurement.* BGS 16E1960 length is 0.96 mm, height is 0.59 mm; BGS 16E2037 length is 1.12 mm, height is 0.66 mm.

*Description.* Valves strongly preplete, S2 weakly sigmoidal, heteromorphic velum extending from mid-posterior and terminating slightly below the antero-cardinal corner. Hinge line straight and long, slightly shorter than the total length of the domicilium. Lateral surface finely reticulate.

*Discussion.* *Levisulculus* cf. *michiganensis* differs from Kesling's 1960 type material in possessing more finely reticulate lateral surface ornament. The Girvan specimen also lacks a posteroventral spine, which may be due to preservation as Canadian specimens also lack this feature (see Copeland 1965).

*Occurrence.* Late Ordovician (early Katian) Craighead Limestone Formation, Girvan district, southwest Scotland (Williams & Floyd 2000; Mohibullah *et al.* 2010), locality 6a.

Genus **EUPRIMITES** Hessland, 1949

*Type species.* *Euprimites reticulogranulatus* Hessland, 1949 emend. Jaanusson, 1957. From the Early Ordovician strata of the Siljan district, Dalecarlia, Sweden.

*Occurrence.* From the Late Ordovician (late Katian) strata of Scotland (Floyd *et al.* 1999; Williams *et al.* 2001a), the Ordovician of Baltoscandia (Jaanusson 1957; Meidla 1996), and Siberia (Meidla 1996).

**Euprimites (Euprimites) limus** Floyd, Williams & Rushton, 1999 Pl. 3, figs 8, 9

1999 *Euprimites (Euprimites) limus* sp. nov. Floyd, Williams & Rushton, figs 4d, e.

2001a *Euprimites (Euprimites) limus* Floyd, Williams & Rushton, 1999; Williams *et al.*, fig. 5dd.

*Holotype.* A heteromorphic right valve, external mould BGS 16E895 (pl. 3, fig. 8).

*Diagnosis.* Species of *Euprimites* with heteromorph having a broad flange-like velum, which, in lateral view, has a rounded ventral margin.

*Material.* Five well-preserved valves (including counterparts) from the Lady Burn Formation: BGS 16E895, 16E1000/1001, 16E1004/1005, 16E1008/1009, 16E1290/1291.

*Measurements.* Based on BGS, 16E1290/1291, 16E895, 16E1000/1001, 16E1004/1005, 16E1008/1009, length 1.4-1.5 mm. The holotype (BGS 16E895) is 1.5 mm long and 0.9 mm high.

*Description.* (After Floyd *et al.* 1999) Valves weakly preplete. Dorsal plica absent. S2 well-developed, deep and broad, L2 indistinct and slightly constricted adjacent to S2; zygial arch absent. Tecnomorph with a narrow flange-like velum, which, in lateral view, has a rounded ventral margin: velum extends from the mid-anterior to the mid-posterior region. In the heteromorphy the velum is anteriorly and antero-ventrally more convex and broad where it forms the dolon. Surface has fine reticulation and granulation.

*Discussion.* The narrow flange-like tecnomorphic velum of *Euprimites limus* differentiates it from the type and other species of *Euprimites*. This is the only record of *Euprimites* from the Ordovician of Scotland.

*Occurrence.* Late Ordovician (late Katian; *anceps* graptolite Biozone), Lady Burn Formation, Girvan district, southwest Scotland (Floyd *et al.* 1999; Williams *et al.* 2001a), locality 12.

Subfamily MARTINSSONOPSAE Schallreuter, 1967

Genus **EOAQUAPULEX** Levinson, 1968

*Type species.* *Diploopsis socialis* Levinson, 1961; by original designation Levinson, 1968, p. 248.

*Occurrence.* From the Ordovician of Scotland (Williams *et al.* 2001a; Mohibullah *et al.* 2011), Oklahoma (Williams & Siveter 1996), Virginia (Kraft 1962), Missouri (Keenan 1951), Ontario (Copeland 1965), Mackenzie District, Canada (Copeland 1974), Baffin Island, Canada (Copeland 2000), southern Ireland (Orr 1987), northern England (Jones & Holl 1868) and the Baltic region (Schallreuter & Siveter 1985).

**Eoaquapulex** cf. **socialis** (Levinson, 1961) Pl. 2, fig. 4

2001a *Eoaquapulex* cf. *socialis* (Levinson, 1961); Williams *et al.*

2011 *Eoaquapulex* cf. *socialis* (Levinson, 1961); Mohibullah *et al.*

*Material.* A single left valve, part and counterpart (GLAHM 114085)

*Measurement.* Length 1.6 mm, height 1 mm.

*Description.* Valves weakly preplete and non-sulcate. Valves surface evenly convex, the anterior margin is more broadly rounded than the posterior. A narrow tecomorphic velum extends from mid-anterior to mid-posterior. Carapace surface smooth.

*Discussion.* The dorsal margin is more arched from a lateral aspect in the Girvan specimen than for comparable material from Oklahoma (Harris 1957).

*Occurrence.* From the lower Ardwell Farm Formation, Girvan, district, southwest Scotland (Williams *et al.* 2001a; Mohibullah *et al.* 2011), locality 5.

Family uncertain

Genus **DUOARCUS** Mohibullah *et al.*, 2010

*Type Species.* By original designation, *Duoarcus levigatus* Mohibullah *et al.* 2010.

*Diagnosis.* (After Mohibullah *et al.* 2010) Ventral margin marked by an acute, arcuate bend on both the left and right valves that, from a ventral aspect, forms two opposing bow-shapes.

*Discussion.* *Duoarcus levigatus* resembles *Eoaquapulex socialis* (Levinson, 1961) in lateral, dorsal and ventral outlines but the anterior lateral outline of *D. levigatus* is more rounded than in *E. socialis*. Both taxa also have a similar bow-shaped structure along the ventral margin of the valves, manifested as a marked bend in *D. levigatus* whereas in *E. socialis* it is formed from a velar ridge. No heteromorphic dimorph is known for *Duoarcus*.

*Duoarcus* also show some similarities with *Schmidtella* Ulrich, 1892, in having an epicline dorsum, smooth, non-sulcate, asymmetrical and umbonate valves, and the larger left valve overlapping the smaller right valve. *Duoarcus* differs from *Schmidtella* in having a ventral bow-shaped bend on both the valves, which are absent in *Schmidtella*. In addition, the distinct channel developed along the ventral margin in the type species *Schmidtella crassimarginata* Ulrich, 1892 is absent in *Duoarcus*.

*Occurrence.* Only from the Craighead Limestone Formation, Girvan district, southwest Scotland (Mohibullah *et al.* 2010), locality 6C.

**Duoarcus levigatus** Mohibullah *et al.*, 2010

Pl. 2, figs 6-9

2010 *Duoarcus levigatus* Mohibullah *et al.*, p. 932, figs 7b, c, e, f.

*Diagnosis.* As for the genus which is monotypic.

*Holotype.* A carapace GSE15348 (Mohibullah *et al.* 2010, fig. 7e), from the Late Ordovician (early Katian) Craighead Limestone Formation (locality 6c), Girvan district, southwest Scotland.

*Material.* Twenty carapaces, one left valve and a broken specimen (BGS collections). All specimens appear to be tecnomorphs.

*Measurement.* Length ranges from 0.58-1.39 mm; maximum valve height is 1.05 mm. The holotype is 0.93 mm long and 0.72 mm high and is therefore probably a juvenile.

*Description.* (After Mohibullah *et al.* 2010) Valves preplete, non-sulcate and smooth. Lateral outline sub-circular, longitudinal and transverse outlines sub-triangular. Lateral surface convex, the posterior is more convex than the anterior and strongly flattened posteriorly. Dorsum epicline; the left valve is larger and overlaps the right valve ventrally. Ventrally an acute bend on both valves forms opposing bow-shaped structures (pl. 2, fig. 8). The ventral valve contact is straight.

*Discussion.* *Duoarcus levigatus* resembles '*Hyperchilarina*' *angularis* Harris, 1957 in having both the valves strongly flattened posteriorly and ventrally and both have opposing bow-shaped bends when seen in a ventral aspect. *D. levigatus* differs from '*H.*' *angularis* in being more tumid anteriorly, whereas the latter is more acutely pointed. Further study might reveal that these two species are congeneric, but neither are assignable to *Hyperchilarina*. A bow-shaped bend on the ventral margin of each valve and the lack of admarginal spines on the left valve differentiate both *D. levigatus* and *H. angularis* from the type-species *Hyperchilarina ovata* Harris, 1957 (see Williams & Vannier 1995).

*Occurrence.* Only from the Craighead Limestone Formation, Girvan district, southwest Scotland (Mohibullah *et al.* 2010), locality 6c.

Family HITHIDAE Schallreuter, 1964

Subfamily SARVININAE Schallreuter, 1966

Genus **DISTOBOLBINA** Sarv, 1959

*Type species.* By original designation, *Distobolbina nabalaensis* Sarv, 1959.

*Occurrence.* Ordovician of Scotland (Williams & Floyd 1999; Williams *et al.* 2001a; Mohibullah *et al.* 2010), England (Williams *et al.* 2001a, b) Baffin Island, Canada (Copeland 2000) and Baltoscandia (Henningsmoen 1954; Meidla 1996).

**Distobolbina** sp. Pl. 1, fig. 4

2000 *Distobolbina* sp. Williams & Floyd, 2000, figs 5s, u.

2010 *Distobolbina* sp. Mohibullah *et al.*, fig. 6k.

*Material.* A single right valve BGS 16E1958. No additional specimens were recovered from extensive recollecting at Craighead Quarry.

*Measurement.* Length 0.74 mm, height 0.5 mm.

*Description.* Valve preplete, lateral surface pustulose, L2 well defined. Unisulcate, S2 deep and well developed, tecnomorphic velar ridge appears to be absent.

*Discussion.* Preplete shape, unisulcate valves and spaced pustulose ornament are typical for *Distobolbina* species, but the specimen from the Craighead Limestone appears to lack a tecnomorphic velar ridge, differentiating it from the type species *D. nabalensis* Sarv, 1959 and other species of *Distobolbina*. This is the only record of *Distobolbina* from Scotland.

*Occurrence.* Late Ordovician (early Katian) Craighead Limestone Formation, Girvan district, southwest Scotland (Williams & Floyd 2000; Mohibullah *et al.* 2010) locality 6a.

Superfamily PRIMITIOPSACEA Swartz, 1936

Family PRIMITIOPSIDAE Swartz, 1936

Genus Uncertain

**Primitiopsid sp.** Pl. 1, figs 9, 10

2010 Primitiopsacean sp. Mohibullah *et al.*, figs 6l, n.

*Material.* Three carapaces (BGS GSE15345, GSE15416, GSE15417).

*Measurement.* Based on all collections, length 1.63-1.73 mm, height 1.07-1.25 mm. Figured specimen (BGS GSE15345) length 1.73 mm, height 1.25 mm.

*Description.* Carapace sub-ovate with maximum height posterior, and therefore valves slightly postplete. Unisulcate, S2 and dorsal plica weakly developed. The left valve is larger and overlaps the right valve along the posterior and ventral margin. Velum is well developed posteriorly, where it forms the boundary wall of the dolonal antrum. It is demarcated from the lateral valve surface by a weak furrow. Surface smooth.

*Discussion.* Primitopsid sp. is a rare element of the Craighead Limestone Formation and represents the only record of a primitiopsacean from the Ordovician of Scotland. The velum resembles the morphology of the primitiopsacean *Anisocyamus* Martinsson, 1960, in being restricted to the posterior part of the valve. In the Scottish material though, the velar ridge is demarcated from the lateral valve surface by a weak furrow that is absent in *Anisocyamus*.

*Occurrence.* Late Ordovician (early Katian) Craighead Limestone Formation, Girvan district, southwest Scotland (Mohibullah *et al.* 2010), locality 6c.

Palaeocopa? Family uncertain

Genus **NINGULELLA** Warshauer & Berdan, 1982

*Type species.* By original designation; *Ningulella paupera* Warshauer & Berdan, 1982, pl. 15, figs 11-13), a carapace, USNM 271078, from the Strodes Creek Member of the Lexington Limestone, Kentucky, USA.

*Diagnosis.* (Modified from Warshauer & Berdan 1982) Valves ample to weakly postplete, lateral outline sub-rectangular, hinge line straight and long. Valves nearly equal in size; right valve weakly overlaps the left valve along the ventral and posterior margins. Carapace smooth.

*Discussion.* See Warshauer & Berdan (1982).

*Occurrence.* From the Ordovician of Kentucky (Warshauer & Berdan 1982). Possibly from Oklahoma (Williams & Siveter 1996) and southwest Scotland (Mohibullah *et al.* 2010).

**Ningulella?** sp. Pl. 3, fig. 10

2010 *Ningulella?* sp. Mohibullah *et al.*, p. 939, figs 8o, r.

*Material.* A single carapace, GSE15366.

*Measurement.* Length 0.9 mm; height 0.6 mm.

*Description.* Non-sulcate, lateral outline sub-rectangular, valves weakly postplete, nearly equal in size, the right valve weakly overlaps the left one along the posterior margin. Surface smooth and non-sulcate.

*Discussion.* *Ningulella?* sp. differs from the type species *N. paupera* in having right over left valve overlap only along the posterior margin whereas in the type

species the valve overlap is marked along both the ventral and posterior margins. Due to simple morphology and poor preservation the assignment is tentative.

*Occurrence.* Late Ordovician (Katian) Craighead Limestone Formation, Girvan district, southwest Scotland (Mohibullah *et al.* 2010), locality 6c.

Suborder BINODICOPA Schallreuter, 1972

Family DREPANELLIDAE Ulrich & Bassler, 1923

Genus **KINNEKULLEA** Henningsmoen, 1948

*Type-species.* *Kinnekullea waerni* Henningsmoen, 1948, by original designation. From the Late Ordovician Black Tretaspis Shale, Kinnekulle, Västergötland, Sweden.

*Occurrence.* From the Ordovician of southwest Scotland (Floyd *et al.* 1999, Williams *et al.* 2000, 2001a; Mohibullah *et al.* 2010), northern England (Williams *et al.* 2001b), Ireland (Orr 1987) and the Baltic region (Meidla 1996).

**Kinnekullea comma** (Jones, 1879) Pl. 3, fig. 5

1879 *Beyrichia comma*, Jones (sp. nov.), p. 219, pi. 15, figs 9a-c.

1881 *B. comma*, Jones; Salter and Etheridge (*in* Ramsay), p. 409.

1886 *B. comma*, Jones; Jones and Holl, p. 362.

1892 *Beyrichia comma*, Jones; Smith, p. 158.

1893 *Beyrichia (Primitia) comma*, Jones; Jones, pp. 301, 305.

1899 *Beyrichia comma* (Jones); Peach and Horne, p. 690.

1934 *Beyrichia?* (*Bollia?*) *comma* Jones; Bassler and Kellett, p. 190.

1999 *Kinnekullea comma* (Jones, 1879); Floyd, Williams & Rushton, p. 20-21, figs 4i, 7a-f.

2000 *Kinnekullea comma* (Jones, 1879); Williams *et al.* 2000, p. 163-164, figs 1a, b.

2001a *Kinnekullea comma* (Jones, 1879); Williams *et al.*, fig. 5ee.

*Type specimen.* Rock slab NHM UK PM In20008, from the Starfish Beds, contains the 'syntypes' of *K. comma*, including the specimens figured by Jones (1879, pi. 15, figs 9a-c), but none of the specimens on this slab, can be matched exactly with Jones' figured specimens (see Floyd *et al.* 1999 for further details).

*Material and measurements.* More than 20 specimens from the Starfish Beds, NHM UK PM In20008, PM In20040 (part and counterpart), PM 1979.28.75: 12 specimens (including counterparts) from the Lady Burn Formation, BGS 16E897, 16E898, 16E903, 16E904, 16E911 16E912, 16E913, 16E914, 16E915, 16E916, 16E934/16E935, 16E962, 16E963, 16E984/16E985, 16E940, 16E941 and an external mould (GSE15418) from new collections.

*Measurement.* Specimens from the Starfish Beds are 0.95-1.20 mm (NMH PM 1979.28.75) and 1.00-1.10 mm long (NHM UK PM In20008, In20040). Those from the Lady Burn Formation are 0.75-1.00 mm in length, possibly representing two moult stages.

*Diagnosis.* (After Floyd *et al.* 1999) *Kinnekullea* species with its arcuate lobe terminated in a short, posterodorsally projecting narrow spine.

*Description.* (After Floyd *et al.* 1999) Valves postplete to subamplete. Dorsal margin straight, remainder of lateral valve outline convex. Well-developed, sub-circular L2 connects ventrally to 'comma'- shaped arcuate lobe. Arcuate lobe terminated posteriorly in a short, posterodorsally projecting narrow spine. Valves smooth and without any adventral and marginal structures.

*Occurrence.* From the Late Ordovician (Katian) Lady Burn and South Threave Formation, Girvan district, southwest Scotland (Floyd *et al.* 1999, Williams *et al.* 2001a, localities 12, 13), Cautley Mudstone Formation of northern England (Williams *et al.* 2000, 2001b, Potrane Limestone of Ireland (Orr 1987) and possibly from the Late Ordovician of Northern Ireland (Pomeroy) and the Baltic region (Floyd *et al.* 1999).

**Kinnekullea** n. sp. Pl. 3, fig. 4

2010 *Kinnekullea* sp. Mohibullah *et al.*, p. 939, fig. 6e.

*Material.* A single carapace (GSE15343).

*Measurement.* Length 0.53 mm, height 0.37 mm.

*Description.* The valves of *Kinnekullea* n. sp. are amplete, the dorsal margin is concave, and the ventral margin is convex. *Kinnekullea* n. sp. is characterized by its raised, circular muscle spot (85 µm in diameter) that is sited in the adductorial depression. This muscle spot is circumvented on three sides by a stout lobe that forms a recumbent 'n' shape, the closed end of the 'n' pointing anteriorly. Surface smooth.

*Discussion.* Its distinctive lobal morphology, while typical of *Kinnekullea*, serves to distinguish this taxon from all other species of *Kinnekullea* (for which, see Floyd *et al.* 1999). The species is not named because of limited material.

*Occurrence.* Late Ordovician (early Katian) Craighead Limestone Formation, Girvan district, southwest Scotland (Mohibullah *et al.* 2010), locality 6c.

Suborder LEIOCOPA Schallreuter, 1973

Superfamily PARAPARCHITACEA Scott, 1959

Family JANNUSSONIDAE Schallreuter, 1971

Genus **HEMIAECHMINOIDES** Morris & Hill, 1952

*Type species.* By original designation; *Hemiaechminoides monospinus* Morris and Hill, 1952, from the Mid Silurian strata of Tennessee, USA.

*Diagnosis.* (After Meidla 1996) Valves amplete, lateral shape oval or elongate oval. Dorsal margin short. Right valve overlaps the left along the free margin. Left valve is characterized by a prominent spine centro- to postero-dorsally.

*Discussion.* (see Meidla 1996 p. 99).

*Occurrence.* Ordovician of Scotland (Mohibullah *et al.* 2010), Baltoscandia (Meidla 1996; Schallreuter 1971); Silurian of North America (Morris & Hill 1952) and Bohemia (Příbyl 1988).

**Hemiaechminoides** sp. Pl. 3, fig. 1

2010 *Hemiaechminoides* sp. Mohibullah *et al.*, p. 939, fig. 8i.

*Material.* A single carapace (GSE15362).

*Measurement.* Length 0.45 mm, height 0.31 mm.

*Description.* Carapace small (0.45 mm long), lateral shape oval, valves amplete. Hinge line straight. Left valve has boss (35 µm in diameter) situated centro-dorsally. Right valve weakly overlaps the left valve along the free margin. Surface smooth and non-sulcate.

*Discussion.* The position of the dorsal boss in *Hemiaechminoides* sp. is equivalent to the spine in *Hemiaechminoides minusculus* Meidla, 1986. The type-species *Hemiaechminoides monospinus* Morris & Hill, 1952 has the boss situated centro- to posterodorsally on the left valve. *Hemiaechminoides* sp. may be conspecific with the Baltic type species but due to poor preservation our assignment is limited to generic level. This is the first record of *Hemiaechminoides* from the Ordovician of Scotland.

*Occurrence.* Late Ordovician (Katian) Craighead Limestone Formation, Girvan district, southwest Scotland (Mohibullah *et al.* 2010), locality 6c.

Superfamily APARCHITACEA Jones, 1901

Family APARCHITIDAE Jones, 1901

Genus **BALTONOTELLA** Sarv, 1959

*Type species.* By original designation (Sarv, 1959, p. 161) *Macronotella kuckersiana* Bonnema, 1909.

*Diagnosis.* (After Meidla 1996) Carapace sub-circular to oval, valves asymmetrical, the larger right valve overlaps the smaller left valve along the entire free margin. The left valve may have admarginal structures such as a row of denticles or spines. Hinge line short and straight. Valves reticulate, punctate or smooth.

*Occurrence.* Ordovician of southwest Scotland (Williams *et al.* 2001a, Mohibullah *et al.* 2011), Oklahoma (Williams & Siveter 1996; Williams & Vannier 1995), Virginia (Kraft 1962), New York (Swain 1962), Pennsylvania (Swain 1962), Minnesota (Swain *et al.* 1961), Ontario (Copeland 1965), Baffin Island (Copeland 2000), district of Franklin and district of Mackenzie (Copeland, 1977a, 1982) Canada, and Baltoscandia (Meidla 1996).

**Baltonotella parsispinosa** (Kraft, 1962)      Pl. 3, figs 2, 3

1957 *Aparchites fimbriatus* (Ulrich); Swain, p. 560-561, pl. 61, figs 13a-c.

1961 *Aparchites fimbriatus* (Ulrich); Swain *et al.*, p. 351-353, text-fig. 2, pl. 46, figs 1a,b.

1962 *Aparchites parsispinosus* Kraft, n. sp., p. 30, pl. 2, figs 12-13, pl. 5, figs 1, 2, text-figs 7g-h.

1962 *Aparchites fimbriatus* (Ulrich); Kraft p. 28-29, pl. 2, figs 1-11, pl. 3, fig. 3, text-figs 1g-e.

1962 *Aparchites fimbriatus* (Ulrich); Swain.

1965 *Aparchites fimbriatus?* (Ulrich); Copeland, p. 29, pl. 2, figs 5, 13.

1977a *Leperditella?* sp.; Copeland, pl. 2, fig. 10.

1982 *Aparchites fimbriatus* (Ulrich); Copeland, pl. 9, fig. 1.

1995 *Baltonotella parsispinosa* (Kraft, 1962); Williams & Vannier, p. 12, figs 4.1-4.7, pl. 1, figs 9, 11, 14.

1996 *Baltonotella parsispinosa* (Kraft, 1962); Williams & Siveter, pl. 2, fig. 10.

2001a *Baltonotella parsispinosa* (Kraft, 1962); Williams *et al.*

2011 *Baltonotella parsispinosa* (Kraft, 1962); Mohibullah *et al.*, figs 4e, h.

*Holotype.* A left valve, USNM 136581, (Kraft 1962, p. 30, pl. 2, figs 12a-c) from the Late Ordovician Edinburg Formation Virginia.

*Material.* Two calcitic carapaces GLAHM 114368 and BGS GSE 15387 and an external mould (BGS GSE 15390).

*Measurement.* GSE 15387, length 1.88 mm, height 1.6 mm, GSE 15390, length 1.58 mm, height 1.30 mm. Seven moult stages of *Baltonotella parsispinosa* are recorded from the Bromide Formation of Oklahoma (see Williams & Vannier 1995) with a size range of 1.21-3.15 mm in length. The Virginian type specimen of Kraft (1962) is 0.94 mm long and 0.67 mm high, and is probably a juvenile, whereas another figured specimen is larger with a length of 2.38 mm and height of 1.75 mm.

*Diagnosis.* *Baltonotella* with cardinal spines and spaced marginal denticles on the left valve.

*Description.* Carapace sub-circular, Valves amplete and convex, left valve with spaced marginal denticles. The larger right valve markedly overlaps the smaller left valve along the ventral, posterior and anterior margins. Hinge line straight

and about half the total length of the valves. Carapace smooth or punctate and non-lobate.

*Discussion.* As a result of differential preservation, the number of spaced marginal spines on the left valve varies and in some cases may be completely absent (see also Williams and Vannier 1995).

*Occurrence.* Late Ordovician lower Ardwell Farm Formation, Girvan district, southwest Scotland (Williams *et al.* 2001a; Mohibullah *et al.* 2011, locality 5), Bromide Formation of Oklahoma (Williams & Siveter 1996), Lincolnshire and Edinburg formations of Virginia (Kraft 1962), Hatter and Benner formations of Pennsylvania (Swain 1957, 1962), Day Point, Crown Point and Valcour formations of New York (Swain 1957, 1962), Decorah Formation of Minnesota (Swain *et al.* 1961), Silliman's Fossil Mount, Franklin district, Canada (Copeland 2000), Lower Esbataottine Formation, Mackenzie district, Canada (Copeland 1982), the Liskeard Formation of Ontario, Canada (Copeland 1965).

Genus **VANNIERIA** n. gen.

*Derivation of name.* After Jean M.C. Vannier, University of Lyon, for his extensive contributions to Palaeozoic ostracod taxonomy.

*Type species.* *Schmidtella transversa* Harris, 1957

*Diagnosis.* Valves amplete, non-sulcate and strongly umbonate. Lateral outline sub-elliptical. Dorsum epicline and deeply excavated, dorsal margin gently arched. Surface smooth.

*Discussion.* The smooth, non-sulcate and convex valves and right over left valve overlap suggests its position in the *Aparchitidae*.

*Occurrence.* From the Girvan district, southwest Scotland (Mohibullah *et al.* 2010, 2011) and Oklahoma, USA.

**Vannieria transversa** (Harris, 1957) Pl. 4, figs 3-8

1957 *Schmidtella transversa* Harris n. sp., p. 169, pl. 4, figs 11a-c.

1996 '*Schmidtella*' *transversa* Harris; Williams & Siveter, pl. 2, fig. 3.

2010 '*Schmidtella*' cf. *transversa* Harris; Mohibullah *et al.*, figs 5b, 6m, p, r.

2011 '*Schmidtella*' *transversa* Harris; Mohibullah *et al.*, fig. 4d.

*Holotype.* MCZ 5447 from the Tulip Creek Formation, Ordovician, Oklahoma, USA.

*Material.* More than 50 carapaces and an external mould.

*Measurement.* Based on all Craighead Limestone specimens in the BGS collection, length 0.49-0.79 mm, height 0.3-0.46 mm. The figured specimen (GSE15341) length 0.72, height 0.42 mm, (GSE15355) length 0.51 mm, height 0.33 mm. The figured specimen from the Ardwell Farm Formation is 1.30 mm long and 0.80 mm high. The holotype (MCZ 5447) from Tulip Creek Formation is 0.55 mm long and 0.32 mm high.

*Diagnosis.* As for the genus which is monotypic.

*Description.* Valves amplete, non-sulcate and strongly umbonate. Lateral outline sub-elliptical. Dorsum epicline and deeply excavated, dorsal margin gently arched, ventral margin convex. The anterior margin is more sharply rounded than the posterior. The larger right valve overlaps the smaller left valve along the entire ventral and anterior margins. Valve contact straight. Surface smooth.

*Discussion.* *Vannieria transversa* resembles '*Macronotella*' *upsoni* Harris, 1957 in general shape, umbonation and valve overlap, but lacks the narrow flattened margin of the smaller left valve.

*Occurrence.* Late Ordovician (early Katian) Craighead Limestone Formation and lower Ardwell Farm Formation Girvan district, southwest Scotland (Mohibullah *et al.* 2010, 2011) (locality 6c) and Tulip Creek and the Bromide formations of Oklahoma (Harris 1957; Williams & Siveter 1996).

Suborder PLATYCOPA Sars, 1866

Family LEPERDITELLIDAE Ulrich & Bassler, 1906

Genus **LEPERDITELLA** Ulrich, 1894

*Type species.* Designated Coryell and Schenk, 1941, p. 176, *Leperditella rex* (new name for *L. inflata* (Ulrich, 1892)).

*Diagnosis.* (Modified from Ulrich 1894) Non-sulcate, or with a weak sulcal depression. Lateral outline subovate. The left valve is larger and overlaps the smaller right valve along the ventral margin. Carapace smooth or punctate.

*Occurrence.* From the Ordovician of Scotland (Williams & Floyd 2000; Williams *et al.* 2001), Oklahoma (Harris 1957; Williams & Siveter 1996; Utah (Berdan 1988), Kentucky (Warshauer & Berdan 1982), Iowa (Kay 1940), Minnesota (Ulrich 1894). Also from the Late Ordovician strata of the District of Mackenzie (Copeland 1974), Ontario, Canada (Copeland 1965) and the Ordovician of the Baltic region (Sarv 1959).

***Leperditella girvanensis*** n. sp. Pl. 4, fig. 13, Pl. 5, fig. 1, 2

2000 *Leperditella* sp., Williams & Floyd, figs 5o, p, r.

2001a *Leperditella* sp., Williams *et al.* fig. 5l.

2010 *Leperditella* sp. Mohibullah *et al.*

*Derivation of name.* After the Girvan District, southwest Scotland.

*Holotype.* A right valve BGS 16E1959 from the Late Ordovician (early Katian) Craighead Limestone Formation (locality 6a), Girvan district, southwest Scotland.

*Material.* 14 valves BGS (Keyworth) 16E1955, 16E1956, 16E1936, 16E1959, 16E1933, 16E1941, 16E2028, 16E1948, 16E1931, 16E2032, 16E2851, 16E1963, 16E1964, GLAHM 114035.

*Measurement.* Based on BGS collections, length ranges from 1.15-2.1 mm. Length of the holotype (BGS 16E1959) 1.54 mm, height 0.93 mm; figured specimen (16E1965) length 1.84 mm, height 1.14 mm; (BGS 16E1964) length 1.92 mm, height 1.25 mm.

*Diagnosis.* Non-sulcate and slightly postplete valves thickened into a node postero-cardinally. Valve surface finely punctate.

*Description.* Valves weakly postplete, lateral outline sub-ovate. Anterior margin is more sharply convex than the posterior, outline of dorsal margin slightly sinuous, ventral margin convex. The larger left valve overlaps the smaller right valve along the ventral margin. Valves surface finely punctate.

*Discussion.* The presence of punctate ornamentation, weakly postplete outline and the sinuous dorsal margin differentiates *Leperditella girvanensis* from the type species *Leperditella rex* Coryell and Schenk, 1941. *Leperditella girvanensis* resembles *Leperditella tumida* (Ulrich, 1892) in its sinuous dorsal outline, but the later is more tumid posteriorly, strongly postplete and the left over right overlap extends from the ventral to posterocardinal corner whereas in *Leperditella girvanensis* the left over right valve overlap is only along the ventral margin.

*Occurrence.* Late Ordovician (early Katian) Craighead Limestone Formation, Girvan district, southwest Scotland (Williams & Floyd 2000; Mohibullah *et al.* 2010) locality 6a.

Order PODOCOPIDA Sars, 1866

Suborder METACOPINA Sylvester-Bradley, 1961

Family STEUSLOFFINIDAE Schallreuter, 1984

Genus **STEUSLOFFINA** Teichert, 1937

*Type species:* Teichert 1937, p. 120-122, pl. 24, figs 2-4; *Steusloffina ulrichi* Teichert, 1937, from a beach section between Nugsanarsuk and Qarman, east coast of Melville Peninsula, Canada, Late Ordovician.

*Diagnosis.* (Modified from Teichert 1937) Valves markedly preplete, such that the posterior lateral outline tapers to less than one-half of the width of the anterior. Valves convex mid-dorsally, forming a distinctive cusp that overreaches an epicline dorsum. Larger left valve with well-developed bow-shaped projection that overlaps the smaller right valve along the entire ventral margin. Free margin of valves convex throughout.

*Discussion.* *Steusloffina* species are distinguished by lateral shape, possession of a lateral spine, and by characteristic pustulose ornament.

*Occurrence.* Late Ordovician (Katian) strata of Scotland (Mohibullah *et al.* 2010), North America (Hessland & Adamczak 1974), Baltoscandia (Schallreuter 1968; Meidla 1996), Uzbekistan, (Melnikova & Michailova 1999), Altai (Melnikova 2010), northern India (Schallreuter *et al.* 2008), Late Ordovician and Early Silurian strata of Arctic Canada (Teichert 1937; Copeland 1983, 1989), Early Silurian strata of Iran (Hairapetian *et al.* 2011) and questionably from the Ordovician of Argentina (Salas 2002).

***Steusloffina cuneata*** (Steusloff, 1895) Pl. 5, figs 6, 7, 9, 10

1895 *Primitia cuneata* n. sp. Steusloff, p. 782, pl. 58, figs 5 a-b.

1918 *Primitia cuneata* Steusloff; Kruizinga, 131.

- 1924 *Bairdia* ? *cuneata* Steusloff. sp., *Krausella cuneata* Steusloff. sp.; Kummerow, pp. 408, 435, 436; pl. 21 (numbered 20), figs 17 a-c.
- 1934 *Bairdia cuneata* Steusloff; Bassler & Kellet, pp. 55, 169.
- 1937 *Steusloffina cuneata* (Steusloff), Teichert, p. 121.
- ?1937 *Steusloffina ulrichi* n. sp., Teichert, p. 120, pl 24, figs 2-5.
- 1938 *Bairdia* cf. *cuneata* (Steusloff); Thorslund & Westergård, p. 30, 31.
- 1956 *Steusloffina diversa* sp. n. Stumbur, p. 192, pl. 3, figs 7-9.
- 1960 *Steusloffina cuneata* (Steusloff); Krandievski, p. 175.
- 1960 *Steusloffina cuneata* (Steusloff); Sarv, p. 242, Table. 1.
- 1961 *Steusloffina cuneata* (Steusloff); Sohn, 13, 43, 84-85; pl. 6, fig. 17.
- 1962 *Steusloffina cuneata* (Steusloff); Sarv, p. 96, pl. 1 (S. 97).
- 1963 *Steusloffina cuneata* (Steusloff); Männil, Abb. 6.
- 1967 *Steusloffina cuneata* (Steusloff); Schallreuter, 616.
- 1968 *Steusloffina cuneata* (Steusloff); Schallreuter, p. 138-141, figs 12-15.
- 1972 *Steusloffina cuneata* (Steusloff); Pranskevičius, p. 142, pl. 28, figs 3-4.
- 1974 *Steusloffina cuneata* (Steusloff); Hessland & Adamczak, p. 61, pl. 1, figs 1-4, text-figs 1-2.
- 1983 *Steusloffina cuneata* (Steusloff), 1895; Copeland, p. 201-204, figs 23.2 (1-8)

1984 *Steusloffina cuneata* (Steusloff); Sarv & Meidla, pp. 8, 11.

1989 *Steusloffina cuneata* (Steusloff); Nölvak *et al.*, p. 90.

1992 *Steusloffina cuneata* (Steusloff); Sidaravičienė, pp. 202-203, pl. 52, fig. 11.

1999 *Steusloffina cuneata* (Steusloff, 1895); Melnikova & Michailova; pl. 6, p. 394, figs 10a, b.

1996 *Steusloffina cuneata* (Steusloff, 1895); Meidla, p. 122, pl. 25, figs 4-6.

2001b *Steusloffina cuneata* (Steusloff, 1895); Williams *et al.* p. 594, fig. 3t.

2005 *Steusloffina cuneata* (Steusloff); Schallreuter *et al.*, p. 107.

2008 *Steusloffina cuneata* (Steusloff, 1895); Schallreuter *et al.*, p. 201, fig. 8C.1.

2010 *Steusloffina cuneata* (Steusloff, 1895); Mohibullah *et al.*, p. 926, figs 7h, i, l, o.

2010 *Steusloffina cuneata* (Steusloff, 1895); Melnikova; pl. 6, fig. 10.

2011 *Steusloffina cuneata* (Steusloff, 1895); Hairapetian *et al.*, p. 648, figs 4f, g.

*Lectotype.* Designated Schallreuter, 1968, p. 138, fig.12; a carapace GG no. 114-25A (Institute of Geography and Geology, Greifswald University, Germany).

*Material.* More than 50 complete specimens (all carapaces).

*Measurements.* Based on all Girvan specimens, length 1.08 mm-1.5 mm, height 0.63-0.83 mm. Figured specimen (GSE15352) length 1.5 mm, height 0.84 mm, (GSE15354) length 1.4 mm, height 0.82 mm. The size range of Girvan

specimens overlaps the type specimen of Schallreuter (1968) and the figured specimen from India, both of them are 1.63 mm in length. The sizes of *Steusloffina cuneata* from the Early Silurian strata of Iran (Hairapetian *et al.* 2011) are smaller, ranging in length from 0.81-0.87 mm.

*Diagnosis.* *Steusloffina* with a variably developed, small mid-central to mid-ventrally situated spine having a diameter of 120  $\mu\text{m}$ . Valves otherwise without ornament. Posterior lateral shape varies from gently convex and half the height of the anterior, to markedly acuminate.

*Description.* Valves preplete: posterior valve height about one-half that of anterior valve height. Dorsal outline weakly convex mid-dorsally, forming a weak dorsal cusp that encapsulates the epicline dorsum. Valves non-sulcate and smooth. Larger left valve overlaps the smaller right valve with a bow-shaped projection that gives the strongest overlap through the mid-ventral part of the ventral surface. Lateral spine absent.

*Discussion.* Teichert (1937, p. 121) clearly recognised the similarity between his new species *Steusloffina ulrichi* and *S. cuneata*, stating that *ulrichi* differs from *cuneata* “in that the anterior margin is slightly more prominent in its ventral half”. This is a weak basis for differentiating *Steusloffina* species which are known to have quite variable shapes within species (e.g. see Schallreuter 1968, fig. 13; herein Pl. 5, figs 6, 7). *Steusloffina cuneata* is known from both smooth (Hessland & Adamczak 1974; Meidla 1996; Mohibullah *et al.* 2010) and spine-bearing forms (Copeland 1983; Meidla, 1996 & Schallreuter *et al.* 2008), with some authors recording both (e.g. Schallreuter 1968; Meidla 1996). All of the

specimens from the Craighead Limestone Formation lack lateral spines. Both spine-bearing and non-spinose forms of *Steusloffina cuneata* occur in single samples, for example in the 'Moe-2 section' of Estonia (Meidla 1996).

*Occurrence.* From the Late Ordovician (Katian) Craighead Limestone Formation, Girvan district southwest Scotland (Mohibullah *et al.* 2010, locality 6c), Late Ordovician (Katian) Rysedorph Hill Conglomerate, North America (Hessland & Adamczak 1974). Also from the Late Ordovician strata of Baltoscandia (Schallreuter 1968; Meidla 1996), Uzbekistan (Melnikova & Michailova 1999), Altai, Russia (Melnikova 2010), India (Schallreuter *et al.* 2008), Early Silurian Bescie Formation of Arctic Canada (Copeland 1983), and Early Silurian strata of Iran (Hairapetian *et al.* 2011).

***Steusloffina cf. ulrichi*** (Teichert, 1937)                      Pl. 5, figs 3-5

2010 *Steusloffina cf. ulrichi* Teichert; Mohibullah p. 939, figs 7k, n, q.

*Material.* A single carapace GSE 15358.

*Measurement.* 0.61 mm, height 0.32 mm.

*Description.* Valves preplete; the anterior outline is more broadly rounded than the posterior. Hinge line straight and long, slightly less than the total length of the carapace. Carapace length almost twice the height. The larger left valve overlaps the smaller right valve. The valves are smooth and non-spinose.

*Discussion.* This single specimen referred to *Steusloffina* cf. *ulrichi* resembles the type species *Steusloffina ulrichi* Teichert 1937, but the valves of that species are more tumid than in the Girvan specimen.

Genus **MEDIANELLA** Neckaja, 1966

*Type species.* *Medianella aequa* (Stumbur, 1956)

*Occurrence.* Ordovician and Early Silurian strata of Baltoscandia (Meidla, 1996), Ordovician (?) of Argentina (Salas 2002), British Isles (Vannier *et al.* 1989) and Late Ordovician strata (?) of Scotland (Mohibullah *et al.* 2010).

?**Medianella longa** (Stumbur, 1956) Pl. 6, figs 2-4

2010 *Medianella* cf. *longa* (Stumbur, 1956); Mohibullah *et al.*, figs 8a, d.

*Material.* A single carapace GSE15359.

*Measurement.* Length 1.30 mm, height 0.67 mm.

*Discussion.* With its smooth valves, elongate lateral shape, length about double the height, and the larger left valve overlapping the smaller right valve along the anterior, posterior and ventral margins, this species resembles *M. longa*. Poor preservation precludes firm assignment to Stumbur's *M. longa* (1956).

*Occurrence.* Late Ordovician (early Katian) Craighead Limestone Formation, Girvan district, southwest Scotland (Mohibullah *et al.* 2010), locality 6c.

Family BALTICELLIDAE Schallreuter, 1968

Genus **BALTICELLA** Thorslund, 1940

*Type species.* By original designation; *Balticella oblonga* Thorslund, 1940, p. 179 from the Ordovician lower Chasmops limestone, Sweden.

*Diagnosis.* (Modified from Kraft 1962) Valves bisulcate, S2 deep and extending approximately half way to ventral margin. S1 very short and shallow. L2 usually distinct. Dorsal margin slightly sinuous from a lateral aspect. Length is about twice the height, the left valve projects beyond the right and strongly overlaps the right valve; the overlap is more marked along the ventral margin. Surface smooth, reticulate or pustulose.

*Occurrence.* Late Ordovician strata of southwest Scotland (Williams *et al.* 2001a; Mohibullah *et al.* 2010), Oklahoma (Williams & Siveter 1996), Virginia (Kraft 1962), Pennsylvania (Swain 1962) and the Baltic region (Thorslund 1940; Schallreuter & Siveter 1985; Vannier *et al.* 1989).

**Balticella deckeri** (Harris, 1931) Pl. 5, fig. 11

1931 *Leperditella? deckeri* n. sp. Harris, p. 89, pl. 14, figs 5a-c.

1957 *Balticella deckeri* (Harris); Harris, p. 242, pl. 8, figs 7a-c.

1957 *Balticella deckeri* subsp. *elongata* n. subsp.; Harris, p. 242, pl. 8, fig. 8.

1962 *Balticella deckeri* (Harris); Kraft p. 57, pl. 13, figs 16, 17, pl. 14, figs 1-10.

1962 *Balticella deckeri* (Harris); Swain p. 738, pl. 111, fig. 12.

1968 *Balticella deckeri elongata* Harris; Schallreuter, p. 135.

1996 *Balticella deckeri* (Harris, 1957); Williams & Siveter, pl. 3, fig. 3.

2001b *Balticella deckeri* (Harris, 1957); Williams *et al.*, fig. 5d.

*Lectotype.* Designated here, (Harris 1957; pl. 8, fig 7a). In the Harvard Museum of Comparative Zoology, but without a reference number. Figured by Harris 1931, pl. 14, figs 5a-c. *Balticella deckeri* specimens were re-photographed by Harris (1957, pl. 8, figs 7a-c). The type specimen is not referred to any of the published figures in Harris's publications. From 'Decker's bed 24', Bromide Formation, Oklahoma Highway 99 (loc.1).

*Material.* An external mould and its counterpart (A18499b). Despite an extensive search of the Balclatchie Formation at Penwhapple Burn, no further specimens could be recovered.

*Measurement.* Length 1.24 mm, height, 0.72 mm.

*Diagnosis.* *Balticella* with well-developed S1 and S2, and prominent L2. Valves smooth.

*Description.* Carapace lateral outline sub-quadrate, valves amplete to slightly preplete. Bisulcate, S1 shallow, S2 deep extending halfway towards the ventral margin. L2 distinct and confluent with the anterior lobal area. Left valve overlaps the right along ventral, posterior and anterior margins; the strongest overlap is along the ventral margin. Valves smooth.

*Discussion.* *Balticella deckeri* differs from the type species *Balticella oblonga* Thorslund, 1940, by having a more pronounced anterior lobe, a spine on the

preadductorial node (see Kraft's 1962 material from Virginia) and by the lack of fine tuberculate ornament.

*Occurrence.* From the Balclatchie Formation of the Girvan district, southwest Scotland (Williams *et al.* 2001a, locality 1), Bromide Formation of Oklahoma (Williams & Siveter 1996), Lincolnshire and Edinburg formations of Virginia (Kraft 1962), and the Loysburg Formation of Pennsylvania (Swain 1962).

**Balticella** n. sp. Pl. 5, figs 8, 12

2010 *Balticella* sp. nov. Mohibullah *et al.*, p. 939, fig 6a.

*Material.* A single carapace (MPA49672).

*Measurement.* Length 1.54 mm, height 1.00 mm.

*Description.* Valves weakly postplete and bisulcate, S1 shallow and S2 deep. L2 indistinct. Both the anterior and posterior margins are convex. Dorsal margin sinuous from a lateral aspect, ventral margin slightly concave. Both valves have a diminutive posteroventral spine. The larger left valve overlaps the smaller right valve along the ventral, posterior and anterior margins. Valves smooth.

*Discussion.* The diminutive posteroventral spine and indistinct preadductorial node differentiate *Balticella* n. sp. from *Balticella deckeri* (Harris, 1957) and from the Baltic type-species *Balticella oblonga* Thorslund, 1940. The species is retained in open nomenclature because it is known only from a single specimen.

*Occurrence.* Late Ordovician (early Katian) Craighead Limestone Formation of the Girvan district, southwest Scotland (Mohibullah *et al.* 2010) locality 6c.

Genus **MONOCERATELLA** Teichert, 1937

*Type species.* By original designation Teichert, 1937, *Monoceratella teres* p. 116, pl. 23, figs 2-5, from a beach section between Nugsanarsuk and Qarman, east coast of Melville Peninsula, Canada, Late Ordovician.

*Diagnosis.* Unisulcate, with weakly developed S2 as a broad shallow depression. Internal sulcament well developed corresponding in position to the weak external S2. A spine projects ventrally from the lateral surface, ventral and posterior of the adductorial region.

*Discussion.* *Monoceratella teres* is very similar to *Monoceratella obliqua* from the descriptions and figures of Teichert, 1937, and the two may be conspecific.

*Occurrence.* From the Ordovician of southwest Scotland (Williams & Floyd 2000; Mohibullah *et al.* 2010), Oklahoma (Williams & Siveter 1996), Pennsylvania (Swain 1962) New York (Swain 1962), Virginia (Kraft 1962) Greenland (Teichert 1937) and Arctic Canada (Copeland 1977a).

**Monoceratella teres** Teichert, 1937                      Pl. 6, fig. 1

1937 *Monoceratella teres* Teichert, p. 116, pl. 23, figs 2-5.

1937 *Monoceratella obliqua* Teichert, p. 55, pl. 6, figs.

1962 *Monoceratella teres* Teichert; Swain, pl. 111, figs 4a, b.

1962 *Monoceratella teres* Teichert; Kraft, pl. 13, figs 5-15, text-figs 7p, q; 10d, e.

2000 *Monoceratella teres* Teichert, 1937; Williams & Floyd, fig. 5m.

2001a *Monoceratella teres* Teichert, 1937; Williams *et al.*, fig. 5o.

2010 *Monoceratella teres* Teichert, 1937; Mohibullah *et al.*, fig. 8q.

*Holotype.* Without a reference number, referred to Teichert, 1937, p. 114-116, pl. 23, figs 2-5, from a beach section between Nugsanarsuk and Qarman, east coast of Melville Peninsula, Canada, Late Ordovician.

*Material.* A left valve, GLAHM A1379.

*Measurement.* Length 1.7 mm, height, 1.05 mm.

*Diagnosis.* *Monoceratella* with S2 developed as a broad shallow depression. Valves with a central ovate muscle spot and a stout spine with a broad base developed on the posteroventral margin. No cardinal projections.

*Description.* Valves preplete, S2 weakly developed as a broad shallow depression. A prominent stout spine with a broad base is developed on the posteroventral margin. Both the posterior and anterior valve margins are convex, the posterior is sharply convex whereas the anterior is more gently convex. Dorsal margin is slightly sinuous from a lateral aspect. The larger left valve overlaps the smaller right valve. Valves smooth.

*Discussion.* Its central ovate muscle spot, stout posteroventral spine, and absence of cardinal projections clearly distinguish *M. teres* from other *Monoceratella* species.

*Occurrence.* From the Late Ordovician Craighead Limestone Formation of the Girvan district, southwest Scotland (Williams & Floyd 2000; Mohibullah *et al.* 2010 locality 6a), the Lincolnshire and Edinburg formations of Virginia (Kraft 1962), the Hatter and Benner formations of Pennsylvania (Swain 1962), the Crown Point Formation of New York (Swain 1962), and the Ordovician of northern Greenland (Teichert 1937).

Family KRAUSELLIDAE Berdan, 1961

Genus **KRAUSELLA** Ulrich, 1894

*Type species.* By original designation *Krausella inaequalis* Ulrich, 1894, from the Late Ordovician Platteville Formation, Dixon, Illinois, North America.

*Diagnosis.* (Modified from Kraft, 1962) Carapace elongate, dorsal lateral outline arched. The larger left valve strongly overlaps the smaller right valve along the ventral margin and weakly overlaps the dorsal margin along the cardinal corners. Dorsum weakly to moderately epicline. Right valve has a posteroventral spine; left valve without spine or with slightly drawn out posteroventral corner. Valves smooth and non-sulcate.

*Occurrence.* Ordovician of Scotland (Williams *et al.* 2001a; Mohibullah *et al.* 2010, 2011), Oklahoma (Harris 1957; Williams & Siveter 1996) Virginia (Kraft

1962), New York (Swain 1962), Pennsylvania (Swain 1962), Iowa, Minnesota (Kay 1940), Utah (Berdan 1988) Ontario, (Copeland 1965), district of Mackenzie (Copeland 1974, 1982), district of Franklin (Copeland 1977a) and Baffin Island Canada (Copeland 2000), and the Baltic region (Meidla 1996).

**Krausella arcuata** Ulrich, 1894 Pl. 6, fig. 12

1894 *Krausella arcuata* n. sp., Ulrich, p. 692, pl. 44, figs 47-53.

1940 *Krausella arcuata* Ulrich, 1894; Kay, p. 267.

1957 *Krausella arcuata* Ulrich, 1894; Harris, p. 255, pl. 10, figs 5a-c.

?1965 *Krausella* sp. cf. *K. arcuata* Ulrich, 1894; Copeland, p. 47, pl. 3, figs 11-13.

1974 *Krausella arcuata* Ulrich, 1894; Copeland, p. 28.

2010 *Krausella arcuata* Ulrich, 1894; Mohibullah *et al.*, fig. 8h.

*Holotype.* Carapace, USNM 41717. From the Guttenberg Member, Decorah Formation (Kay, 1940).

*Material.* A single carapace, GSE15364.

*Measurements.* The specimen is 1.85 mm long.

*Diagnosis.* *Krausella* with a weakly epicline dorsum and narrow admarginal ridge towards the anterior end of the right valve. Right valve is drawn out into a stout spine, left valve lacks spine.

*Description.* Carapace elongate, valves strongly convex. The larger left valve overlaps the smaller right valve along the ventral margin and towards the cardinal corners. Dorsum epicline. Right valve with a triangular posteroventral spine, left valve without spine. Right valve has a narrow admarginal ridge towards the anterior. Surface smooth.

*Occurrence.* From the Late Ordovician Craighead Limestone Formation of Scotland, (Mohibullah *et al.* 2010, locality 6a), Bromide Formation of Oklahoma (Williams & Siveter 1996), Decorah Formation of Iowa and Minnesota (Kay 1940) and the Bucke Formation of Ontario (Copeland 1965).

**Krausella variata** Kraft, 1962     Pl. 6, figs 5-7

1962 *Krausella variata* n. sp., Kraft, p.63-66, pl. 17, figs 1-23, pl. 18, figs 1a-b, 14m, 15a, b.

1962 *Krausella variata* Kraft, 1962; Swain, pl. 111, figs 7a-f.

1996 *Krausella variata* Kraft, 1962; Swain, p. 99.

2001a *Krausella variata* Kraft, 1962; Williams *et al.*, figs 5f, g, j.

2011 *Krausella variata* Kraft, 1962; Mohibullah *et al.* fig. 4c.

*Holotype.* A carapace USNM 136593 (Kraft, 1962, pl. 17, figs 1a-d), from Strasburg Junction, Edinburg Formation, Virginia.

*Material.* 11 external moulds BGS GSE 15385, GLAHM 114361, GLAHM 114362, GLAHM 114363, GLAHM 114364, GLAHM 114369, GLAHM 114371, GLAHM 1143082, GLAHM 114083, GLAHM 1143084, A18512.

*Measurements.* (BGS GSE 15385) length 1.5 mm, height 0.82 mm; (GLAHM 1143082) length 0.95 mm, height 0.57 mm, (GLAHM 1143084), length 1.56 mm, height 0.75 mm.

*Diagnosis.* *Krausella* species with elongate to sub-elliptical carapace, left valve slightly triangular; dorsal margin strongly and evenly curved into posterior and anterior margins.

*Description.* Carapace elongate to sub-elliptical, non-sulcate. Dorsal margin strongly convex and evenly curved towards the anterior and posterior. Valves smooth, the larger left valve overlaps the right valve along the ventral, anterior and posterior margins.

*Discussion.* The holotype of *Krausella variata* (Kraft, 1962; pl. 17, figs 1a-d) resembles *Krausella arcuata* Ulrich, 1894 in overall shape and ventral overlap. However, other specimens of *Krausella variata* figured by Kraft (1962; pl. 63, figs 14, 15, 17) differ from *Krausella arcuata* by having a less elongate left valve.

*Occurrence.* From the lower Ardwell Farm Formation of the Girvan district southwest Scotland (Mohibullah *et al.* 2011), the Lincolnshire and Edinburg Formation of Virginia (Kraft 1962), the Day Point and Crown Point formations of New York (Swain 1962), and the Glenwood and Platteville formations of Minnesota (Swain 1996).

**Krausella** n. sp.     Pl. 6, fig. 14

1999 Podocope sp. 2, Floyd, Williams & Rushton, fig. 4a

2001a *Krausella* sp.; Williams *et al.*, figs 5f, g, j.

*Material.* At least four carapaces and their counterparts on slabs NHM UK PM In20008 and NHM UK PM In20041.

*Measurements.* Based on NHM UK PM In20041, length 1.58 mm, height 0.76 mm.

*Discussion.* *Krausella* n. sp. is characterized by its elongate carapace outline, posteroventral spine on the right valve and left over right valve overlap which is typical for species of *Krausella* Ulrich, 1894. It differs from *Krausella arcuata* Ulrich, 1894 by having a diminutive posteroventral spine, concave ventral margin (from a lateral aspect) and less convex dorsal margin.

*Occurrence.* From the Starfish Beds, South Threave Formation, Girvan district, southwest Scotland (Floyd *et al.* 1999; Williams *et al.* 2001a) locality 13.

#### Family LONGISCULIDAE Neckaja, 1966

#### Genus **LONGISCULA** Neckaja, 1958

*Type species.* By original designation *L. arcuaris* Neckaja, 1958, Mid Ordovician Echinospaerites beds, north-western part of Russia.

*Diagnosis.* (After Meidla 1993) Carapace sub-oval to sub-triangular in lateral view, elongate to oval with acuminate ends in dorsal view. The larger left valve overlaps the smaller right valve along the ventral and anterodorsal margins.

Surface smooth or granulated.

*Occurrence.* Ordovician of Scotland (Mohibullah *et al.* 2010), Argentina (Salas 2002), Baltoscandia (Meidla 1993, 1996), Podolia, Bohemia (?), China, Uzbekistan, Altai (Melnikova & Michailova 1999; Melnikova 2010; Meidla 1993); early Silurian strata of Baltoscandia, Uzbekistan, Eastern Siberia, Tian-Shan, Urals and Altai (Meidla 1986, 1993, Melnikova and Michailova 1999; Melnikova 1986; Neckaja 1966).

**Longiscula** sp.      Pl. 6, figs 8, 9

2010 *Longiscula* cf. *perfecta* Meidla, 1993; Mohibullah *et al.*, p. 928, figs 8b, e

*Material.* A single carapace, GSE15360.

*Measurement.* Length 0.63 mm; height 0.28 mm.

*Description.* Carapace sub-ovate, length of carapace about twice the height. Both the anterior and posterior margins are strongly convex. Dorsal margin arched, with anterior margin being slightly steeper than the posterior. In lateral outline the ventral margin is slightly concave. The lateral outline of the right valve has more distinct ventral concavity than the left valve. The larger left valve strongly overlaps the smaller right valve along the ventral margin but only weakly overlaps along the anterior and posterior margins. Valve surface smooth.

*Discussion.* *Longiscula* sp. resembles *Longiscula perfecta* Meidla, 1993 in having strongly convex valves. The lateral shape of the Girvan specimen is concave at the mid-ventral whereas in *Longiscula perfecta* the ventral concavity is more towards the anterior. A second specimen (GSE15365; Pl. 6, figs 10, 11,

13), 0.66 mm also seems referable to *Longiscula* but its specific designation is uncertain.

*Occurrence.* From the Late Ordovician (early Katian) Craighead Limestone Formation of the Girvan district, southwest Scotland (Mohibullah *et al.* 2010), locality 6c.

#### Ostracoda *incertae sedis*

The following taxa were described by Jones (1893) from the Mill Formation of the Whitehouse Group, sourced from the Girvan foreshore. They comprise poorly preserved mould material. I consider these taxa to be nomina dubia. In addition, a few other taxa including '*Primitia*' *krausei*, '*Primitia*' *ulrichiana*, '*Primitia*' *elongata*, '*Beyrichia*' *kloedeni infecta* (NHM UK number PM In 20030 equivalent to rock slab no. 116 of Jones 1893), '*Beyrichia*' *kloedeni* (NHM UK number PM In 20010 equivalent to rock slab no. 119), '*Uruchia*'? sp. (NHM UK number In 20021 equivalent to rock slab no. 123) and '*Cypridina*' *grayae* (NHM UK 20016 equivalent to no. 118 rock slab) cannot be matched between specimens on the rock slabs and those illustrations given by Jones (1893). They are not discussed further here.

**'*Primitia*' *girvanensis*** Jones, 1893      Pl. 7, fig. 5

1893 *Primitia girvanensis* sp. nov. Jones, p. 298, pl. 13, figs 7-9.

2001a '*Primitia*' *girvanensis* Jones, 1893; Williams *et al.*, fig. 5aa.

*Material.* Several specimens housed in the Natural History Museum London: In 20024 and In 20011 (equivalent to rock slabs numbers 114 and 115 of Jones, 1893, p. 299). *Primitia girvanensis* occurs in mudstones associated with several other ostracod taxa described by Jones (1893) including *Aparchites leperditoides*, *Aparchites subovatus* and *Sulcuna preacurrens*.

*Measurement.* Based on the right valve on rock slab (NHM UK PM In 20024), length 1.2 mm, and height 0.75 mm.

*Discussion.* All specimens in Jones' collection are decalcified moulds. Internal moulds indicate the presence of a L2 and an S2, and also suggest evidence for punctate ornament. However, there is insufficient information by which to diagnose this species and it should be restricted to its type material.

**'Sulcuna' preacurrens** Jones, 1893

1893 *Sulcuna preacurrens* sp. nov. Jones, p. 304, pl.14. figs 10-11.

*Material.* Several specimens in the NHM UK numbered as In 20030 and In 20024 (equivalent to rock slabs no. 116 and 115 as referred to in Jones 1893, p. 305).

*Measurement.* Based on the specimen on rock slab (NHM UK PM In 20030), length 1.0 mm, height 0.51 mm.

*Discussion.* All specimens in Jones' collection are decalcified moulds. A L2 and S2 can be seen in the specimens but other diagnostic features cannot be recognized due to poor preservation.

**‘Aparchites’ leperditoides** Jones, 1893

1893 *Aparchites leperditoides*, sp. nov. Jones, pl. 12 figs 10a-c.

*Material.* Several specimens housed in the Natural History Museum London. Numbers are: In 20024, In 20030 and In 20021 (equivalent to rock slabs 115, 116 and 123 as referred to in Jones 1983).

*Measurements.* Based on specimen on rock slab NHM UK PM In 20021, length 1.3 mm, height 0.75 mm.

*Discussion.* All specimens are decalcified moulds, the internal mould on rock slab 115 has a straight hinge line, no ornament, and lobation, but other diagnostic features are absent.

**‘Aparchites’ subovatus** Jones, 1893 Pl. 7, fig. 2

1893 *Aparchites subovatus* sp. nov., Jones, pl. 13, figs 4 & 5.

1893 ‘*Aparchites*’ *subovatus* Jones, 1893; Williams *et al.*, fig. 5y.

*Material.* Specimens on NHM UK PM In 20024 and PM In 20019 (equivalent to rock slabs 115 and 117 in Jones, 1893).

*Measurements.* Based on specimen on rock slab NHM UK PM In 20019, length 1.42 mm, height 0.67 mm.

*Discussion.* The material represents a decalcified mould, the valve is elliptical in shape, the posterior is gently rounded whereas the anterior is sharply rounded. No other diagnostic characters can be recognised.

**‘Beyrichia’ impar** Jones, 1893

1893 *Beyrichia impar* sp. nov., Jones, pl. 14, fig. 5.

*Material.* NHM UK In 20009 (equivalent to rock 113 as referred to in Jones, 1893, p. 303).

*Measurement.* Based on specimen on rock slab NHM UK PM In 20009, length 0.9 mm, height 0.58 mm.

*Discussion.* A decalcified external mould of a right valve showing a narrow curved median lobe and a sulcus, but no other distinctive characters.

**‘Primitia’ mundula** var. **fimbriata** Jones, 1893      Pl. 7, fig. 1

1893 *Primitia mundula* var. *fimbriata* sp. nov., Jones, pl. 13 fig. 11.

*Material.* A decalcified internal mould NHM UK 20016 (equivalent to no. 118 on rock slab as referred to in Jones, 1893, p. 299).

*Measurement.* Based on the specimen on rock slab (NHM UK PM In 20016), length 1.3 mm, height 0.82 mm.

*Discussion.* There is a well-developed L2 and S2. The posterior margin has marginal spines but no other diagnostic features can be distinguished and this taxon should be restricted to its type material.

**‘Primitia’ mundula** var. **kloedeniana** Jones, 1893                      Pl. 7, fig. 6

*Primitia mundula* var *kloedeniana* sp. nov., Jones, Pl. 13, figs 12-15.

*Material.* Several decalcified internal moulds NHM UK PM In 20037, PM In 20013, PM In 20019, PM In 20030 and PM In 20016 (equivalent to nos 116, 117, 120, 122 and 118 on rock slabs as referred to in Jones, 1893).

*Measurement.* Based on the specimen on rock slab NHM UK PM In 20016, length 1.04 mm, height 0.49 mm.

*Discussion.* All specimens are decalcified moulds. Internal moulds indicate the presence of a S2, but this is insufficient to recognize its systematic position.

**‘Primitia’ grayae** Jones, 1893

1893 *‘Primitia’ grayae* sp. nov., Jones, pl. 13, fig. 10.

*Material.* A left valve internal mould on rock slab PM In 20013 (equivalent to rock slab no. 120 as referred to in Jones, 1893, pl. 13, fig. 10).

*Measurement.* Based on the figured specimen (PM In 20013) length 0.6 mm, height 0.4 mm.

*Discussion.* The decalcified mould of *Primitia grayae* shows a sulcus and a punctate lateral surface. No other diagnostic characters are available to determine its systematic position.

**'Ulrichia' girvanensis** Jones, 1893      Pl. 7, fig. 4

1893 *Ulrichia girvanensis* sp. nov., Jones, pl. 14, fig. 8.

*Material.* Decalcified internal moulds on rock slab PM In 20021 (equivalent to rock slab no. 123 as referred to in Jones, 1893, pl. 14, fig. 8).

*Measurement.* Based on the specimen on rock slab PM In 20021, length 1.1 mm, height 0.6 mm.

*Discussion.* A decalcified internal mould with L2 and S2 and straight hinge line, but no other diagnostic characters are present to provide a firm taxonomic assignment.

**'Beyrichia' kloedeni** M'Coy      Pl. 7, figs 7

*non Beyrichia kloedeni* M'Coy, 1846, p. 58.

1893 *Beyrichia kloedeni* M'Coy; Jones, pl. 14, fig. 3.

*Material.* Decalcified moulds on rock slab PM In 20016 and PM In 20010 (equivalent to rock slabs no. 123 and 119 as referred to in Jones, 1893, pl. 14, figs 3 & 4).

*Measurement.* NHM UK PM In 20016 length 1.2 mm, height 0.75 mm, NHM UK PM In 20010 length 1.0 mm, height 0.55 mm.

*Discussion.* The decalcified material referred to *Beyrichia kloedeni* by Jones (1893) possesses a S2 and L2, and a straight hinge line, but these are insufficient to determine its systematic position. There is no evidence for cruminal dimorphism and it is not possible to establish the relationships of this material with *Beyrichia* M'Coy, 1846.

### **Biostratigraphical significance**

While North American Ordovician successions have highly refined graptolite and conodont biozonations (Sweet 1983, 1984; Bergstrom 1986; Finney 1986; Bauer 1994) no such schemes are yet devised for North American ostracods. In some cases attempts have been made at an ostracod biozonation such as the use of the *Monoceratella teres* and *Aparchites kauffmanensis* biozones for the Late Ordovician successions of New York and Pennsylvania (Swain 1962) but these are loosely defined and not applied elsewhere, probably due to strong inter-basinal faunal variation (see chapter 5). Nevertheless, there are some widespread and short-ranging species that have greater biostratigraphic potential. Thus, *Balticella deckeri* and *Eurychilina sunbloodensis* appear to have ranges restricted to the Sandbian (*gracilis* and *bicornis* biozones) and are of interregional value for correlating the Balclatchie Formation of the Girvan district with the Bromide Formation of Oklahoma and the lower Esbataottine Formation of the Mackenzie District, Canada. *Hippula ventrospinosa* appears to be indicative of the *bicornis* Biozone and enable correlation of the lower Ardwell Farm Formation with the Edinburg Formation of Virginia. The late Katian

*Kinnekullea comma* has great biostratigraphic value for inter-regional correlation of the *anceps* graptolite biozone (Floyd *et al.* 1999; Williams *et al.* 2000) between Scotland, and equivalent stratigraphic levels in England, Ireland and the East Baltic (see Orr 1987; Williams *et al.* 2001a; Floyd *et al.* 1999).

### **Palaeoecology**

The ostracod assemblages of much of the Late Ordovician succession of the Girvan district comprise low-diversity faunas that have largely been transported and deposited into deep shelf mudstones. Most ostracod workers use the juvenile to adult ratio to recognise transported versus in situ assemblages (Boomer *et al.* 2003). However, the Late Ordovician ostracod faunas of Girvan are represented by low abundance (see appendix 7) and such techniques cannot be applied. However, the disarticulated valves in most of the successions such as in the lower Ardwell Farm, Lady Burn, South Threave and Balclatchie formations supports the idea that the fauna is not in situ. The associated trilobite and brachiopod assemblages in these formations are also represented mostly by disarticulated valves (Williams 1962; Tripp 1980a; Harper 2001). In addition, these successions represent a mixed shallow and deep water fauna together which suggests high energy conditions, an unstable shelf and active down-slope transport of the shallow shelf fauna and sediments (see Figs 7, 8; Ingham 1978; Harper 2001; Ebbestad 2008).

Many of these ostracod faunas may have had their origins in carbonate ramp settings of the inner and mid shelf, exemplified by such taxa as *Balticella deckeri* or *Baltonotella parsispinosa* that are known from such settings in the

Ordovician succession of North America (Kraft 1962; Williams & Siveter 1996; Williams *et al.* 2001). This includes the faunas of the Balclatchie Formation, lower Ardwell Farm Formation, Lady Burn Formation and the South Threave Formation (Floyd *et al.* 1999; Mohibullah *et al.* 2011; see chapter 3). The exception is the fauna of the Craighead Limestone Formation that is of high diversity and is autochthonous, representing a shallow marine assemblage dominated by palaeocopes and an open marine assemblage dominated by podocopes, leiocopes, some palaeocopes and rare binodicopes (Williams & Floyd 2000; Mohibullah *et al.* 2011). The rich palaeocope and rare binodope occurrences in the Craighead Limestone Formation accords with the Vannier *et al.* (1989) lithofacies distribution model which suggests palaeocope dominance in carbonates and binodope abundance in clastics.

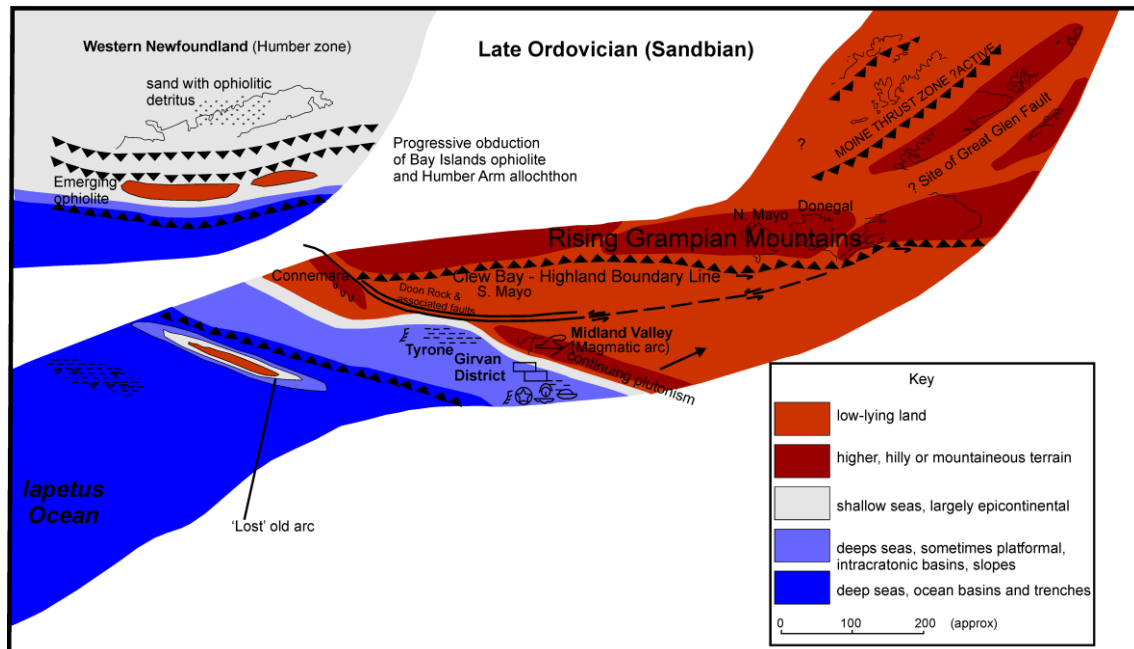


Figure 7. Regional palaeogeographic setting for the Girvan district in the Sandbian. Adapted from Bevins *et al.* (1992).

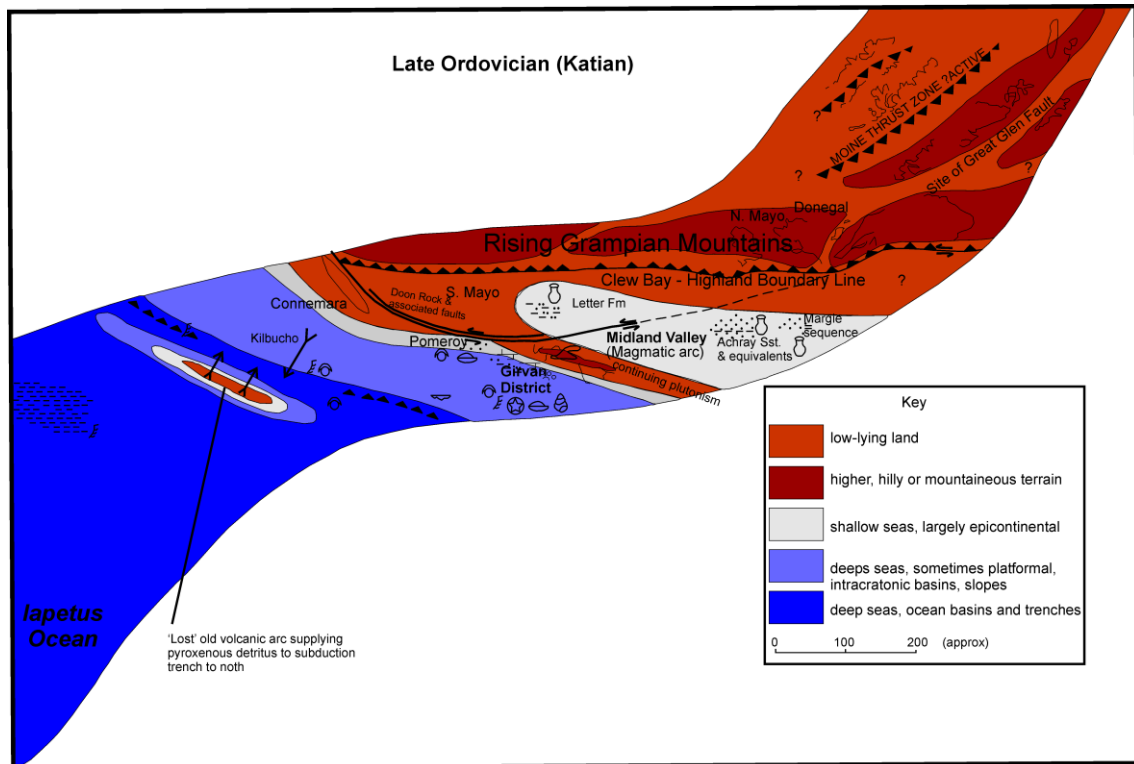


Figure 8. Regional palaeogeographic setting for the Girvan district in the Katian.

Adapted from Bevins *et al.* (1992).

## Biogeography

For more than two decades Ordovician ostracod assemblages have been widely used in determining the palaeogeographic positions of ancient continents (Schallreuter & Siveter 1985; Vannier *et al.* 1989; Williams *et al.* 2003; Meidla *et al.* in press). Laurentian Ordovician ostracod faunal similarities and exchange with the neighbouring continents Baltica and Avalonia have been discussed in detail by Schallreuter and Siveter (1985) and Williams *et al.* (2003). Herein, chapter 5 discusses the biogeographic distribution patterns of Ordovician ostracods of the palaeocontinent Laurentia, that demarcate a 'Mid-continent' and a southern 'Marginal' province for the Late Ordovician. The marginal faunas of Laurentia formed the earliest links with the Baltic region by the Mid

Ordovician (early Darriwilian) with the earliest species-level links between the Baltic region and the marginal faunas of Girvan during the early Katian (also see Mohibullah *et al.* 2010; figs 7, 8). Other Ordovician shallow water faunal groups of Girvan such as brachiopods, trilobites and gastropods show similar biogeographic patterns by showing progressive similarities with Baltica and Avalonia from Katian times onwards (Harper 2001; Ebbestad 2008). Thus, the distribution pattern of Girvan ostracods and other shallow water groups strongly supports palaeomagnetic studies which suggest the close proximity of the palaeocontinents Laurentia, Baltica and Avalonia during the Late Ordovician (Cocks & Torsvik 2002).

PLATE 1

The plates include images of a few taxa that are not formally described in the text, but are included here for completeness. These taxa are: (Palaeocope sp. 1, Palaeocope sp. 2, *Aparchites* sp. 1, *Aparchites* sp. 2, cf. *Schmidtella minuta* Harris, 1957, *Longiscula?* sp. and Podocope sp. 1).

***Oepikella tunnicliffi* Williams & Floyd, 2000**

Craighead Limestone Formation, *D. clingani* Biozone (*caudatus* Subzone, locality 6a).

- 1 Holotype, heteromorphic right valve (BGS 16E1961). Lateral view (stereo-pair), scale bar 1.0 mm.
- 2 Juvenile tecnomorphic valve (BGS 16E1967). Ventral view, scale bar 0.75 mm.
- 3 Tecnomorphic right valve (BGS 16E1965). Lateral view, scale bar 1.0 mm

***Distobolbina* sp.**

Craighead Limestone Formation, *D. clingani* Biozone (*caudatus* Subzone, locality 6a).

- 4 Tecnomorphic right valve (BGS 16E1958). Lateral view (stereo-pair), scale bar 0.38 mm.

***Hallatia* cf. *labiosa* (Ulrich, 1894)**

Ardwell Farm Formation at Pinmerry, *C. bicornis* graptolite Biozone (locality 5).

- 5 Silicon rubber cast of external mould of left valve (BGS GSE 15389). Lateral view (stereo-pair), scale bar 0.3 mm.

***Kiesowia* sp.**

Craighead Limestone Formation, *D. clingani* Biozone (*caudatus* Subzone, locality 6c).

- 6 Carapace (BGS GSE15344), left Lateral view (stereo-pair); scale bar 0.3 mm.

***Levisulculus* cf. *michiganensis* Kesling, 1960b**

Craighead Limestone Formation, *D. clingani* Biozone (*caudatus* Subzone, locality 6a).

- 7 Tecnomorphic right valve (BGS 16E1960). Lateral view, scale bar 0.43 mm.
- 8 Partly exfoliated heteromorphic left valve (BGS 16E2037). Lateral view, scale bar 0.5 mm.

***Primitiopsid* sp.**

Craighead Limestone Formation, *D. clingani* Biozone (*caudatus* Subzone, locality 6c).

- 9, 10 Carapace (BGS GSE15345). Right lateral view (stereo-pair); oblique lateral view, scale bar 0.5 mm.

***Platybolbina* cf. *punctata* (Kraft, 1962)**

Craighead Limestone Formation, *D. clingani* Biozone (*caudatus* Subzone, locality 6a).

- 11 Tecnomorphic left valve (GLAHM A1382). Lateral view, scale bar 0.75 mm.

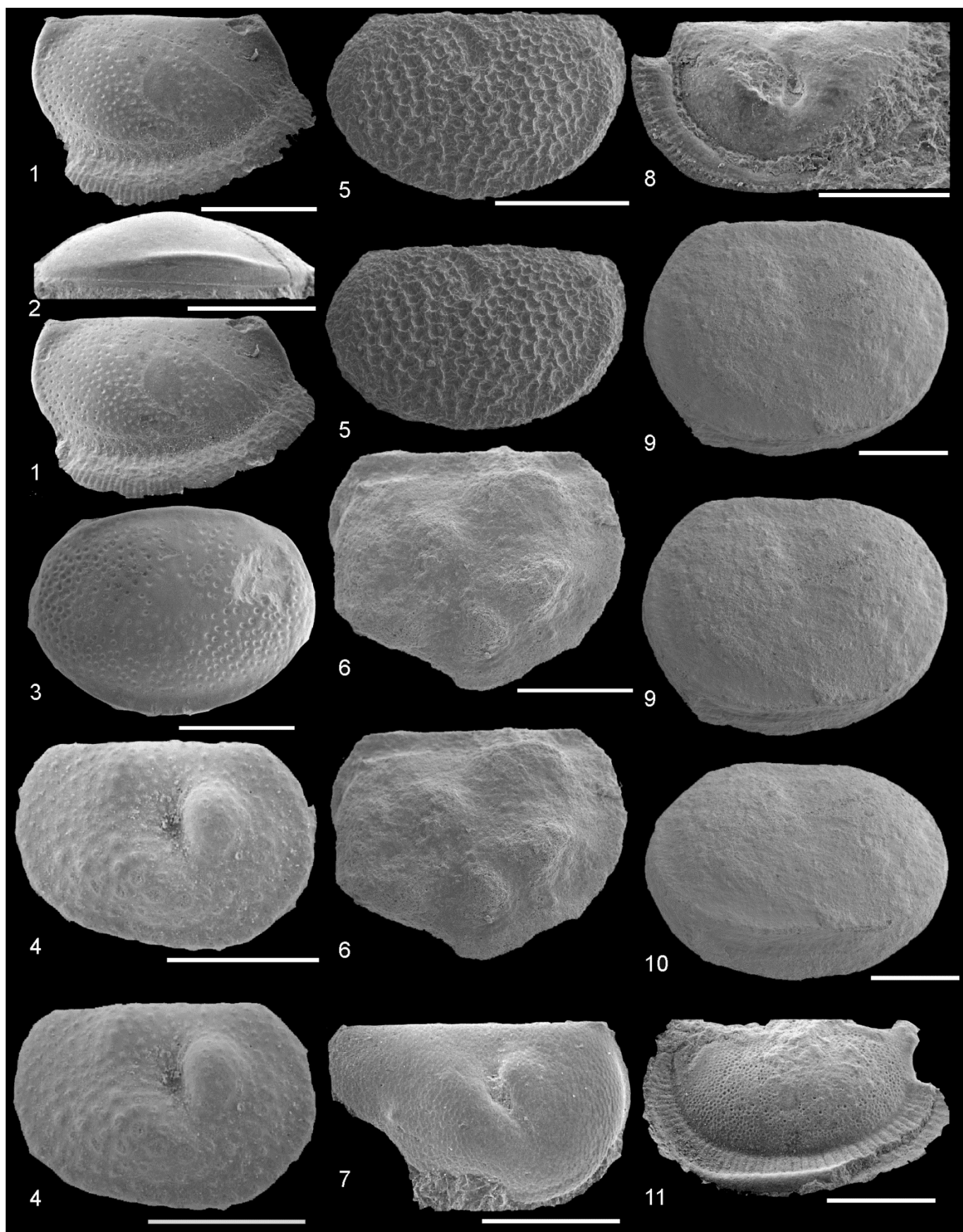


PLATE 2

***Platybolbina cf. punctata* (Kraft, 1962)**

Craighead Limestone Formation, *D. clingani* Biozone (*caudatus* Subzone, locality 6a).

- 1 Silicon rubber cast of external mould of tecomorphic right valve (BGS 16E 1986). Lateral view, scale bar 0.75 mm.

***Hippula ventrospinosa* (Kraft, 1962)**

Ardwell Farm Formation at Pinmerry, *C. bicornis* graptolite Biozone (locality 5).

- 2 Silicon rubber cast of heteromorph right valve (BGS GSE 15383). Lateral view (stereo-pair), scale bar 0.5 mm.
- 3 Heteromorphic left valve (BGS GSE 15384). Lateral view (stereo-pair), scale bar 0.5 mm.

***Eoaquapulex cf. socialis* (Levinson, 1961)**

Ardwell Farm Formation at Pinmerry, *C. bicornis* graptolite Biozone (locality 5).

- 4 Internal mould of left valve (GLAHM 114085). Lateral view, scale bar 0.5 mm.

***Palaeocope* sp. 1**

Craighead Limestone Formation, *D. clingani* Biozone (*caudatus* Subzone, locality 6a).

- 5 Right valve (BGS 16E2038). Lateral view, scale bar 0.5 mm.

***Duoarcus levigatus* Mohibullah et al., 2010**

Craighead Limestone Formation, *D. clingani* Biozone (*caudatus* Subzone, locality 6c).

- 6 Carapace (BGS GSE15347). Right lateral view, scale bar 0.5 mm.
- 7 Carapace (BGS GSE15350). Dorsal view, scale bar 0.5 mm.
- 8 Carapace (GSE15349). Ventral view (stereo-pair), scale bar 0.5 mm.
- 9 Holotype, Carapace (BGS GSE15348). Left lateral view (stereo-pair), scale bar 0.5 mm.

***Eurychilina sunbloodensis* Copeland, 1974**

Balclatchie Formation at Penwhapple Burn, *C. bicornis* graptolite Biozone (Locality 1).

- 10 Heteromorphic right valve (GLAHM 114089). Lateral view (stereo-pair), scale bar 0.69 mm.

***Vittella* sp.**

Lady Burn Formation, *anceps* graptolite Biozone (locality 12).

- 11 Juvenile right valve, internal mould (BGS 16E919). Lateral view, scale bar 0.45 mm.

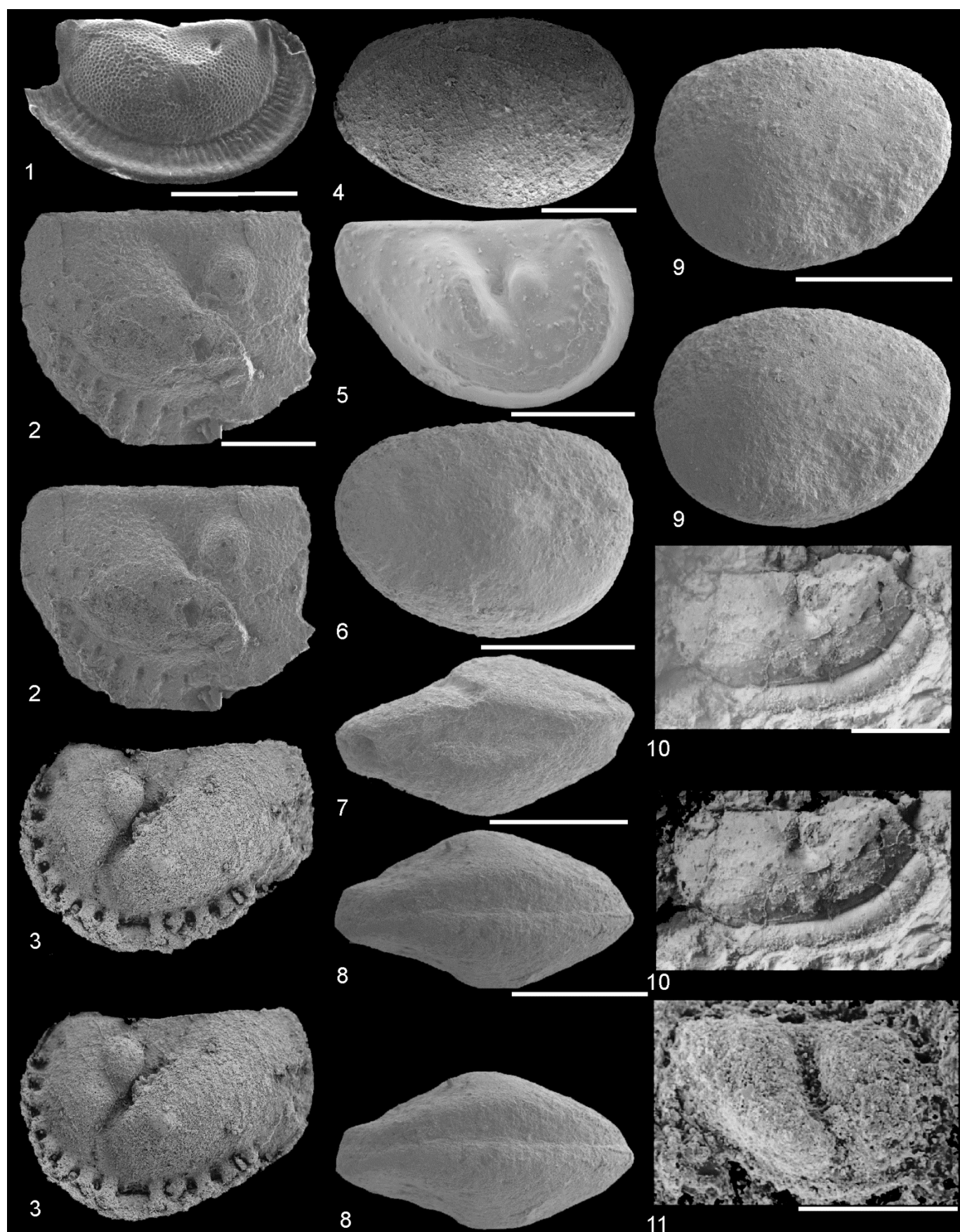


PLATE 3

***Hemiaechminoides* sp.**

Craighead Limestone Formation, *D. clingani* Biozone (*caudatus* Subzone, locality 6c).

- 1 Carapace (BGS GSE15362). Left lateral view (stereo-pair), scale bar 0.2 mm.

***Baltonotella parsispinosa* (Kraft, 1962)**

Ardwell Farm Formation at Pinmerry, *C. bicornis* graptolite Biozone (locality 5).

- 2 Silicon rubber cast of external mould of left valve (BGS GSE 15387). Lateral view (stereo-pair), scale bar 0.5 mm.  
3 Carapace (BGS GSE 15390). Oblique lateral view of left valve, scale bar 0.5 mm.

***Kinnekullea* n. sp.**

Craighead Limestone Formation, *D. clingani* Biozone (*caudatus* Subzone, locality 6c).

- 4 Carapace (BGS GSE15343). Right lateral view (stereo-pair), scale bar 0.25 mm.

***Kinnekullea comma* (Jones, 1879)**

Lady Burn Formation, *anceps* graptolite Biozone (locality 12).

- 5 Silicon rubber cast of external mould of left valve (BGS 16E900). Lateral view (stereo-pair), scale bar 0.43 mm.

***Aparchites* sp. 1**

Craighead Limestone Formation, *D. clingani* Biozone (*caudatus* Subzone, locality 6c).

- 6, 7 Carapace (BGS GSE15342). Right lateral and oblique lateral views, scale bar 0.5 mm.

***Euprimites limus* Floyd, Williams & Rushton, 1999**

Lady Burn Formation, *anceps* graptolite Biozone (locality 12).

- 8 Silicon rubber cast of external mould of heteromorphic right valve, holotype (BGS 16E895). Lateral view, scale bar 0.5 mm.  
9 Silicon rubber cast of external mould of tecnomorphic right valve (BGS 16E1005). Lateral view, scale bar 0.5 mm.

***Ningulella?* sp.**

Craighead Limestone Formation, *D. clingani* Biozone (*caudatus* Subzone, locality 6c).

- 10, 11 Carapace (BGS GSE15366). Right lateral and left lateral views, scale bar 0.5 mm.

***Palaeocope* sp. 2**

Starfish Beds, South Threave Formation, *anceps* graptolite Biozone (*pacificus* Subzone, locality 13).

- 12 Silicon rubber cast of right valve (BGS 16E900). Lateral view, scale bar 0.6 mm.

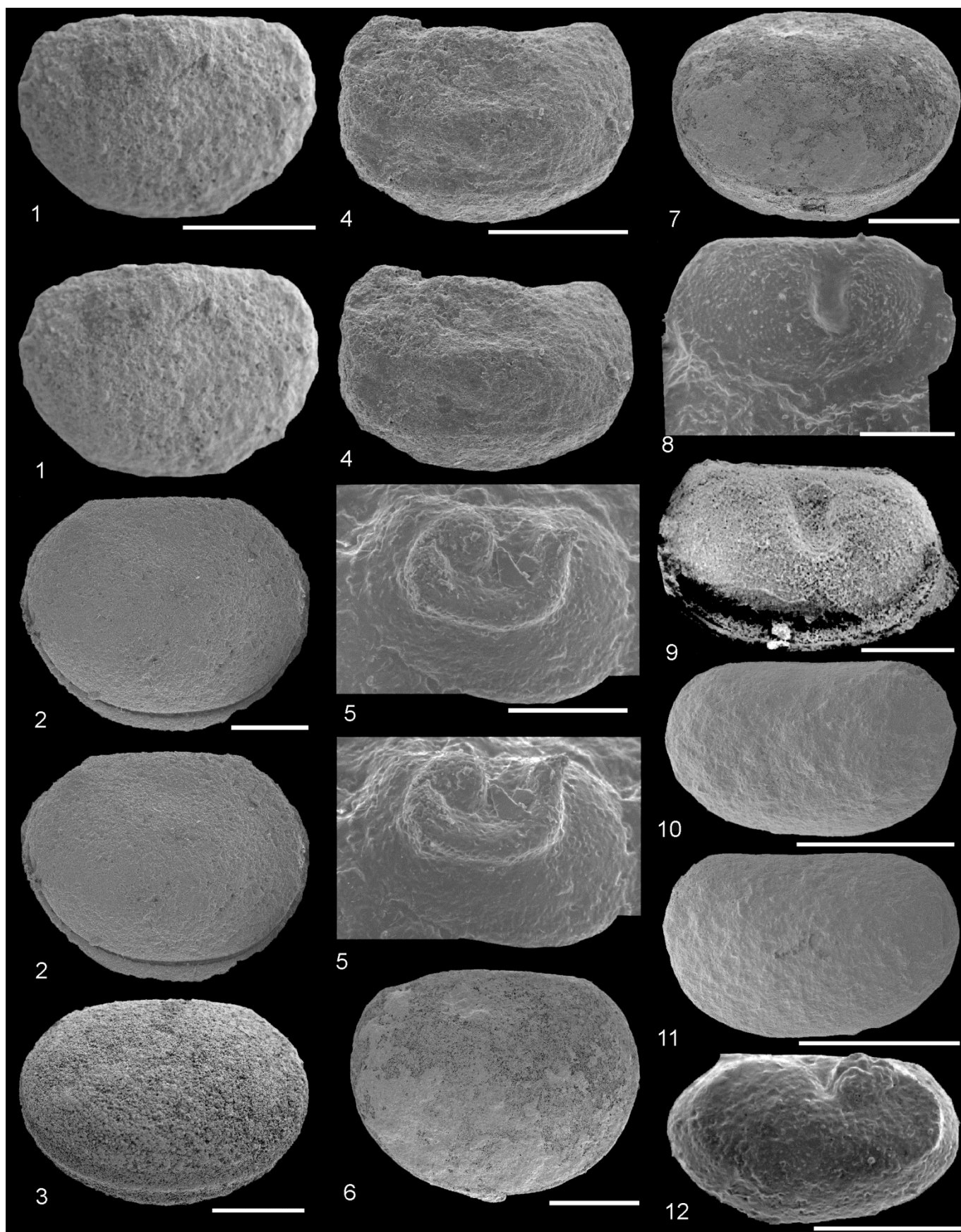


PLATE 4

***Aparchites* sp. 2**

Craighead Limestone Formation, *D. clingani* Biozone (*caudatus* Subzone, locality 6c).

- 1, 2 Carapace (BGS GSE15363). Left lateral view (stereo-pair); ventral view, scale bar 0.5 mm.

***Vannieria transversa* (Harris, 1957)**

Craighead Limestone Formation, *D. clingani* Biozone (*caudatus* Subzone, locality 6c).

- 3 Carapace (BGS GSE15356). Left lateral view (stereo-pair), scale bar 0.3 mm.  
4 Carapace (BGS GSE15341). Ventral view, scale bar 0.2 mm.  
5 Carapace (BGS 15357). Dorsal view, scale bar 0.2 mm.  
6 Carapace (BGS GSE15419). Left lateral view, scale bar 0.2 mm.  
8 Carapace (BGS GSE15420). Right lateral views, scale bar 0.2 mm.

Ardwell Farm Formation at Pinmerry, *C. bicornis* graptolite Biozone (locality 5).

- 7 Silicon rubber cast of left valve (GSE 15386). Lateral view (stereo-pair), scale bar 0.5 mm.

**cf. '*Schmidtella*' *minuta* Harris, 1957**

Craighead Limestone Formation, *D. clingani* Biozone (*caudatus* Subzone, locality 6c).

- 9-12 Carapace (BGS GSE15346). Right lateral, dorsal, right lateral (stereo-pair) and ventral views, scale bar 0.5 mm.

***Leperditella girvanensis* n. sp.**

Craighead Limestone Formation, *D. clingani* Biozone (*caudatus* Subzone, locality 6a).

- 13 Left valve (BGS 16E1964). Lateral view, scale bar 0.86 mm.  
14 Right valve (BGS 16E1963). Lateral view, scale bar 1 mm.

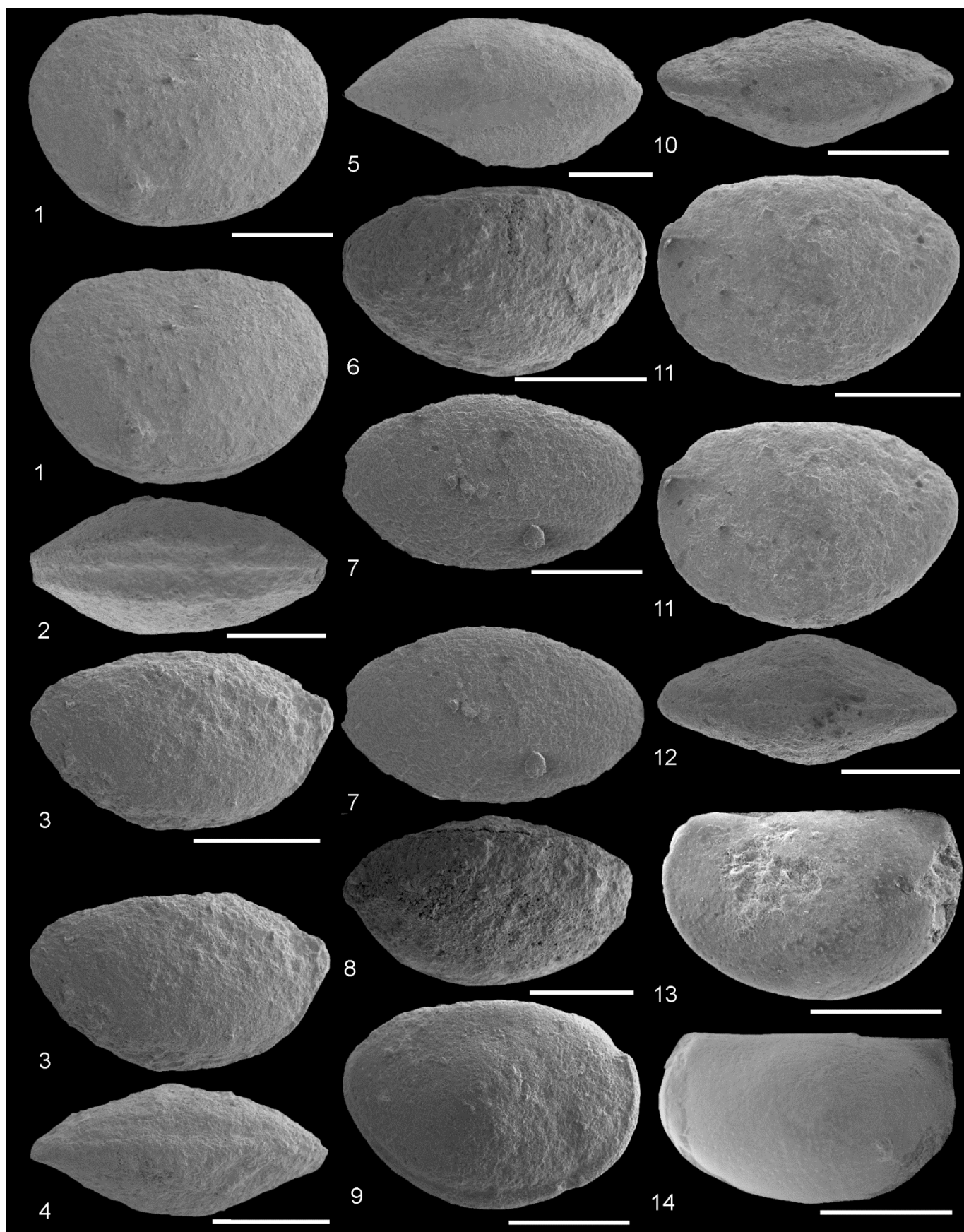


PLATE 5

***Leperditella girvanensis* n. sp.**

Craighead Limestone Formation, *D. clingani* Biozone (*caudatus* Subzone, locality 6a).

- 1 Holotype left valve (BGS 16E1959). Lateral view (stereo-pair), scale bar 0.75 mm.
- 2 Right valve (BGS 16E1965). Lateral view, scale bar 0.75 mm.

***Steusloffina cf. ulrichi* (Steusloff, 1895)**

Craighead Limestone Formation, *D. clingani* Biozone (*caudatus* Subzone, locality 6c).

- 3-5 Carapace (BGS GSE15358). Left lateral view (stereo-pair); right lateral view; ventral view, scale bar 0.2 mm.

***Steusloffina cuneata* (Steusloff, 1895)**

Craighead Limestone Formation, *D. clingani* Biozone (*caudatus* Subzone, locality 6c).

- 6 Carapace (BGS GSE15352). Right lateral view, scale bar 0.5 mm.
- 7 Carapace (BGS GSE15354). Left lateral view (stereo-pair), scale bar 0.5 mm.
- 9 Carapace (BGS GSE15353). Dorsal view, scale bar 0.5 mm.
- 10 Carapace (BGS GSE15351). Ventral view, scale bar 0.5 mm.

***Balticella deckeri* (Harris, 1931)**

Balclatchie Formation at Penwhapple Burn, *C. bicornis* graptolite Biozone (Locality 1).

- 11 Silicon rubber cast of external mould of left valve (GLAHM 18499b). Lateral view (stereo-pair), scale bar 0.75 mm.

***Balticella* n. sp.**

Craighead Limestone Formation, *D. clingani* Biozone (*caudatus* Subzone, locality 6c).

- 8, 12 Carapace (BGS MPA49672). Right lateral (stereo-pair) view; left lateral (stereo-pair) view, scale bar 0.5 mm.

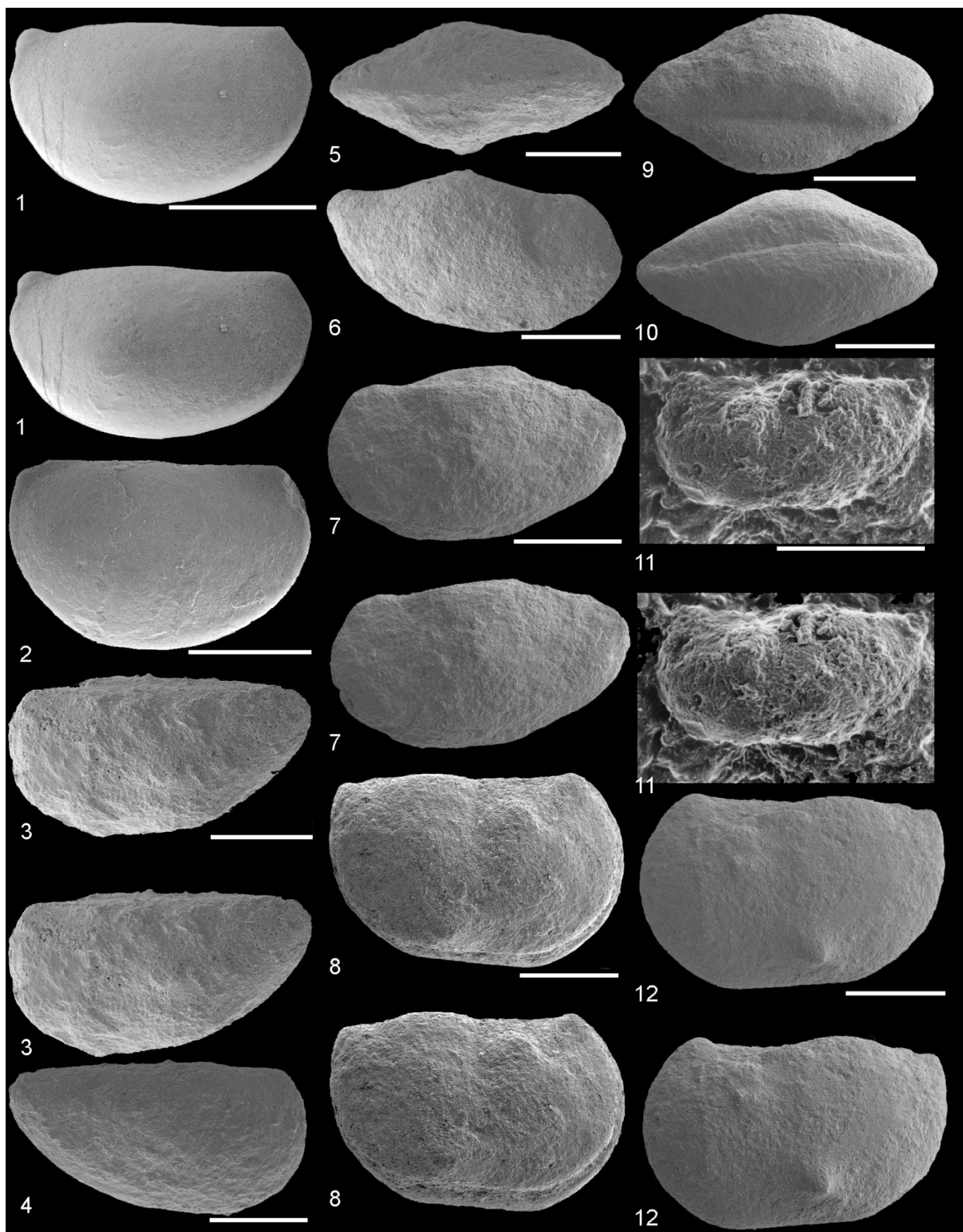


PLATE 6

***Monoceratella teres* Teichert, 1937**

Craighead Limestone Formation, *D. clingani* Biozone (*caudatus* Subzone, locality 6a).

- 1 Left valve (GLAHM A1379). Lateral view (stereo-pair), scale bar 0.75 mm.

**?*Medianella longa* (Stumbur, 1956)**

Craighead Limestone Formation, *D. clingani* Biozone (*caudatus* Subzone, locality 6c).

- 2-4 Carapace (GSE15359). Left lateral view (stereo-pair); ventral view; right lateral view, scale bar 0.5 mm.

***Krausella variata* Kraft, 1962**

Ardwell Farm Formation at Pinmerry, *C. bicornis* graptolite Biozone (locality 5).

- 5 Silicon rubber cast of external mould of right valve (BGS GSE 15385) Lateral view (stereo-pair), scale bar 0.5 mm.  
6 Silicon rubber cast of external mould of right valve (GLAHM 114084). Lateral view, scale bar 0.5 mm.  
7 Silicon rubber cast of external mould of right valve (GLAHM 114082). Lateral view, scale bar 0.5 mm.

***Longiscula* sp.**

Craighead Limestone Formation, *D. clingani* Biozone (*caudatus* Subzone, locality 6c).

- 8, 9 Carapace (BGS GSE15360). Left lateral (stereo-pair) and right lateral views, scale bar 0.2 mm.

***Longiscula?* sp.**

Craighead Limestone Formation, *D. clingani* Biozone (*caudatus* Subzone, locality 6c).

- 10-11, 13 Carapace (BGS GSE15365). Right lateral (stereo-pair) view; dorsal view; left lateral view, scale bar 0.2 mm.

***Krausella arcuata* Ulrich, 1894**

Craighead Limestone Formation, *D. clingani* Biozone (*caudatus* Subzone, locality 6c).

- 12 Carapace (BGS GSE15364). Right lateral view (stereo-pair), scale bar 0.5 mm.

***Krausella* n. sp.**

Starfish Beds, South Threave Formation, *anceps* graptolite Biozone (*pacificus* Subzone, locality 13).

- 14 Carapace (NHM UK PM In20041). Right lateral view, scale bar 0.79 mm.

***Podocope* sp. 1**

Craighead Limestone Formation, *D. clingani* Biozone (*caudatus* Subzone, locality 6c).

- 15 Left valve (BGS 16E1957). Lateral view, scale bar 0.75 mm.

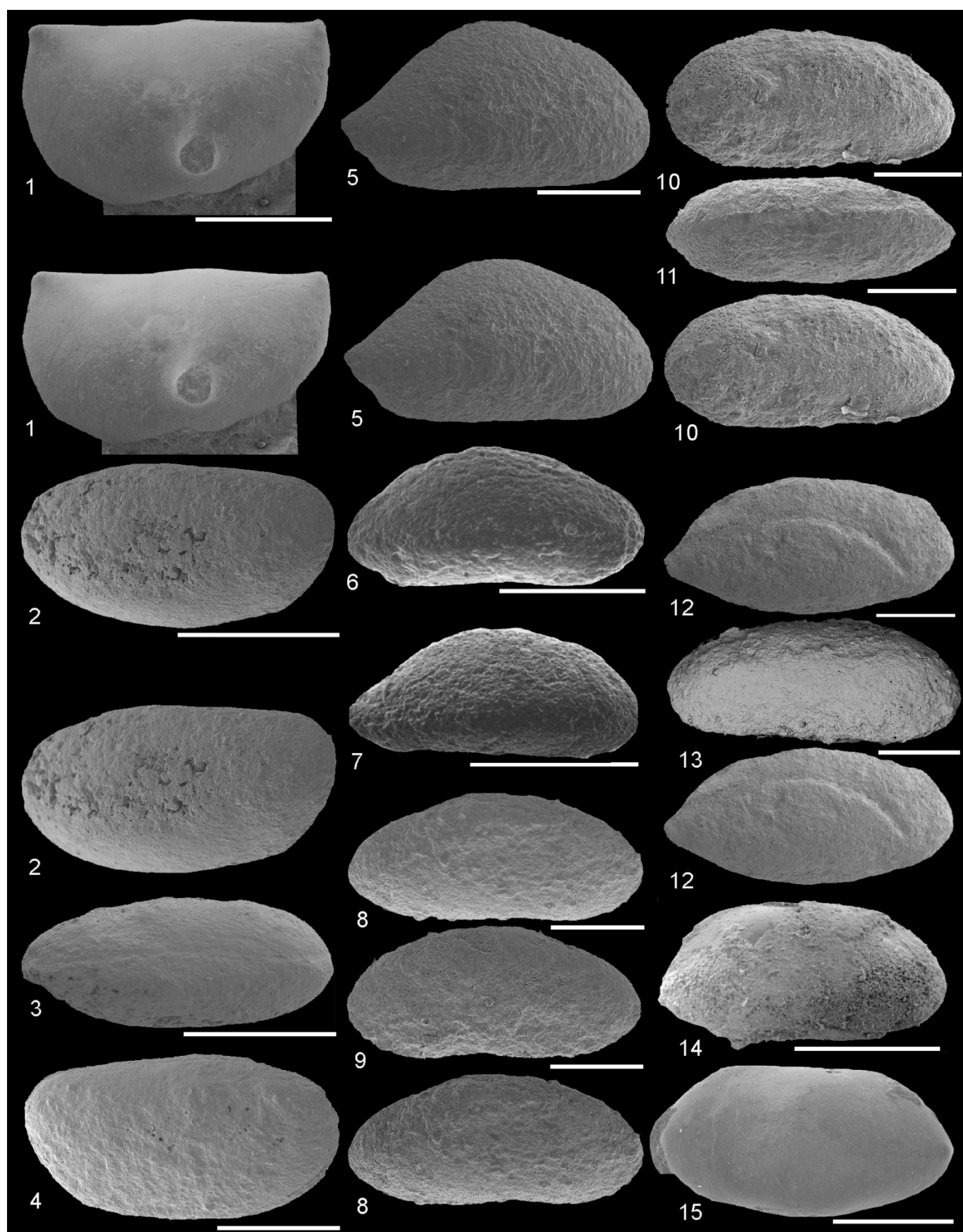


PLATE 7

**‘*Primitia*’ *mundula* var. *fimbriata* Jones, 1893**

Mill Formation, *complanatus* graptolite Biozone (locality 11).

- 1 Right valve (NHM UK PM In 20016). Lateral view, scale bar 0.5 mm.

**‘*Aparchites*’ *subovatus* Jones, 1893**

Mill Formation, *complanatus* graptolite Biozone (locality 11).

- 2 Right valve (NHM UK PM In 20019). Lateral view, scale bar 0.5 mm.  
3 Rock slab (NHM UK PM In 20030) with specimen of ‘*Sulcuna*’ *preacurrens* Jones, 1893. scale bar 0.5 mm.

**‘*Ulrichia*’ *girvanensis* Jones, 1893**

Mill Formation, *complanatus* graptolite Biozone (locality 11).

- 4 Right valve (NHM UK PM In 20021). Lateral view, scale bar 0.5 mm.  
8 Rock slab (NHM UK PM In 20021) with specimen of ‘*Ulrichia*’ *girvanensis* Jones, 1893. scale bar 0.5 mm.

**‘*Primitia*’ *girvanensis* Jones, 1893**

Mill Formation, *complanatus* graptolite Biozone (locality 11).

- 5 Right valve (NHM UK PM In 20024). Lateral view, scale bar 0.357 mm.

**‘*Primitia*’ *mundula* var. *kloedeniana* Jones, 1893**

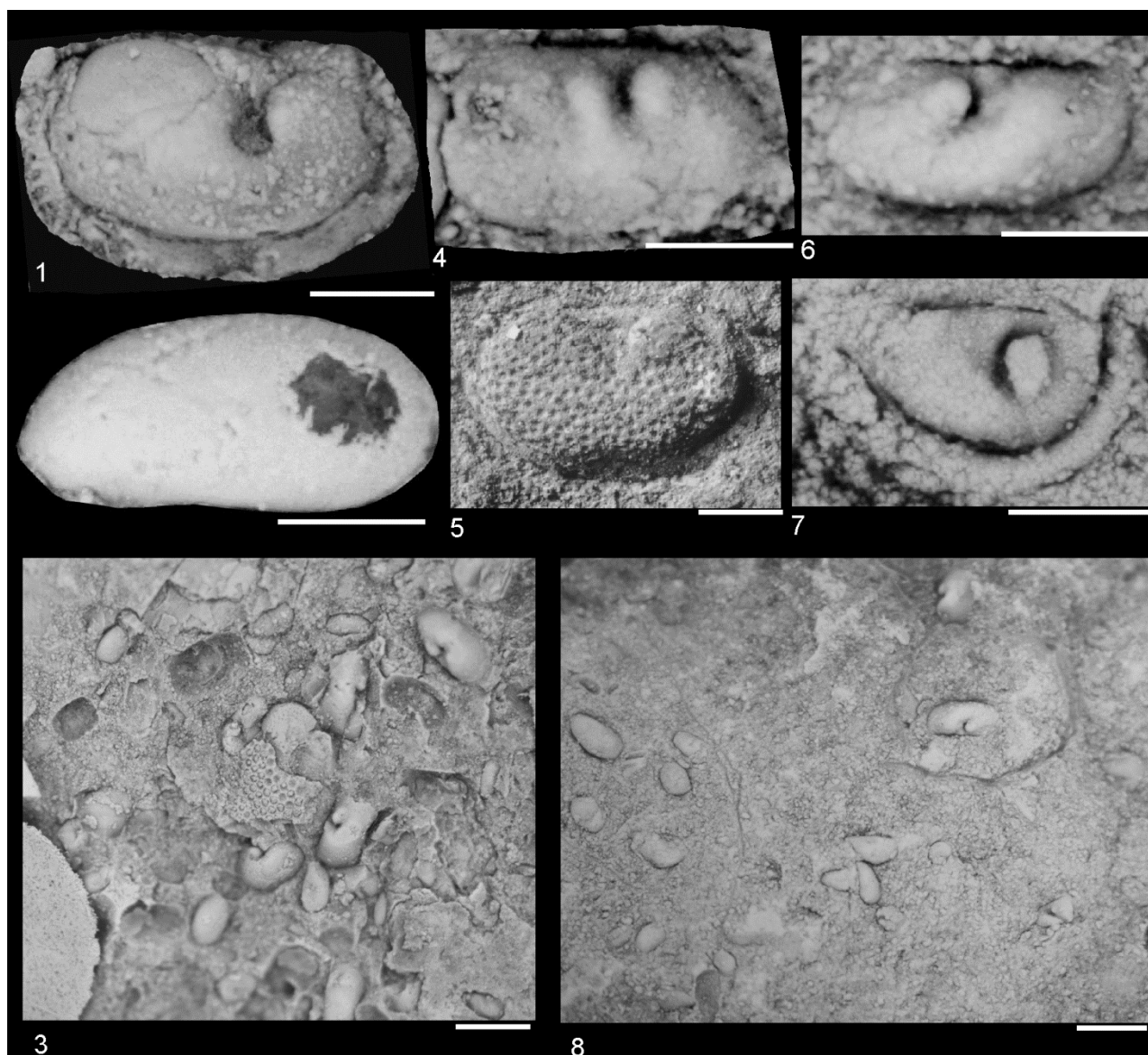
Mill Formation, *complanatus* graptolite Biozone (locality 11).

- 6 Left valve (NHM UK PM In 20019). Lateral view, scale bar 0.5 mm.

**‘*Beyrichia*’ *kloedeni* Jones, 1893**

Mill Formation, *complanatus* graptolite Biozone (locality 11).

- 7 Right valve (NHM UK PM In 20010). Lateral view, scale bar 0.5 mm.



## Chapter 3: Late Ordovician (Sandbian) ostracods from the Ardwell Farm Formation, southwest Scotland

### Abstract

The lower part of the Late Ordovician Ardwell Farm Formation of the Girvan district in southwest Scotland yields a low-diversity ostracod fauna comprising six species. Many of these ostracods are biostratigraphically short-ranging North American taxa limited to an interval equivalent to the *gracilis* and *bicornis* graptolite biozones. These species include *Hippula ventrospinosa* and *Baltonotella parsispinosa* that permit inter-regional correlation with the Sandbian strata of the USA and Arctic Canada. This chain of correlation is also confirmed by chitinozoans, such as *Belonechitina hirsuta*, that occur with the ostracods in the Ardwell Farm Formation. Although allochthonous, mostly represented by disarticulated valves and transported by turbidity currents into a deep water clastic-rich basin, the ostracod fauna of the Ardwell Farm Formation resembles other Ordovician deep-water ostracod biotopes, characterised by podcope ostracods and low species-diversity. Alternatively the ostracods might simply have been transported from a carbonate ramp setting.

### Introduction

The Lower Palaeozoic of the Girvan district, southwest Scotland preserves a thick succession of Ordovician marine shelf clastics and subordinate shallow marine carbonates (Fig. 1). Fossils include graptolites and deep water shelly assemblages in the Ordovician mudstones, which alternate with sandstones, conglomerates and carbonates that bear rich shallow marine shelly assemblages. The juxtaposition of a

range of different lithologies and environmental settings from shallow to deep shelf provides excellent opportunities for precise biostratigraphical correlation (Harper & Stewart 2008).

The Ordovician fauna and flora of Girvan have been long studied for inter-regional biostratigraphical correlation and also serve as a means of establishing the biogeographical context of southwest Scotland during the Early Palaeozoic, prior to the closure of the Iapetus Ocean (Williams 1962; Tripp 1980a, b; Williams *et al.* 2001a; Harper & Stewart 2008; Mohibullah *et al.* 2010). Ostracods form a component of the Girvan Ordovician faunas and are present mainly in shallow marine, but also in deeper marine deposits as transported allochthonous fauna. They have been reported from the Ordovician succession of Girvan since the middle of the nineteenth century (M'Coy 1851). The earlier published records by M'Coy (1851), Jones (1879, 1893), Peach & Horne (1899), Anderson & Pringle (1946) and Siveter (1978) were essentially reconnaissance reports and gave preliminary taxonomic assessments. More recent studies have identified extensive ostracod faunas and have attempted to define their biostratigraphical, palaeogeographical and palaeoecological potential (e.g. Floyd *et al.* 1999; Williams & Floyd 2000; Williams *et al.* 2001a; Siveter 2009) culminating in documentation of the extensive fauna of the Craighead Limestone Formation (Mohibullah *et al.* 2010; Chapter 4). However, the generally poor preservation of the Ordovician ostracod material, mostly recovered as 'crack-out' on limestone slabs and external moulds in mudstones, still precludes precise analysis of much of the Girvan fauna, as in the case of ostracods from the Whitehouse Subgroup of the Girvan foreshore (see Williams *et al.* 2001a).

Here we employ improved methods of microfossil recovery and laboratory techniques for casting material (e.g. Siveter 1984a; Purnell 2003) that enable a detailed analysis of some of the most intractable material. This is important because the ostracods of the Ordovician succession of Girvan provide an additional means of inter-regional correlation with rock units in North America, with which they have a number of species in common (e.g. Williams *et al.* 2001a). The Late Ordovician strata of the Girvan district also yield stratigraphically important ostracod species in common with Late Ordovician faunas from northern England, Wales and the Baltic region (Floyd *et al.* 1999; Williams *et al.* 2000, 2001b). In addition, the ostracods provide stratigraphical ties with trilobites, graptolites, conodonts, brachiopods (e.g. Tripp 1980a, b; Williams & Floyd 2000; Mohibullah *et al.* 2010) and chitinozoans (this chapter) that enable more precise inter-regional correlation.

In this chapter I document the ostracod fauna of the lower part of the Ardwell Farm Formation (Ingham 2000) that forms part of the main Girvan succession and crops out from the Girvan foreshore inland along the Stinchar Valley and also in the Craighead Inlier (Ingham 1992a; Fig. 1). Existing biostratigraphical data (e.g. Williams 1962; Tripp 1980 a, b; Harper & Stewart 2008) indicate that the Ardwell Farm Formation is of Late Ordovician (Sandbian and early Katian) age. Ostracods in the lower Ardwell Farm Formation were first noted in the pilot study of Williams *et al.* (2001a). The ostracod fauna is essentially preserved as decalcified moulds that, nonetheless, preserve details of ornament and lobation. Some of the more thick-shelled ostracods are preserved as carbonate carapaces. This chapter aims to: 1) establish the taxonomic composition and thus the biogeographical affinity of the

ostracod fauna; 2) assess the sedimentological setting of the fauna and reconstruct the primary palaeo-environment; and 3) determine the biostratigraphical significance of the fauna, particularly its correlative value with the Ordovician of North America. We show that even the apparently poorly preserved ostracod material of the lower Ardwell Farm Formation can nevertheless yield important biostratigraphical data.

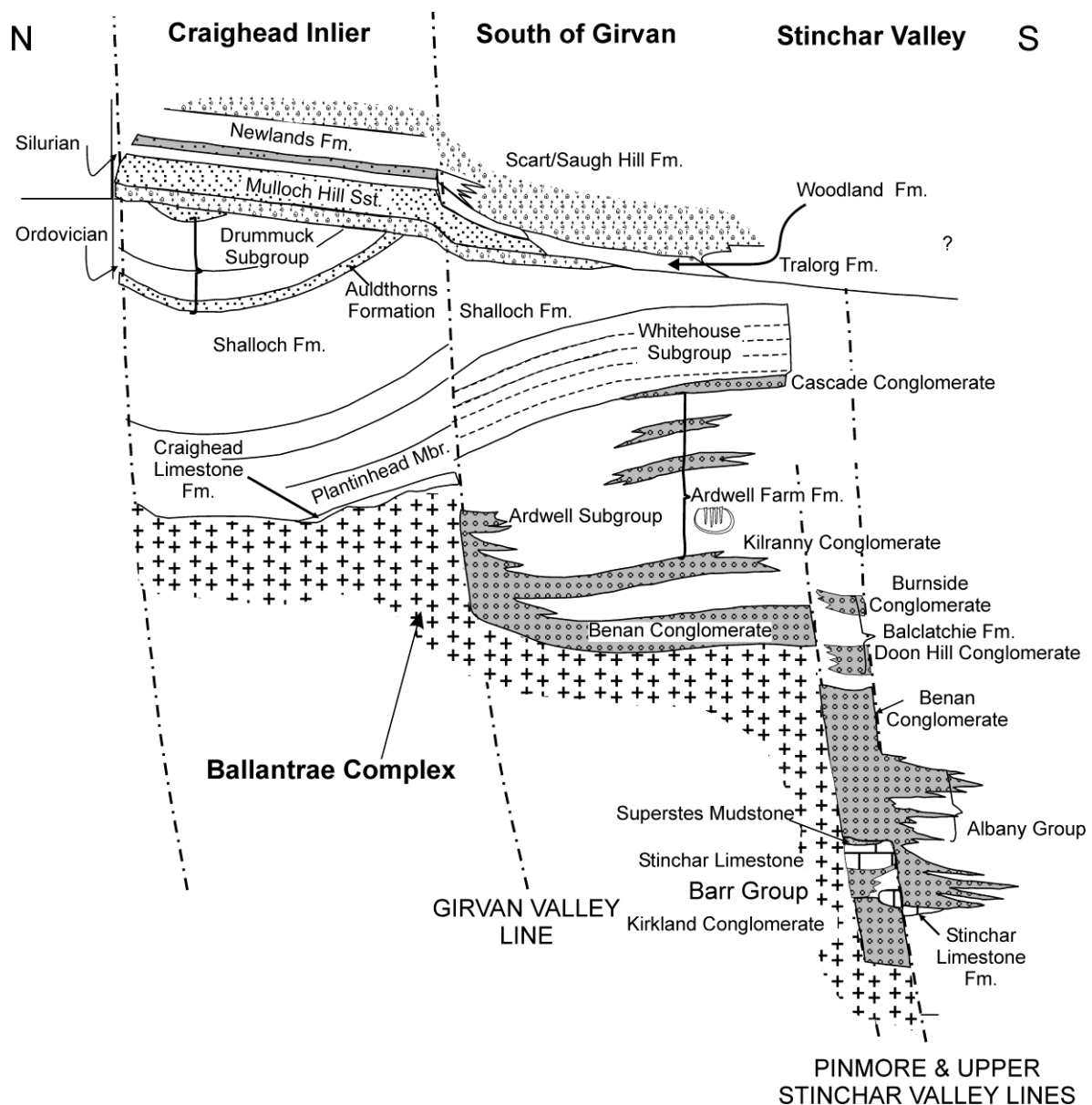


Figure 1. Schematic cross-section showing the lithostratigraphical and structural setting of the Ordovician and Lower Silurian strata of the Girvan district across major faults. Ostracod icon marks the level from which ostracods and chitinozoans were recovered (modified from Ingham 1992a; and Harper & Stewart 2008).

## Geological setting

The Ardwell Subgroup of the Girvan district is part of the Lower Palaeozoic succession of the Midland Valley Terrane of Scotland (Rushton *et al.* 1999), which has a complex lithostratigraphy. Across the major faults of the region there are marked changes in the timing of deposition and thicknesses of the lithofacies comprising the Ardwell Subgroup (Fig. 1). North of the Stinchar Valley Fault, in the Craighead Inlier, the Ardwell Subgroup is dominated by carbonates of the Craighead Limestone Formation (Mohibullah *et al.* 2010), which interdigitate with marine mudstones that contain graptolites indicative of the *clingani* Biozone and thus indicate a late (early Katian) commencement of deposition in this sub-area. The Craighead Limestone Formation is succeeded by mudrocks of the Plantinhead Member (Fig. 1) which represent the more typical motif of clastic Ardwell Subgroup sedimentary rocks that accumulated to the south of the Stinchar Valley Fault from early Sandbian times.

South of the Stinchar Valley Fault the Late Ordovician succession is entirely clastic (Fig. 1). In the Girvan foreshore the Ardwell Subgroup consists of a thick succession of mudstones, siltstones and fine sandstones. The Ardwell Subgroup also underlies a wide area of ground inland along the Stinchar valley to the east (Rushton *et al.* 1999). The Ardwell Subgroup yields trilobites (Tripp 1980a, b), graptolites (Ingham 1992a), brachiopods (Williams 1962; Harper & Stewart 2008) and chitinozoans (Vandenbroucke *et al.* 2003) that indicate that its age south of the Stinchar Valley Fault spans parts of the Sandbian and Katian of the Late Ordovician. Much of the shelly fauna of the Ardwell Farm Formation is transported, representing deep water

assemblages (Harper & Stewart 2008). The intermittent presence of graptolites in the Ardwell Subgroup of both the Girvan foreshore and in the Craighead Inlier also suggests an open marine setting (Ingham 1992a).

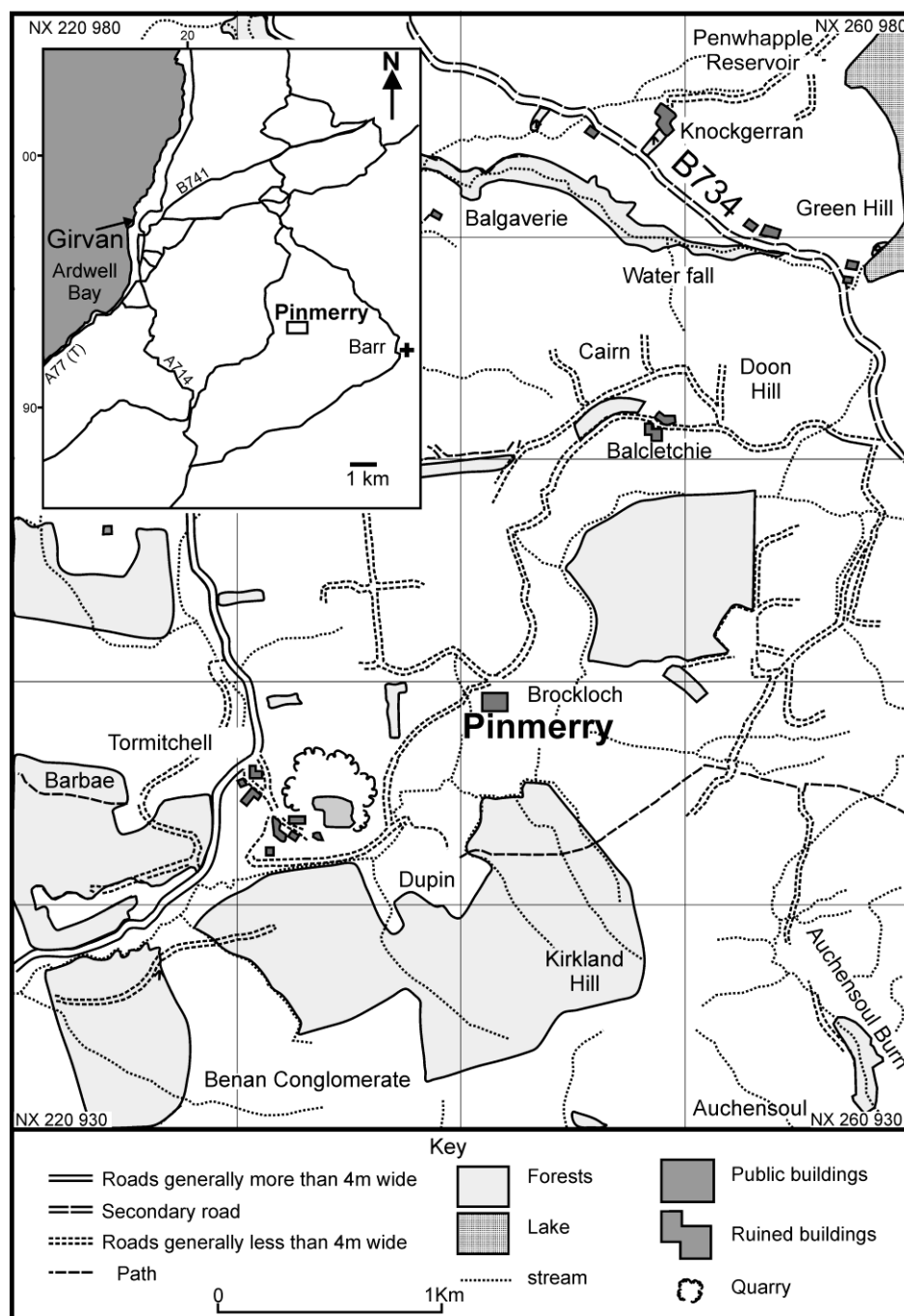


Figure 2. Locality map of Pinmerry Farm (British National Grid Reference NX 241 949), Stinchar Valley, southeast of Girvan.

## Materials and Methods

The ostracod fauna is from a ca 1 m thick interval within a succession of silty mudstones in the lower part of the Ardwell Farm Formation at the now derelict Pinmerry Farm (figs 2, 3). Four visits for sampling yielded a low-diversity ostracod assemblage (Fig. 4). The ostracods are associated with a trilobite fauna described by Tripp (1980b) that include species of *Arthrorhachis*, *Decoroproetus*, *Remopleurides*, *Calyptaulax* and *Harpidella*. Ostracods have not been identified at other localities in the vicinity despite an extensive search of exposures of the Ardwell Farm Formation in nearby track sections. The ostracods are preserved as decalcified moulds with only rare specimens as calcitic crack-out material. External moulds have been cast using silicon rubber compound MM913 (see Purnell 2003). The silicon rubber casts were then mounted on aluminium stubs and coated with the gold/aluminium alloy 'Emitech K500X'. They were examined using a Hitachi S-3600N scanning electron microscope at Leicester University.

We also examined the Ardwell Farm Formation at Pinmerry for chitinozoans, which were recovered from a single sample using standard palynological techniques (see Paris 1981; Fig. 5) at the University of Lille. The resulting organic residue was sieved at 53 µm and handpicked using a palynological microscope set at a magnification of ca 30x. The chitinozoans are rather poorly preserved. They were mounted on SEM stubs, gold-coated and studied with a FEI Quanta 200 SEM at Lille.



Figure 3. Location of strata of the lower part of the Ardwell Farm Formation sampled for ostracods on the eastern (A) and western (B) bank of the stream at Pinmerry Farm. As far as can be discerned, the ostracods occur at only one stratigraphical level striking across the stream bed.

### Biostratigraphical significance of the microfauna

The low-diversity ostracod assemblage comprises six species previously described from, for example, the Ordovician of Oklahoma (Harris 1957; Levinson 1961) and Virginia (Kraft 1962; Fig. 6): *Krausella variata* Kraft, 1962, *Baltonotella parsispinosa* (Kraft, 1962), *Hippula ventrospinosa* (Kraft, 1962), *Eoaquapulex* cf. *socialis* (Levinson, 1961), *Vannieria transversa* (Harris, 1957) and *Hallatia* cf. *labiosa* (Ulrich, 1894) (Fig. 4). The chitinozoan assemblage (Fig. 5) contains rare *Belonechitina hirsuta* (Laufeld, 1967), *Belonechitina?* *robusta* (Eisenack, 1959) and a few hercochitinids, amongst a majority of indeterminate conochitinids. Scolecodonts are also present. This assemblage corresponds relatively well to those described from

the Ardwell Farm Formation on the Girvan foreshore and around Ardwell Farm (Vandenbroucke *et al.* 2003), which contained, amongst others, *Belonechitina hirsuta*, *Belonechitina robusta*, *Hercochitina spinetum* Melchin & Legault, 1985 and *Spinachitina bulmani* Jansonius, 1964.

Previous biostratigraphical assessment indicates that the Ardwell Farm Formation spans part of the Sandbian to early Katian interval, based on brachiopods, trilobites, graptolites and chitinozoans (Williams 1962; Tripp 1980a, b; Ingham 1992a; Harper & Stewart 2008; Vandenbroucke *et al.* 2003). The uppermost part of the Ardwell Farm Formation on the Girvan foreshore near Ardwell Farm contains graptolites of the *clingani* Biozone (Ingham 1992a) that provide a strong biostratigraphical tie with the succession of the Craighead Inlier (where graptolites of this age have been recovered from the Sericoidea Mudstone Member; Tripp 1980a). The lower part of the Ardwell Farm Formation is of Sandbian age based on trilobites and brachiopods that bear similarities with the Edinburg Formation of Virginia (Williams 1962; Tripp 1980b; Harper & Stewart 2008). The new data herein from Pinmerly confirms correlation with the Edinburg Formation (Fig. 6). It also provides evidence for wider correlation to Oklahoma and Arctic Canada. Although there is no associated graptolite data at the Pinmerly locality, the chain of correlation and our comparison with new chitinozoan data, suggests a biostratigraphical age for the ostracod fauna equivalent either to the *gracilis* or *bicornis* graptolite Biozone (for redefinition of Scottish Late Ordovician graptolite biozones see Williams *et al.* 2004 and Zalasiewicz *et al.* 2009).

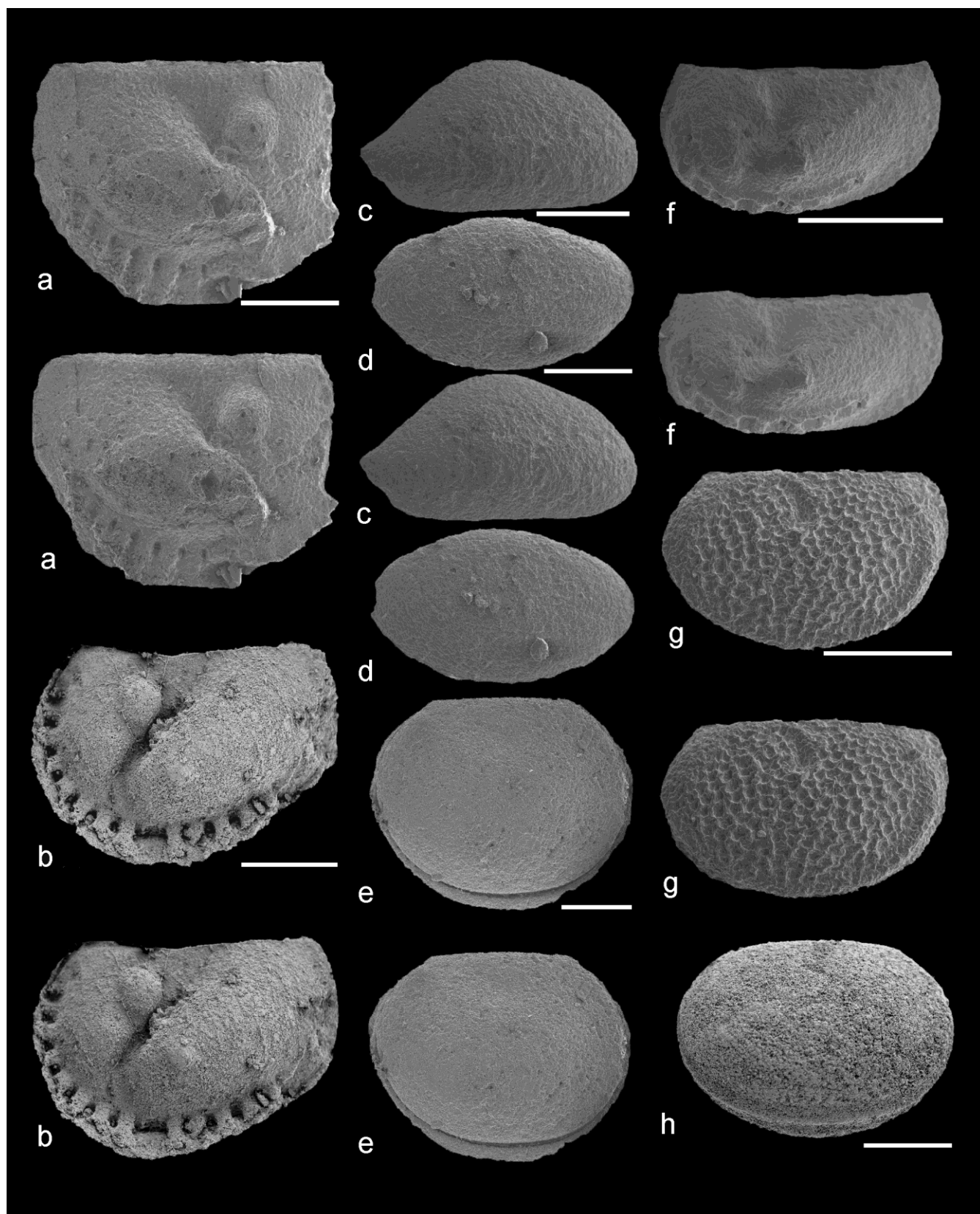


Figure 4. Ostracods from the lower part of the Ardwell Farm Formation at Pinmerry, Girvan. Specimens are deposited in the collections of the British Geological Survey, Keyworth, Nottingham: a, c-g are silicon rubber casts; b and h are calcitic fossil. (a, b) *Hippula ventrospinosa* (Kraft, 1962), (a) GSE 15383 heteromorph right valve, lateral view (stereo-pair) and (b) GSE 15384 heteromorph left valve, lateral view (stereo-pair) respectively. (c) GSE 15385 *Krausella variata* Kraft, 1962, right valve, lateral view (stereo-pair). (d) GSE 15386 *Vannieria transversa* (Harris, 1957), left valve, lateral view (stereo-pair). (e) GSE 15387 *Baltonotella parsispinosa* (Kraft, 1962), left valve of carapace, lateral view (stereo-pair). (f) GSE 15388 *Hippula ventrospinosa* (Kraft, 1962), juvenile, left valve, lateral view (stereo-pair). (g) GSE 15389 *Hallatia* cf. *labiosa* (Ulrich, 1894), left valve, lateral view (stereo-pair). (h) GSE 15390 *Baltonotella parsispinosa* (Kraft, 1962), carapace, oblique lateral view. (a-f, h) Scale bar 0.5 mm; (g) Scale bar 0.3 mm.

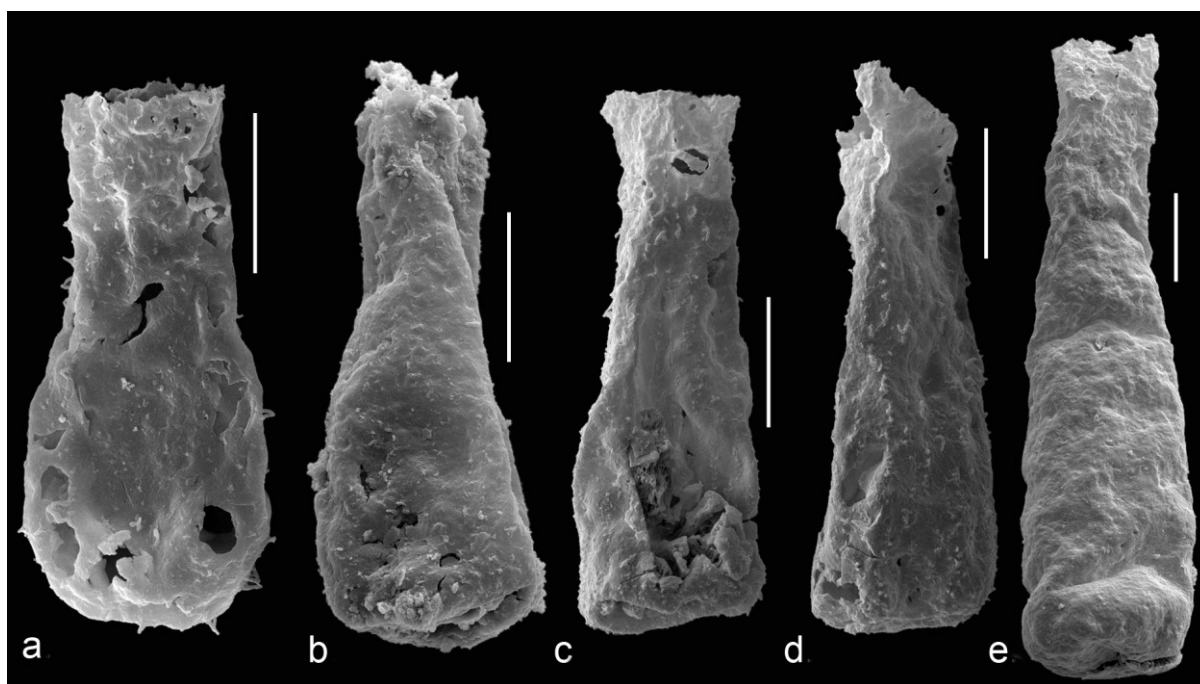


Figure 5. Chitinozoans from the lower part of the Ardwell Farm Formation at Pinmerry. (a) *Belonechitina hirsuta* (170 x 70). (b) *Belonechitina? robusta* (190 x 73). (c) *Hercochitina* sp. (210 x 70). (d) *Hercochitina* sp. (220 x 70). (e) *Conochitina* sp. (360 x 100). All measurements in  $\mu\text{m}$  (L x Dp). Abbreviations, following Paris (1981): L= total length, Dp= chamber diameter. (a-e) Scale bar 50  $\mu\text{m}$ . Chitinozoans kindly identified by Dr Thijs Vandenbroucke (University of Lille).

#### Ostracods

Most of the ostracod species that occur in the lower part of the Ardwell Farm Formation are biostratigraphically important and are short-ranging, representing typical Laurentian forms of Sandbian age. *Krausella variata*, *Baltonotella parsispinosa*, *Hallatia labiosa* and *Eoaquapulex* cf. *socialis* are variously recorded from the Lincolnshire and Edinburg formations of Virginia, while *Hippula ventrospinosa* occurs only in the lower part of the Edinburg Formation (Kraft 1962). Of these species, *Baltonotella parsispinosa* is the most widespread in Sandbian age rocks of North America, and in addition to Virginia, it occurs in the Bromide Formation of Oklahoma (Williams & Siveter 1996), the Decorah Formation of Minnesota (Swain *et al.* 1961), the Hatter and Benner formations of Pennsylvania (Swain 1957), the Lower Esbataottine Formation of the Mackenzie District, Canada (Copeland 1982), Silliman's Fossil Mount of the Franklin District, Canada (Copeland 1977a), and the Valcour Limestone and the Day Point and Crown Point formations of New York (Swain 1957). *Krausella variata*, other than in the Lincolnshire and Edinburg formations, also occurs in the Sandbian Glenwood and Platteville formations of Minnesota (Swain 1996), and the Day Point and the Crown Point formations of New York (Swain 1962). The ostracods of the lower part of the Ardwell Farm Formation also show strong affinities with those of the Bromide Formation of Oklahoma which include *Hallatia labiosa*, *Vannieria transversa* and *Eoaquapulex socialis*. *Hallatia labiosa* is also reported from the Sandbian Decorah Formation of Iowa, the Hull Formation of Ontario (Kay 1934, 1940; Swain 1996), the Crown Point Formation of New York (Swain 1957) and the Cummingsville and Prosser formations of Minnesota (Swain 1996).

System	International standard stages	British regional series and stages		North American regional stages	Scottish graptolite biozones (after Williams <i>et al.</i> 2004)	Conodont biozones	Lithostratigraphy		Arbuckle Mountains Oklahoma	Strasburg Virginia
							Girvan, Scotland			
Ordovician (pars)	Katian ( <i>pars</i> )	Ashgill	Pusgillian	Maysvillian	<i>linearis</i>	<i>superbus</i>	Whitehouse Subgroup ( <i>pars</i> )	Penwhapple Formation	Welling Fm	Martinsburg Fm
			Caradoc		Streffordian			Edenian	<i>clingani</i>	
		Cheneyan		Chatfieldian						
		Burrellian		Turinian	<i>bicornis</i>		Ardmillan Group ( <i>pars</i> )	Plantinhead Member		Bromide Fm
		Aurelucian	Chazyan	<i>gracilis</i>	Ardwell Subgroup			Craighead Limestone Fm	Oranda Fm	
	Sandbian					<i>tvaerensis</i>		Ardwell Farm Formation		Edinburg Fm
						<i>anserinus</i>		Balclatchie Formation		Lincolnshire Fm

Figure 6. Ordovician chronostratigraphy and lithostratigraphy for Girvan, Oklahoma and Virginia. The Sandbian parts of the Ardwell Farm Formation, Bromide Formation and Edinburg Formation are highlighted with light grey ornament (stratigraphy modified after Williams *et al.* 2001a, and Ross *et al.* 1982). Symbols: Fm-Formation; Mbr-Member; Crm-Corbin Ranch Member.

The Lincolnshire, Edinburg and Bromide formations are dated as Sandbian based on conodonts, graptolites, trilobites and brachiopods. The Lincolnshire Formation of Virginia yields trilobites, brachiopods and conodonts that suggest a Sandbian age equivalent to the *gracilis* graptolite Biozone (Cooper & Cooper 1946; Bergström 1971). The Edinburg Formation also yields conodonts and graptolites indicative of the *bicornis* Biozone (Cooper & Cooper 1946; Bergström 1971; see Williams *et al.* 2004, and Zalasiewicz *et al.* 2009 for the equivalent stratigraphic level in Scotland). The Bromide Formation is also considered to be of Sandbian age (Late Whiterockian to Early Mohawkian regional stages) based on the conodonts *Cahabagnathus sweeti*, *Eoplacognathus elongatus* and *Baltoniodus gerdae* recovered from its lower part, and considered equivalent to the *gracilis* graptolite Biozone (Sweet & Bergström 1976; Sweet 1983, 1984; Bauer 1994), while the graptolites

*Dicellograptus flexuosus* and *Amplexograptus maxwelli* from the uppermost beds of the Bromide Formation indicate a level equivalent to the *foliaceus* (= *multidens*) graptolite Biozone (Decker 1935, 1941; Finney 1986) which is also supported by conodont evidence (Sweet & Bergström 1976; Sweet 1983, 1984; Bauer 1994). By a chain of correlation, the ostracod assemblage of the lower part of the Ardwell Farm Formation therefore suggests a Sandbian *gracilis* or *bicornis* graptolite Biozone age, and this is confirmed by our assessment of chitinozoan data from the Pinmerry locality (see below), and this also confirms earlier correlations based on other elements of the fauna (see Ingham 2000, fig. 24).

#### Chitinozoans

Chitinozoans from the Girvan area have been the subject of a reconnaissance study by Vandenbroucke *et al.* (2003), and although their data are currently being revised and refined (work in progress, Thijs Vandenbroucke with Keith Ingham), correlation with these data will furnish finer biostratigraphical precision for the Pinmerry locality. Taxonomical problems remain with *Belonechitina hirsuta* (Vandenbroucke 2008a, pp. 75-76, Vandenbroucke *et al.* 2009a, pp. 228), as it is morphologically close to other small spiny chitinozoans such as *Angochitina communis*, which has stratigraphic potential in Avalonia (Vandenbroucke 2008b). These taxonomic problems cannot be addressed using the poorly preserved material from Pinmerry. Nevertheless, taken at face value, the presence of *B. hirsuta* in the lower part of the Ardwell Farm Formation at Pinmerry suggests a correlation with its occurrences in Canada (Achab 1984, 1989) and Baltoscandia (Nölvak & Grahn 1993). The North American levels with *B. hirsuta* are attributed to the *teretiusculus*, *gracilis* and

*foliaceus* graptolite biozones; those from Baltoscandia are restricted to strata within the *foliaceus* Biozone. This is consistent with reports of graptolites from the “*peltifer*” or “*wilsoni*” Biozone in the lower Ardwell Farm Formation (these biozones are now revised and are equivalent to the *bicornis* Biozone of Williams *et al.* 2004), and species from the *clingani* Biozone in its upper part (Ingham 1992a; Floyd 1999). Traditionally, species of the genus *Hercochitina* are perceived as either exclusively Laurentian (Achab 1988) or more abundant in that palaeocontinent (Achab *et al.* 1992), although they have now been documented from other areas such as Baltoscandia (Grahn & Nölvak 2010; Vandenbroucke 2004).

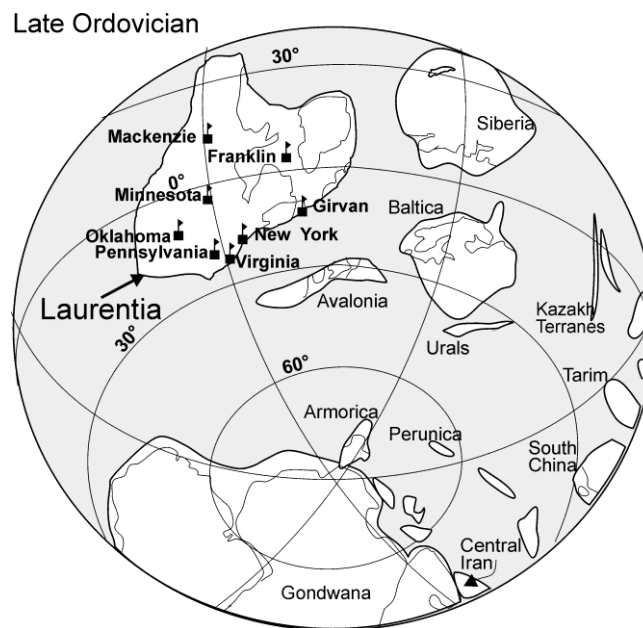


Figure 7. Position of major Sandbian (Late Ordovician) ostracod-bearing localities in Laurentia. The ‘flagpoles’ show the occurrence of *Baltonotella parsispinosa*. Map courtesy of Dr Leonid Popov of the National Museum of Wales, Cardiff.

### **Biogeographical patterns of a palaeo-equatorial ostracod assemblage**

The Ordovician faunas from Girvan have long been known to have strong North American affinities based on similarities of brachiopods, trilobites and ostracods (Williams 1962; Tripp 1980a, b; Floyd *et al.* 1999; Williams & Floyd 2000; Williams *et al.* 2001a; Harper & Stewart 2008; Mohibullah *et al.* 2010). These biogeographical affinities are supported by the ostracod assemblage described herein which shows species-level similarity with Laurentian faunas (see, Kraft 1962; Williams & Siveter 1996), but little affinity with contemporaneous faunas from Avalonia as exemplified by the successions in southern Britain (e.g. see Siveter 2009). This is consistent with palaeogeographical reconstructions for the Sandbian that place the Girvan district along the south-eastern margin of Laurentia and near the palaeoequator (Fig. 7), thus facilitating exchange of faunas with more northern (Arctic Canada) and southern (Oklahoma, Virginia) sub-tropical regions of Laurentia. All of the species documented from the Ardwell Farm Formation show a latitudinal range towards the southern subtropics, of about 15° and 20° palaeolatitude (Oklahoma and Virginia respectively), but none of these taxa are found in Baltica or within the temperate zone Avalonia microplate (Fig. 7). Of the palaeo-equatorial ostracod species found in the lower part of the Ardwell Farm Formation, *Baltonotella parsispinosa* shows the greatest latitudinal range extending from Virginia (palaeolatitude *ca* 15° South) to Arctic Canada (palaeolatitude *ca* 20° North) (Fig. 7).

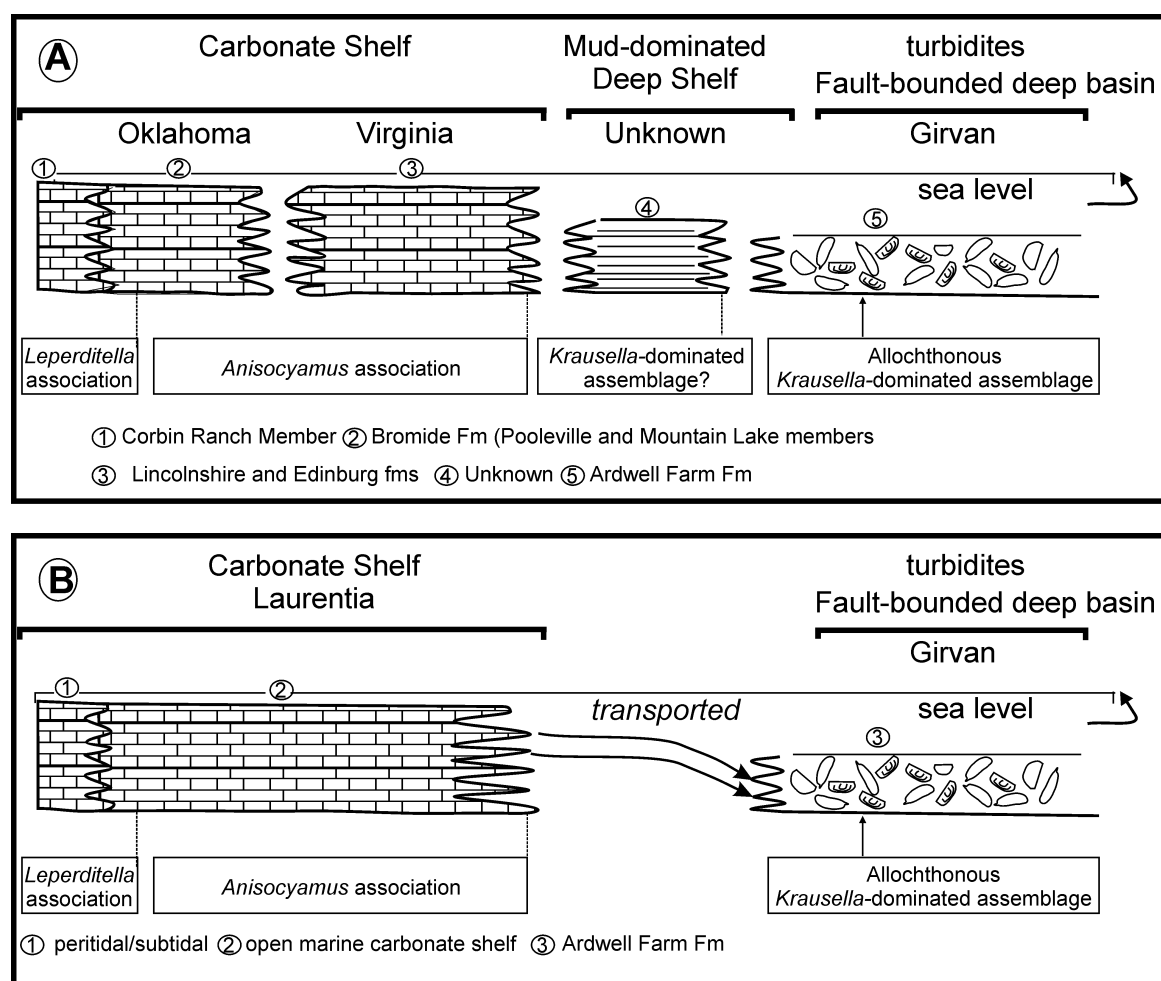


Fig 8. Palaeoenvironmental model for the possible origin of the allochthonous ostracod fauna in the lower part of the Ardwell Farm Formation at Pinmerry, Girvan. Localities for Virginia and Oklahoma as detailed in the text. In (A), 'unknown' refers to the possible original environmental locus of the Ardwell Farm Formation ostracods inferred as a deep-water assemblage. In (B), the ostracods are simply derived from a carbonate ramp by transport.

### Palaeoenvironmental significance of the ostracods: a deep-water biotope?

The Ardwell Farm Formation consists of mudstones, siltstones and sandstones representing a deep-water turbidite lithofacies (Williams 1962; Ingham 1992a). A deep-water allochthonous brachiopod fauna is recorded from the Ardwell Farm Formation on the Girvan foreshore (Harper & Stewart 2008) and the pelagic graptolite fauna also suggests a deep-water environment (Ingham 1992a; Floyd

1999). Ostracods from the lower part of the Ardwell Farm Formation at Pinmerrie also represent an allochthonous fauna that was probably transported by a turbidity current, and they are associated with trilobites thought to have a similar taphonomy (Tripp 1980b). The ostracod and the associated trilobite faunas from the lower Ardwell Farm Formation are largely represented by disarticulated valves (Tripp 1980 a or b) which indicate their transport from shelf to deeper water in a depositional environment interpreted as unstable slope (Ingham 1978; Harper, 1982; 2001).

The original environment of the ostracod fauna cannot be inferred directly from the Ardwell Farm Formation at Pinmerrie, but some reasonable inferences can be made based on the occurrence of the ostracods elsewhere. The low-diversity ostracod assemblage includes the palaeocopes *Hippula ventrospinosa*, *Hallatia* cf. *labiosa*, *Eoaquapulex* cf. *socialis*, the leiocope *Baltonotella parsispinosa* and a podocope *Krausella variata*, the last of these representing the most common element of the fauna (Fig. 8). This low-diversity *Krausella*-dominated assemblage contains species common to the carbonate ramp settings of the Bromide Formation of Oklahoma and the Edinburg Formation of Virginia, both of which yield high-diversity ostracod assemblages of several tens of species (Kraft 1962; Williams & Siveter 1996). *Vannieria transversa*, *Eoaquapulex socialis*, *Baltonotella parsispinosa* and *Hallatia labiosa* are present in the open marine high-diversity *Anisocyamus* Association of the Bromide Formation of Oklahoma (Williams & Siveter 1996; see also Fig. 8). *Krausella variata*, *Baltonotella parsispinosa*, *Hallatia labiosa* and *Hippula ventrospinosa* are present in the high-diversity ostracod assemblage of the Edinburg Formation which also represents a carbonate ramp (Kraft 1962; Carter *et al.* 1988).

The low diversity of the *Krausella*-dominated ostracod assemblage of the Ardwell Farm Formation suggests a possible derivation from an outer shelf, low-diversity ostracod assemblage that has been transported. Other Early Palaeozoic ostracod faunas from outer shelf settings are also of low diversity (see Copeland 1982; Siveter 1984b; Williams *et al.* 2003), and similar diversity patterns are also noted in latest Cenozoic and modern benthic ostracods from equatorial and tropical seas (e.g. Coimbra *et al.* 1999; Ozawa & Kamiya 2005; see Fig. 8). Copeland (1982) identified ostracod bathymetric assemblages for the Late Ordovician Lower Esbataottine Formation of Arctic Canada, which he compared with trilobite biofacies. His open shelf fauna is high-diversity (tens of species), like that of the Bromide and Edinburg formations, but his deep marine assemblage was adapted to a distal shelf edge or upper slope environment, and is low-diversity. It also contains *Baltonotella parsispinosa* and species of *Eoaquapulex*, *Vannieria* and *Krausella*.

Alternatively, the *Krausella*-dominated ostracod assemblage may have been transported from a carbonate ramp setting such as that of the Bromide or Edinburg formations, where diversity at any single horizon typically ranges from one to thirty species (Harris 1957; Kraft 1962; Williams & Siveter 1996). Lower diversity assemblages in this range are thus comparable to the six species recorded from the Ardwell Farm Formation at Pinmerry (see Fig. 8).

## Conclusions

Ostracods recovered from the Ardwell Farm Formation of the Girvan district reveal important new biostratigraphical data for correlating the Ordovician successions of Scotland and North America.

- The ostracod fauna comprises six species, most of which are identified as taxa from the Sandbian strata of North America.
- These provide a biostratigraphical tie, in conjunction with associated chitinozoans, with the *gracilis* or *bicornis* graptolite Biozone and, for example, allow correlation with the Bromide and Edinburg formations of Oklahoma and Virginia respectively.
- They form part of a widespread palaeo-equatorial/tropical assemblage that was typical of Laurentian carbonate-dominated horizons from Oklahoma to Arctic Canada.
- The ostracods may represent a deep-water biotope or a low-diversity assemblage from an adjacent carbonate ramp, and have been transported.

## **Chapter 4: Ostracods from Upper Ordovician (Katian) carbonate lithofacies of the Craighead Limestone Formation, southwest Scotland**

### **Abstract**

The Ordovician Craighead Limestone Formation of southwest Scotland was formed on a carbonate platform on the eastern tropical margin of the Laurentia palaeocontinent during the early Katian (c. 456 Ma). It yields the most diverse and well-preserved ostracod fauna yet recovered from the Scottish Ordovician succession, with some 25 species divisible into two distinct marine biotopes comprising shallow lagoonal and deeper platform margin settings respectively. The ostracods show strong biogeographical links at species-level with Sandbian and early Katian faunas of North America, including *Krausella arcuata*, *Steusloffina cuneata*, *Monoceratella teres* and species of *Levisulculus* and *Platybolbina*. However, many of the ostracod genera that characterise the Craighead Limestone Formation have earlier origins in the Baltica palaeocontinent, suggesting enhanced migration of species from mid (Baltica ca 30°S) to low (Laurentia) latitudes in the late Sandbian and early Katian interval. Such Baltica-originating genera include *Distobolbina*, *Kiesowia* and *Platybolbina*. Notable is the wide biogeographical occurrence of *Steusloffina cuneata*, extending from warm tropical Laurentia to cooler high latitude Gondwana, an enormous latitudinal range for a shelf-dwelling marine species.

## Introduction

Ostracods appear first in the Cambrian (Harvey *et al.* 2012) and had a global distribution from the Early Ordovician onwards (Tinn & Meidla 2004; Salas, *et al.* 2007; Williams *et al.* 2008). The group occurs in all the major palaeocontinental regions of the Ordovician (Schallreuter & Siveter 1985; Vannier *et al.* 1989), where they are characteristic of benthic neritic habitats. Prior to the Silurian, ostracods do not appear to have adopted a pelagic lifestyle (Siveter *et al.* 1991), and may have had limited intercontinental dispersal capability. They are therefore useful for defining the relative palaeogeographic positions of Ordovician continents (Schallreuter & Siveter 1985).

Despite being documented from the mid part of the nineteenth century onwards, the Ordovician ostracods of Scotland are poorly known. This contrasts markedly with the more detailed studies of their southern British counterparts, which are known from the Ordovician of Wales, the Welsh Borderland and northern England (e.g., Siveter 1978, 2009; Jones 1986, 1987; Williams *et al.* 2003). In part, the lack of study reflects the mostly poor preservation of much of the Scottish fauna and also the difficulty of recovering ostracods from highly tectonised rocks. Nevertheless, the Ordovician ostracods of Scotland have wide occurrence (Williams *et al.* 2001a) with the most extensive faunas being recorded from the Girvan district in the south-west of the country (Jones 1879, 1893; Siveter 1978; Siveter & Curry 1984; Floyd *et al.* 1999; Williams & Floyd 2000; Williams *et al.* 2001a). Recent work on the Girvan faunas has documented their biostratigraphical, palaeoecological and palaeogeographical significance (Williams *et al.* 2001a). The best preserved faunas comprise 'crack-out' material from carbonates. Mould material from clastic rocks (e.g., Floyd *et al.* 1999) and silicified material from limestones (e.g. Siveter & Curry

1984) are also reported. In some instances the ostracods co-occur with graptolites, thus allowing precise stratigraphical control on their temporal distribution.

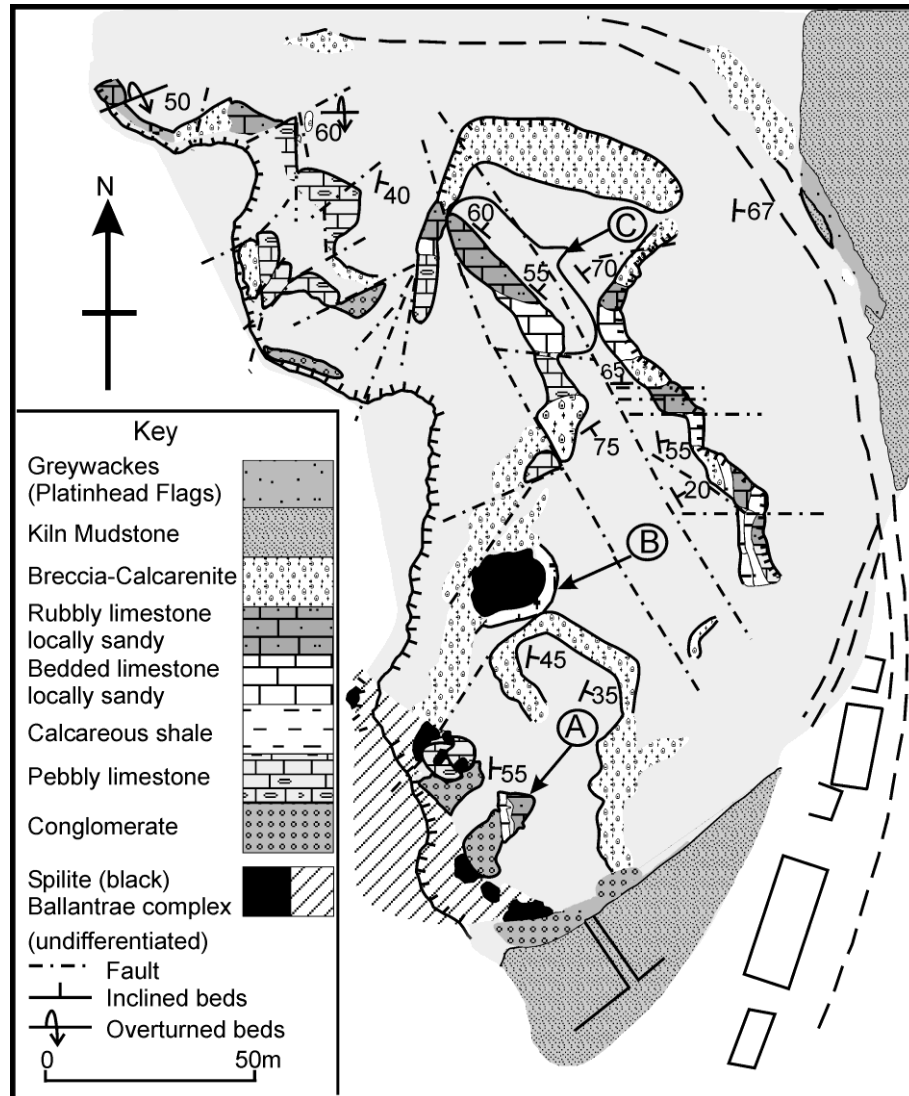


Figure 1. Geological map of Craighead Quarry (redrawn from Williams 1962): 'A', fossil locality of Williams & Floyd (2000); 'B' and 'C', new localities. Locality C, from which 15 samples were taken, yields 18 ostracod species from interbedded mudstone and limestone. Grey shading represents the sub-crop of the Craighead Limestone Formation.

Williams & Floyd (2000) briefly documented an ostracod-bearing horizon at a single locality in the Craighead Limestone Formation of the Girvan district (Fig. 1 locality A).

The fauna was numerically dominated by palaeocopes, especially *Oepikella*, and

had similarities at species level with assemblages from North America. In the present chapter I describe a much more extensive ostracod fauna from fifteen sampled limestone-shale horizons in the northernmost outcrop of the Craighead Limestone Formation at Craighead Quarry, and from one site in massive limestones in the centre of the quarry (Fig. 1). These faunas, amongst the best preserved from the Scottish Ordovician, are quite different from those described by Williams & Floyd (2000). Herein we: a) identify the fauna present in different localities; b) establish the environmental range of the ostracods across four different carbonate lithofacies in the Craighead Limestone Formation; c) document the temporal distribution of the ostracods and compare their ranges with faunas from North America and Scandinavia; and d) elucidate the biogeographical significance of key elements of the fauna.

### **Geological setting of the Craighead Limestone Formation**

The Craighead Inlier forms a lenticular area some 12 km by 2 km of Ordovician-Silurian marine sedimentary and volcanic rocks that are isolated from the main Lower Palaeozoic outcrop at Girvan, southwest Scotland (Fig. 2). The Inlier forms a gently northeast plunging anticline bounded on its southeast side by the Kerse Loch Fault and is unconformably overlain to the northwest by sandstones and conglomerates of the Lower Old Red Sandstone (Upper Silurian-lower Devonian). The oldest rocks of the Inlier comprise spilitic pillow lavas which may be as old as the Floian age Ballantrae Complex to the south, but could be as young as Sandbian (Williams & Floyd 2000). These are unconformably overlain by a Katian-Llandovery succession of shallow marine limestones and clastic sedimentary rocks (Fig. 3) which have yielded a great abundance and variety of macrofauna and microfauna (e.g., Williams 1962; Harper 1982; Bergström 1990; Floyd & Williams 2003).

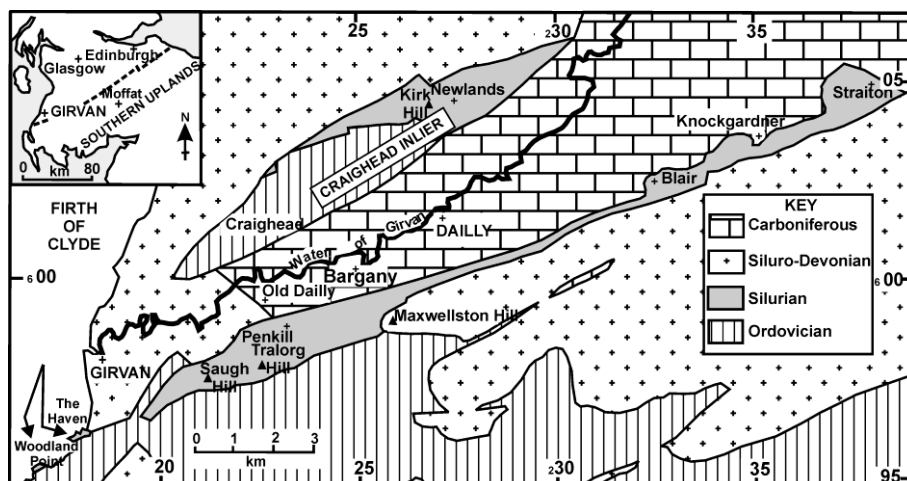


Figure 2. Geological map of the Craighead Inlier (after Williams & Floyd 2000).


Period	Inter- national standard stages	British regional series and stages	Baltic regional stages	North American regional stages	British graptolite biozones	North Atlantic conodont biozones	Craighead Inlier lithostratigraphy			
Ordovician	Hirnantian	Hirnantian	Porkuni	Gamachian	<i>persculptus</i> <i>extraordinarius</i>		Drummuck Subgroup	High Mains Formation		
	Katian	Ashgill	Pirgu		Richmondian	<i>anceps</i>		ordovicianus	South Threave Formation	
				Lady Burn Formation						
				Quarrel Hill Formation						
				Auldthorns Formation						
		Cautleyan	Maysvillian	<i>complanatus</i>	Whitehouse Subgroup	Shalloch Formation				
	Pusgillian	Edenian				[faulted junction]				
	Caradoc			Nabala	clingani Biozone	<i>morrisi</i> Subzone	superbus			
		Streffordian	Rakvere	Chatfieldian						<i>caudatus</i> Subzone
		Cheneyan	Oandu		<i>wilsoni</i>	tvaerensis		Ardwell Subgroup	Plantinhead Formation	
		Sandbian (pars)	Burrellian	Keila					Craighead Limestone Formation (Sericoidea Mudstone Member)	
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Figure 3. Ordovician stratigraphy of the Craighead Inlier (modified after Williams & Floyd 2000).

## Materials and Methods

The new ostracod material comes from fifteen sampled horizons of mudstones interbedded with thin-bedded limestones at the north end of the quarry (Fig. 1 locality

C). Both the limestones and mudstones have been investigated for ostracod content. We have also re-sampled ostracod material from limestone at the locality described by Williams & Floyd (2000), and recovered a single ostracod specimen from the massive limestones in the middle of the quarry (Fig. 1 locality B). Most of the limestone exposure in the quarry is now inaccessible, especially the high faces in the centre of the quarry (Fig. 1), and this has directed our sampling strategy to those parts of the quarry where rock is recoverable.

Mudstones from the Craighead Limestone Formation were treated with a 10% solution of H<sub>2</sub>O<sub>2</sub> in cold water, left for one day, wet-sieved with 1 mm, 500 µm and 250 µm sieves, dried and the residues picked for ostracods under a WILD M8 binocular microscope. The ostracods were then mounted on aluminium stubs, coated with sputter coater 'Emitech K500X' and imaged using a HITACHI S-3600N scanning electron microscope (SEM). Lateral stereo-pairs were captured with 0 and 10° tilt angles; ventral and dorsal stereo-pairs were captured with 0 and 6° tilt angles (see Sylvester-Bradley 1971 for methodology). Ostracods from the locality of Williams & Floyd (2000; see Fig. 1 locality. A) have been extracted as 'crack-out' material from small limestone blocks and prepared mechanically with needles. All of the material is deposited in the collections of the British Geological Survey, Keyworth, Nottingham, UK except GLAHM A1382 and GLAHM A1379 which are deposited in the Hunterian Museum of Glasgow University.

### **Preservation of the ostracods**

The Ordovician ostracods of the Craighead Limestone Formation represent calcitic crack-out material and calcitic valves recovered from mudstones. Ostracods from the

Kiln Mudstone Member and the Sericoidea Mudstone Member of the Craighead Limestone Formation (Fig. 3) are poorly preserved moulds (Williams & Floyd 2000), while the accompanying brachiopods and trilobites are mostly well preserved (Tripp 1980). Ostracods preserved as moulds is a common type of preservation in much of the Ordovician succession of Scotland (e.g., Lady Burn Formation, Lower Ardwell Flags, Stinchar Limestone, Balclatchie Group; see Williams *et al.* 2001a; Siveter 2009) and is also common in England and Wales (see Jones 1986, 1987). The ostracods from carbonates of the Craighead Limestone Formation (Fig. 1 locality A) preserve fine details of the original shell ornament. This type of preservation is common in North American Ordovician carbonates and calcareous mudstones (e.g., Williams & Siveter 1996) and in similar lithologies of the Baltic region (e.g., Meidla 1996) but rare in the Ordovician of Scotland. It is found elsewhere in Scotland only in the Stinchar Limestone at Aldons Quarry and from a limestone clast in the Kirkcolm Formation of the Southern Uplands Terrane (Williams *et al.* 2001a). The ostracods from the mudstones interbedded with thin-bedded limestones yield calcitic valves that range from good to moderate preservation. In some cases the shells have suffered dissolution so that fine details have been lost.

### **Lithofacies of the Craighead Limestone Formation**

A detailed lithofacies analysis identifies four facies types that denote open platform-margin (Lithofacies 1), outer platform/deep shelf (Lithofacies 2), slope (Lithofacies 3) and partly restricted platform settings (Lithofacies 4; Mohibullah *et al.* 2010). The four different lithofacies types identify partly restricted to deeper shelf settings, and indicate that the carbonate platform evolved both shallower and deeper marine environments, with both low to high energy regimes hosting different biota (Fig. 4;

Mohibullah *et al.* 2010). The rubbly limestone in the southern flank of the quarry (Fig. 1 locality A) records a low diversity biota in perhaps the shallowest marine environment represented.

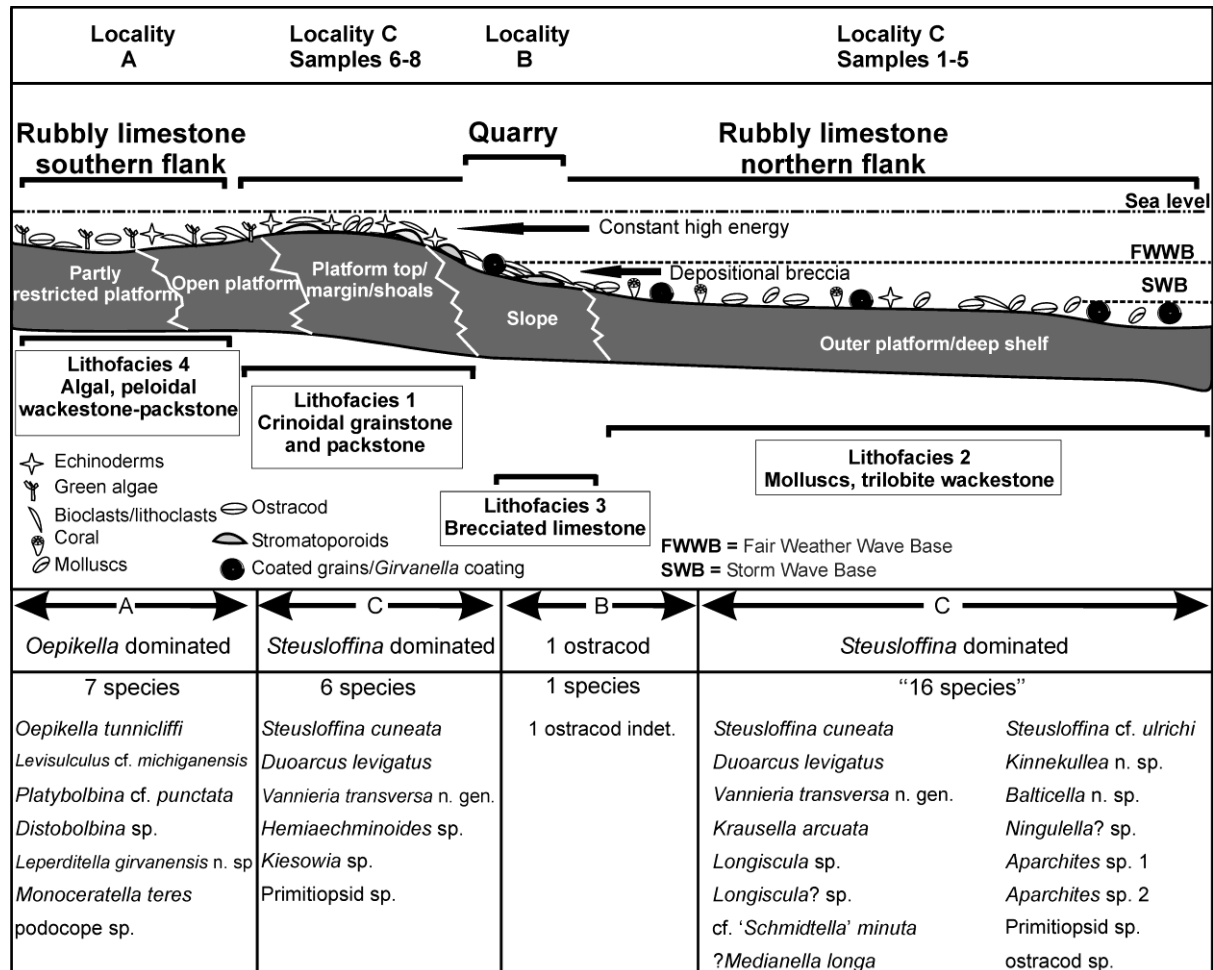


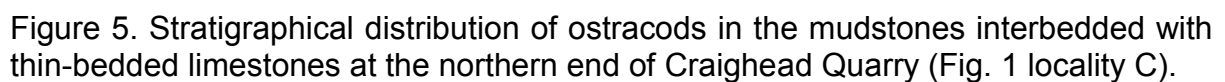
Figure 4. Palaeoenvironmental model for the limestone horizons of the Craighead Limestone Formation at Craighead Quarry (Mohibullah *et al.* 2010). For location of limestone horizons see Fig. 1.

### Ostracod Palaeoecology

Modern marine ostracods are predominantly benthic with high diversity in marine shelf habitats. Their biodiversity decreases in very shallow and very deep shelf marine environments (e.g., Ulst *et al.* 1982; Stepanova *et al.* 2007). Following the principle of uniformitarianism the same patterns may be expected in the Palaeozoic.

Similarly, ostracod diversity is low in very shallow and deep shelf environments in the Ordovician (Copeland 1982; Vannier *et al.* 1989; Williams & Siveter 1996; Williams *et al.* 2003) as well as the Silurian (Siveter 1984). Ordovician ostracods were possibly entirely neritic (Williams *et al.* 2003) and are useful environmental indicators, with some taxa being restricted to shallow marine environments (e.g., the *Leperditella* ostracod association of Williams & Siveter (1996), and some taxa restricted to the deep shelf (Copeland 1982). Copeland (1982) identified bathymetrically controlled ostracod biofacies in the Ordovician Lower Esbataottine Formation of Canada by comparison with the associated trilobite fauna. He distinguished two ostracod assemblages, one restricted to a deeper shelf marine environment and the other tolerant of a wide range of water depths from shallow to deeper shelf, perhaps equivalent, at least in part, to the *Anisocyamus* ostracod association of the Bromide Formation of Oklahoma (Williams & Siveter 1996).

In the Craighead Limestone Formation samples were collected on the basis of accessibility and maximum sediment yield: Some parts of the quarry are inaccessible, and in addition some areas of massive limestone are extremely difficult to sample for ostracods. Nevertheless, we can identify that ostracods occur in at least four lithofacies. The most diverse faunas occur in the limestones of the southern end of the quarry at locality A (Fig. 1: locality A, Fig. 4) and from two lithofacies associations at the northern end of the quarry (Fig. 1: locality C, Figs 4, 5). The ostracods associated with these lithofacies of the southern and northern parts of the quarry are quite distinctive, most likely reflecting adaptations to specific environments, rather than temporally discrete assemblages. Graptolite and other faunal evidence suggest the Craighead Limestone Formation was deposited entirely within the early Katian (Tripp 1980). Of the 25 ostracod species herein recorded from



### **Shallow marine low-diversity ostracod assemblage**

This assemblage is present only in the limestones at the southern end of the quarry (Fig. 1 locality A) and is characterised by *Oepikella tunnicliffi*. It is dominated by palaeocopes, especially *Oepikella* (Fig. 4), and includes species of *Platylbolbina*, *Distobolbina*, *Leperditella girvanensis* n. sp. and *Levisulculus* (see Fig. 6). The podocope *Monoceratella teres* also occurs. This assemblage occurs in a lithofacies representing a shallow platform with restricted open marine influence (Fig. 4). Petrological data (Fig. 4; also see Mohibullah *et al.* 2010) indicate overall low biotic diversity dominated by (fragments of disarticulated) molluscs, trilobites, highly neomorphosed echinoderms, and green algae (dasycladaceans). The elements of this shallow marine assemblage are absent from the lithofacies of the northern part of the quarry where thin-bedded shales and limestone formed in more open marine shelf environments of the carbonate platform (see Mohibullah *et al.* 2010). This shallow marine ostracod assemblage bears similarity to the low-diversity *Leperditella* ostracod association of the Bromide Formation of Oklahoma (Williams & Siveter 1996) that comprises a distinctly different (both taxonomically and in terms of diversity) assemblage from the contemporaneous open marine shelf ostracods of the Bromide Formation.

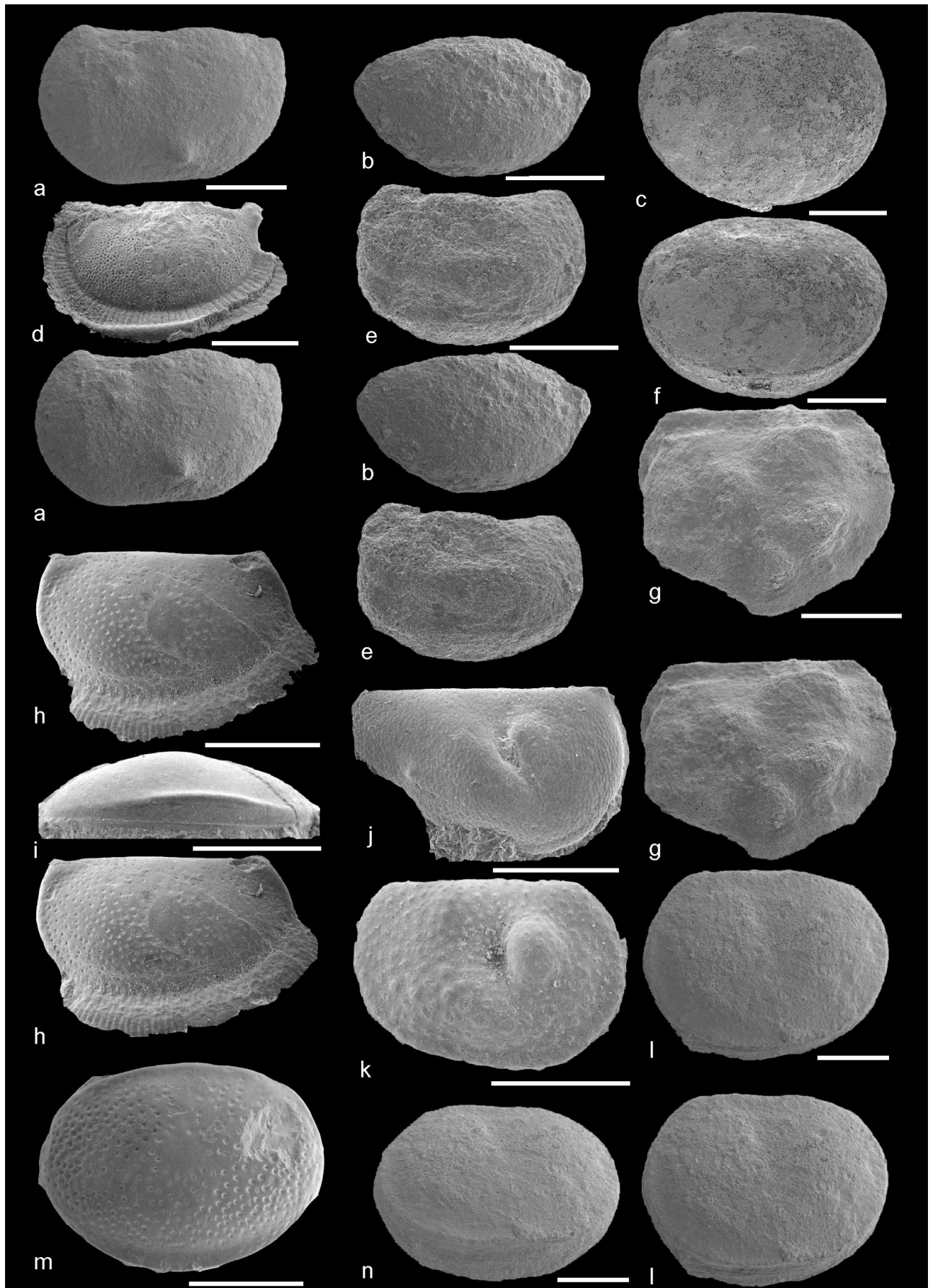


Figure 6. Ordovician ostracods from the Craighead Limestone Formation. (a) MPA49672, *Balticella* n. sp., carapace, left lateral view (stereo-pair). (b) GSE15341, *Vannieria transversa* (Harris, 1957), carapace, left lateral view (stereo-pair). (c, f) GSE15342, *Aparchites* sp. 1, carapace, right lateral and oblique lateral views. (d) GLAHM A1382, *Platybolbina* cf. *punctata* (Kraft, 1962), tecnomorph left valve, lateral view. (e) GSE15343, *Kinnekullea* sp., carapace, left lateral view (stereo-pair). (g) GSE15344, *Kiesowia* sp., carapace, left lateral view (stereo-pair). (h, i, m) *Oepikella tunnicliffi*, Williams & Floyd, 2000: (h) BGS 16E1961, holotype, heteromorphic right valve, lateral view (stereo-pair); (i) BGS 16E1967, juvenile tecnomorphic valve, ventral view; (m) BGS 16E1965 tecnomorph right valve, lateral view. (j) BGS 16E1960, *Levisulculus* cf. *michiganensis* Kesling, 1960b, right valve, lateral view. (l, n) GSE15345, Primitiopsid sp., carapace, right lateral (stereo-pair) and oblique lateral views. (k) BGS 16E1958, *Distobolbina* sp., tecnomorph right valve, lateral view. (a, c, f) Scale bar 0.5 mm; (b) scale bar 0.3 mm; (d) scale bar 0.75 mm; (e) scale bar 0.25 mm; (g) scale bar 0.3 mm; (h, m) scale bar 1.0 mm; (i) scale bar 0.75 mm; (j) scale bar 0.43 mm; (k) scale bar 0.38 mm; (l, n) scale bar 0.5 mm.

### Open marine high diversity ostracod assemblage

This assemblage is characterised by the common occurrence of *Steusloffina*. It is present throughout the interbedded shales and limestones of the northern end of the quarry (Fig. 1 locality C; Figs 6, 7, 8) that represent a marine-facing shallow to deeper platform margin setting. This assemblage shows overall relatively high diversity (18 species) and is dominated by podocopes and leiocopes with some binodicopes and palaeocopes (Figs 4-8). *Steusloffina cuneata*, *Duoarcus levigatus* and *Vannieria transversa* are abundant in both the shallow and deeper platform settings. Rare *Kiesowia* sp. and *Hemiaechminoides* sp., both reported for the first time from Scotland, occur only in the shallower platform margin, whereas most of the other species are present only in the deeper platform. The diversity of podocopes and leiocopes is high, while palaeocopes and binodicopes are less common. This open marine assemblage bears similarity to the *Anisocyamus* ostracod association of Williams & Siveter (1996) in the Bromide Formation of Oklahoma, both of which have species of *Aparchites*, *Schmidtella*, *Krausella* and *Balticella*. The associated

fauna recorded from the limestone is of high diversity and comprises echinoderms, brachiopods, bivalves, gastropods, trilobites, stromatoporoids, bryozoans and the alga *Girvanella*, the shallow platform margin being dominated by crinoids and the deep shelf dominated by molluscs and trilobites (see Mohibullah *et al.* 2010). This ostracod assemblage is quite distinct from the carbonate lithofacies deposited in the restricted lagoonal environment of the platform (Fig. 4; Mohibullah *et al.* 2010).

### **Biostratigraphical significance of the ostracods: an early Katian assemblage**

The Craighead Limestone Formation is of early Katian age based on the occurrence of graptolites referable to the lower part of the *Dicranograptus clingani* Biozone (*caudatus* Subzone) in the interleaved Sericoidea Mudstone Member (Tripp 1980; Williams & Floyd 2000). The shelly fauna of the Craighead Limestone Formation also suggests an early Katian age (Ingham 1992; Leslie & Bergström 1995). The limestones also yield a conodont fauna considered to denote a low level within the *Amorphognathus superbus* Biozone (Bergström 1990). This suggests that the carbonates of the Craighead Limestone Formation are constrained to a fairly short time interval and that the differences in the fauna between the southern (Fig. 1 locality A) and the northern (Fig. 1 locality C) ostracod-bearing carbonates are a function of environment rather than temporal factors.

The ostracod collections of Williams & Floyd (2000) were derived from a single limestone horizon at the southern end of the quarry (Fig. 1 locality A). These ostracods include *Distobolbina*, *Leperditella* and *Oepikella* and show a North American affinity at species-level including *Platybolbina* cf. *punctata*, *Levisulculus* cf. *michiganensis* and *Monoceratella teres* (Figs 6, 8). Of these latter species,

*Levisulculus michiganensis* and *Monoceratella teres* are long-ranging and have widespread geographical occurrence. *Levisulculus michiganensis* is reported from the Sandbian Bony Falls Limestone of Michigan (Kesling 1960b) and also from the lower unit of the Sandbian Bucke Formation in Canada (Copeland 1965). *Monoceratella teres* is referred to as a zone fossil in the eastern United States by Swain (1957). However, this 'biozone' is loosely defined, possessing a long stratigraphical range, being reported from the Sandbian age Lincolnshire and Edinburgh formations of Virginia, the Hatter and Benner formations of Pennsylvania, and the Day Point and Crown Point Limestones of New York (Swain 1957, 1962; Kraft 1962). The presence of *Monoceratella teres* in the early Katian Craighead Limestone Formation is much younger than the North American occurrences and therefore I do not regard it as indicating the '*Monoceratella teres* biozone' per se. *Oepikella tunnicliffi* is a new species reported by Williams & Floyd (2000) only from the Craighead Limestone Formation. However, there are many *Oepikella* species documented from the Late Ordovician strata of the USA (e.g., see Warshauer & Berdan 1982), Arctic Canada (Copeland 1977a, b) and Mid to Late Ordovician (Darriwilian-Katian) strata of the Baltic region (Vannier *et al.* 1989; Meidla 1996). *Platybolbina* cf. *punctata* has close resemblance with the type species *Platybolbina punctata* (Kraft 1962) from the Edinburg Formation (Sandbian) of Virginia (Kraft 1962). Elsewhere in the Laurentian palaeocontinent *Distobolbina* is only documented from the Sandbian succession of Arctic Canada (Copeland 1977a), but is also reported from the Late Ordovician (Sandbian-Katian) strata of the Baltic region (Vannier *et al.* 1989; Williams *et al.* 2003) and late Katian of southern Britain (late Katian) (Williams *et al.* 2001b).

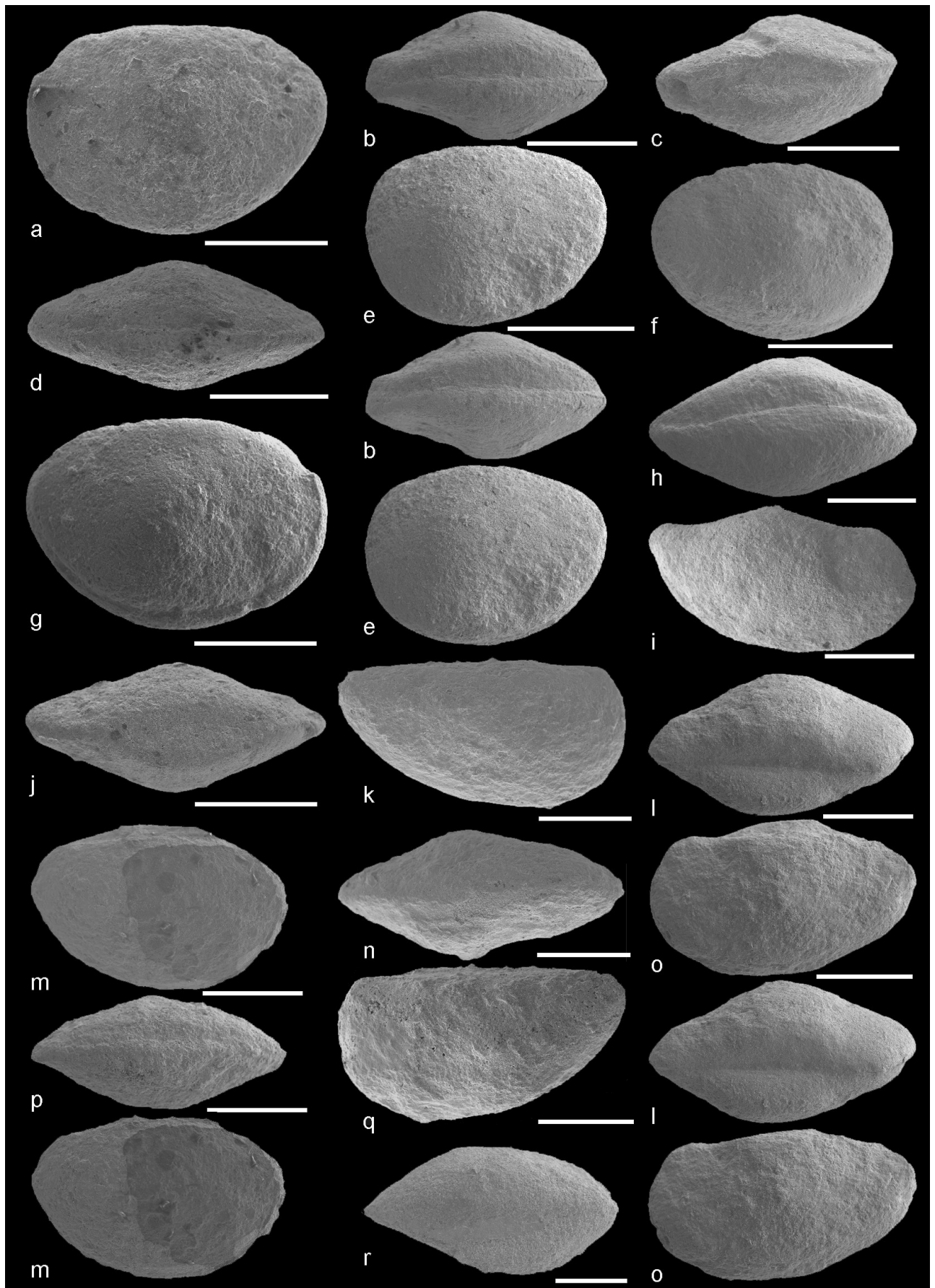


Figure 7. Ordovician ostracods from the Craighead Limestone Formation. (a, d, g, j) GSE15346, cf. '*Schmidtella*' *minuta* Harris, 1957, carapace, left lateral, ventral, right lateral and dorsal views. (f, e, b, c). *Duoarcus levigatus*: (f) GSE15347, carapace, right lateral view: (e) GSE15348 (holotype), carapace, left lateral view (stereo-pair): (b) GSE15349, carapace, ventral view (stereo-pair): (c) GSE15350, carapace, dorsal view. (h, i, l, o) *Steusloffina cuneata* (Steusloff, 1895): (h) GSE15351, carapace, ventral view: (i) GSE15352, carapace, right lateral view: (l) GSE15353, carapace, dorsal view (stereo-pair): (o) GSE15354, carapace, left lateral view (stereo-pair). (m, p, r) *Vannieria transversa* n. gen. (Harris, 1957) (m) GSE15355, carapace, left lateral view (stereo-pair): (p) GSE15356, carapace, ventral view: (r) GSE15357, carapace, dorsal view. (k, n, q) GSE15358, *Steusloffina* cf. *ulrichi* Teichert, 1937, carapace, right lateral, ventral and left lateral views. (a–j, l, o) Scale bar 0.5 mm; (m, p, r, k, n, q) scale bar 0.2 mm.

Sampled horizons at the north end of the quarry (Fig. 1 locality C) have produced eighteen species. These include *Steusloffina cuneata* (Steusloff, 1895), *Balticella* n. sp., *Duoarcus levigatus*, *Krausella arcuata* Ulrich, 1894, *Vannieria transversa* (Harris, 1957), cf. '*Schmidtella*' *minuta* Harris, 1957, *Hemiaechminoides* sp., ?*Medianella longa* (Stumbur, 1956), *Longiscula* sp., *Longiscula?* sp., *Steusloffina* cf. *ulrichi* (Teichert, 1937) and species of *Kiesowia*, *Ningulella?* and *Kinnekullea* (Figs 6–8). Some of these species have potential stratigraphical significance (see below). Collectively they are consistent with the early Katian age indicated by other fossil groups, with the ranges of typical Sandbian and Katian ostracods overlapping (Fig. 9).

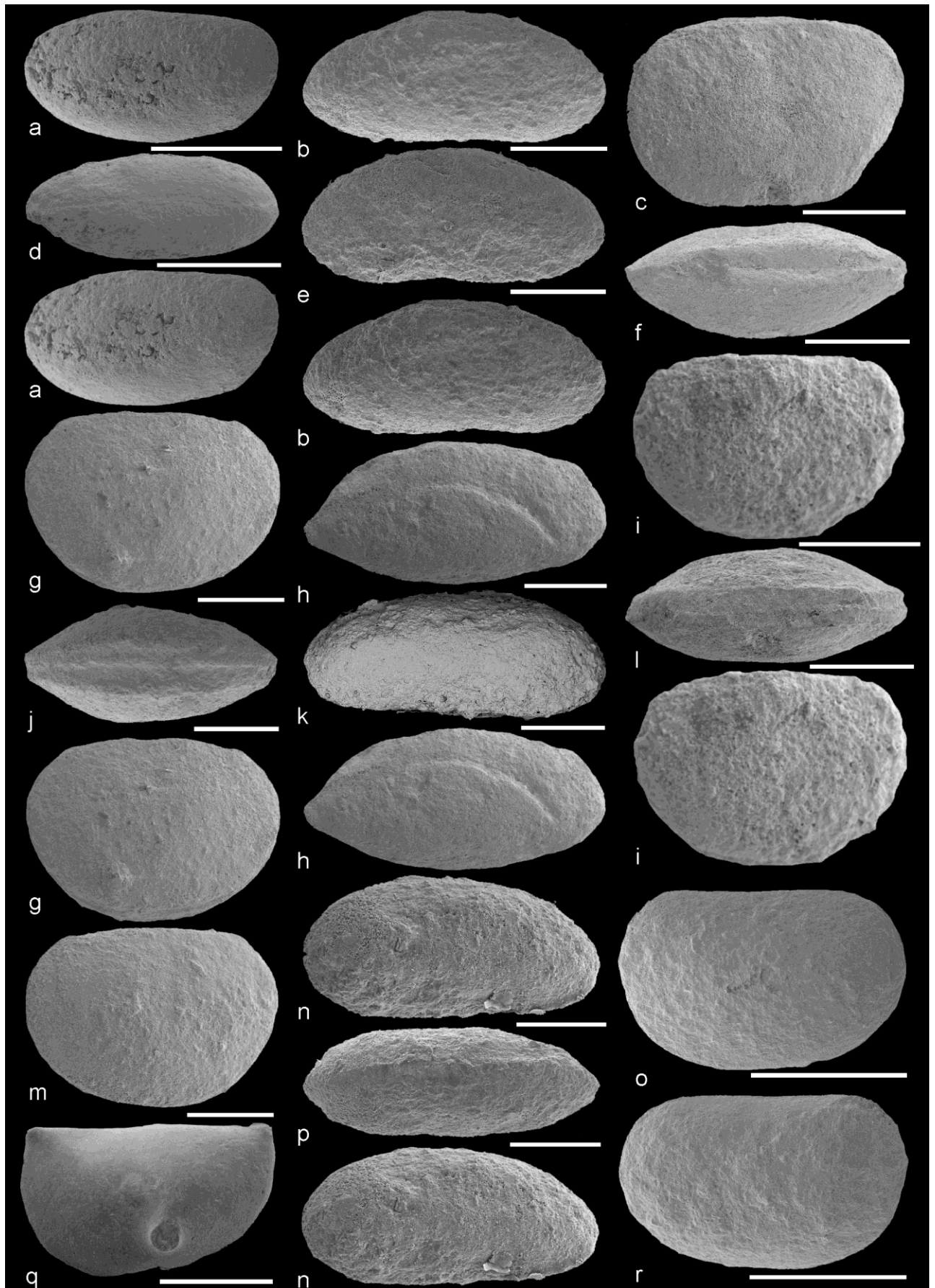


Figure 8. Ordovician ostracods from the Craighead Limestone Formation. (a, d) GSE15359, *?Medianella longa* (Stumbur, 1956), carapace, left lateral (stereo-pair) and ventral views. (b, e) GSE15360, *Longiscula* sp., carapace, left lateral (stereo-pair) and right lateral views. (c, f, l) GSE15361, ostracod sp., carapace, lateral, dorsal and ventral views. (i) GSE15362, *Hemiaechminoides* sp., carapace, left lateral view (stereo-pair). (g, j, m) GSE15363, *Aparchites* sp. 2, carapace, left lateral (stereopair), ventral and right lateral views respectively. (h) GSE15364, *Krausella arcuata* Ulrich, 1894, carapace, right lateral (stereo-pair) view. (k, n, p) GSE15365, *Longiscula?* sp. (Neckaja, 1966), carapace, left lateral, right lateral (stereo-pair) and dorsal views. (q) GLAHM A1379, *Monoceratella teres* (Teichert, 1937), left valve, lateral view. (o, r) GSE15366, *Ningulella?* sp., carapace, left and right lateral views. (a, c, d, f, g, h, j, l, m, o, r) Scale bar 0.5 mm; (b, e, i, k, n, p) scale bar 0.2 mm; (q) scale bar 0.75 mm.

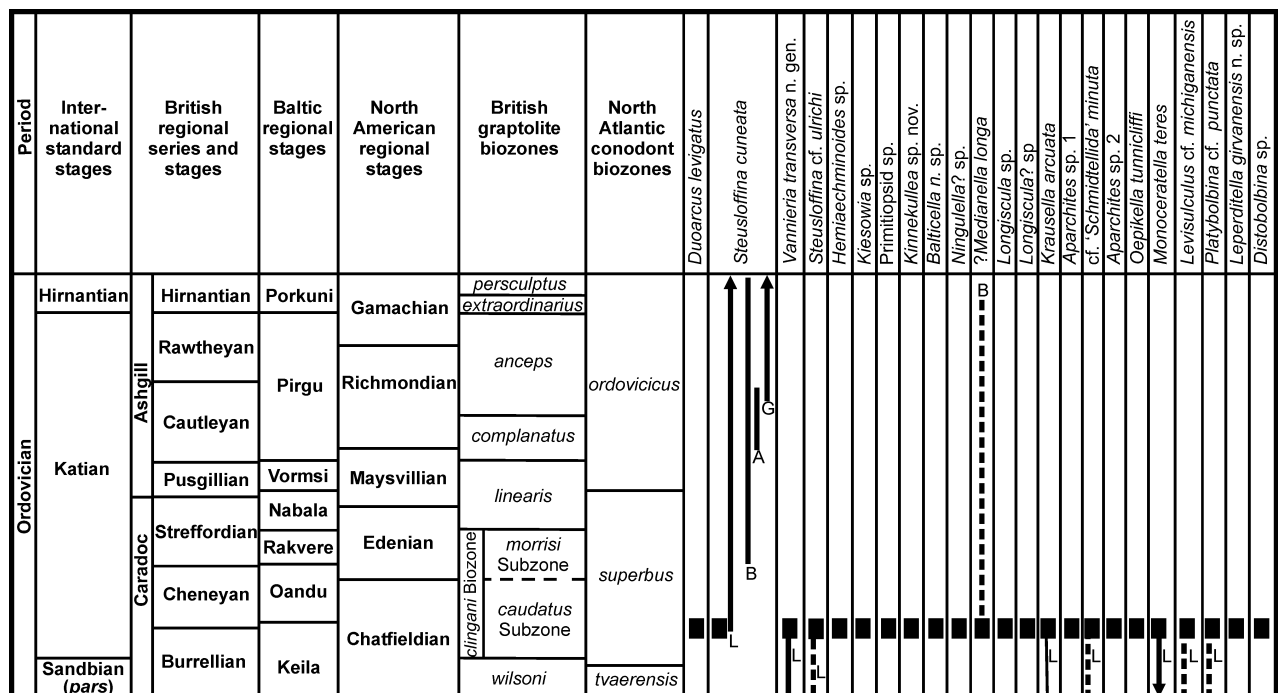


Figure 9. Ostracod species of the Craighead Limestone Formation compared with their stratigraphical ranges in other palaeogeographical areas. Symbols: black square, stratigraphic position of species in the Craighead Limestone Formation; dotted line, represents total range of a species that is tentatively identified at Craighead (as 'cf') with its unequivocal stratigraphical range elsewhere; L, Laurentia; B, Baltica; A, Avalonia; and G, Gondwana.

*Steusloffina cuneata* is long ranging and widespread, being reported from the Upper Ordovician (Katian) of North America (Hessland & Adamczak 1974), the Baltic region (Meidla 1996), Britain (Williams *et al.* 2001b), Kazakhstan (Melnikova 1986) and India (Schallreuter *et al.* 2008) (Figs 9, 10), and from the Lower Silurian of Canada (Copeland 1981, 1983) and Iran (Hairapetian *et al.* 2011). *Steusloffina cuneata* thus

survived the major climatically-driven extinction event of the Late Ordovician that decimated many ostracod assemblages (Schallreuter & Siveter 1985). The presence of *Steusloffina cuneata* in the early Katian Craighead Limestone Formation and Rysedorph Hill Conglomerate of New York are the oldest known occurrences, indicating the possible origin of this species in the Laurentian palaeocontinent, from where it presumably spread out to colonise several palaeocontinents. *Krausella arcuata* is a typical North American species, documented from the Upper Ordovician (Sandbian) Bromide Formation of Oklahoma, the Decorah Formation of Iowa and Minnesota (Kay 1940), the Edinburg and Lincolnshire formations of Virginia (Kraft 1962) and the Day Point Formation of New York (Swain 1957). It is thus a typical Sandbian form, and its occurrence in the Craighead Limestone Formation extends its range into the early Katian. Species of *Kiesowia* are documented from the Late Ordovician Decorah Formation of Iowa (Kay 1940) and from the Middle Ordovician (Darriwilian) to Silurian of the Baltic region (Vannier *et al.* 1989; Meidla 1996). *Medianella longa* (Stumbur, 1956) is recorded from the early to late Katian strata of Estonia and also from the late Katian rocks of the Pskov region in Russia (Meidla 1996). *Medianella longa* has not been reported from other Ordovician successions of Scotland and its identification in the Craighead Limestone Formation remains tentative. The presence of *Kinnekullea* in the Craighead Limestone Formation might also suggest a Laurentian origin for that taxon. Species of *Kinnekullea* are previously reported from the early to late Katian succession of the Baltic region (Vannier *et al.* 1989; Meidla 1996), late Katian strata of northern England (Williams *et al.* 2001b) and late Katian strata of the Girvan District, Scotland (Floyd *et al.* 1999). *Balticella* species are documented from Sandbian age strata in the Bromide Formation of Oklahoma (Harris 1957), the Edinburg Formation of Virginia (Kraft 1962), the

Balclatchie Conglomerate of the Girvan District (Williams *et al.* 2001a) and the Baltic region (Meidla 1996). Again, the record from the Craighead Limestone Formation extends the range of *Balticella* into the Katian. *Hemiaechminoides* species are known from early to late Katian strata of the Baltic region and Silurian of North America (Meidla 1996).

### **Early Katian ostracod biogeography and the Craighead Limestone fauna**

During the Ordovician, Girvan formed part of the south-eastern margin of the Laurentia palaeocontinent (figs 10, 11; Bergström 1990; Rushton *et al.* 1996). It was separated from the Baltic region (Baltica palaeocontinent) and from southern Britain (Avalonia microcontinent) by an arm of the Iapetus Ocean (Cocks & Fortey 1982; McKerrow *et al.* 1991; Cocks & Torsvik 2005). In the Late Ordovician these palaeocontinents converged as a result of the northward movement of Avalonia and the subduction of the Iapetus Ocean and the closure of the Tornquist Sea (Pickering *et al.* 1988; Cocks *et al.* 1997; Cocks 2000; Cocks & Torsvik 2005). This is supported by evidence of increasing similarity between the ostracod faunas of these regions (Schallreuter & Siveter 1985; Vannier *et al.* 1989; Williams *et al.* 2003). In the following subsections we discuss the biogeographical affinities of the Craighead Limestone Formation ostracod faunas in terms of their Laurentia and Baltica origins.

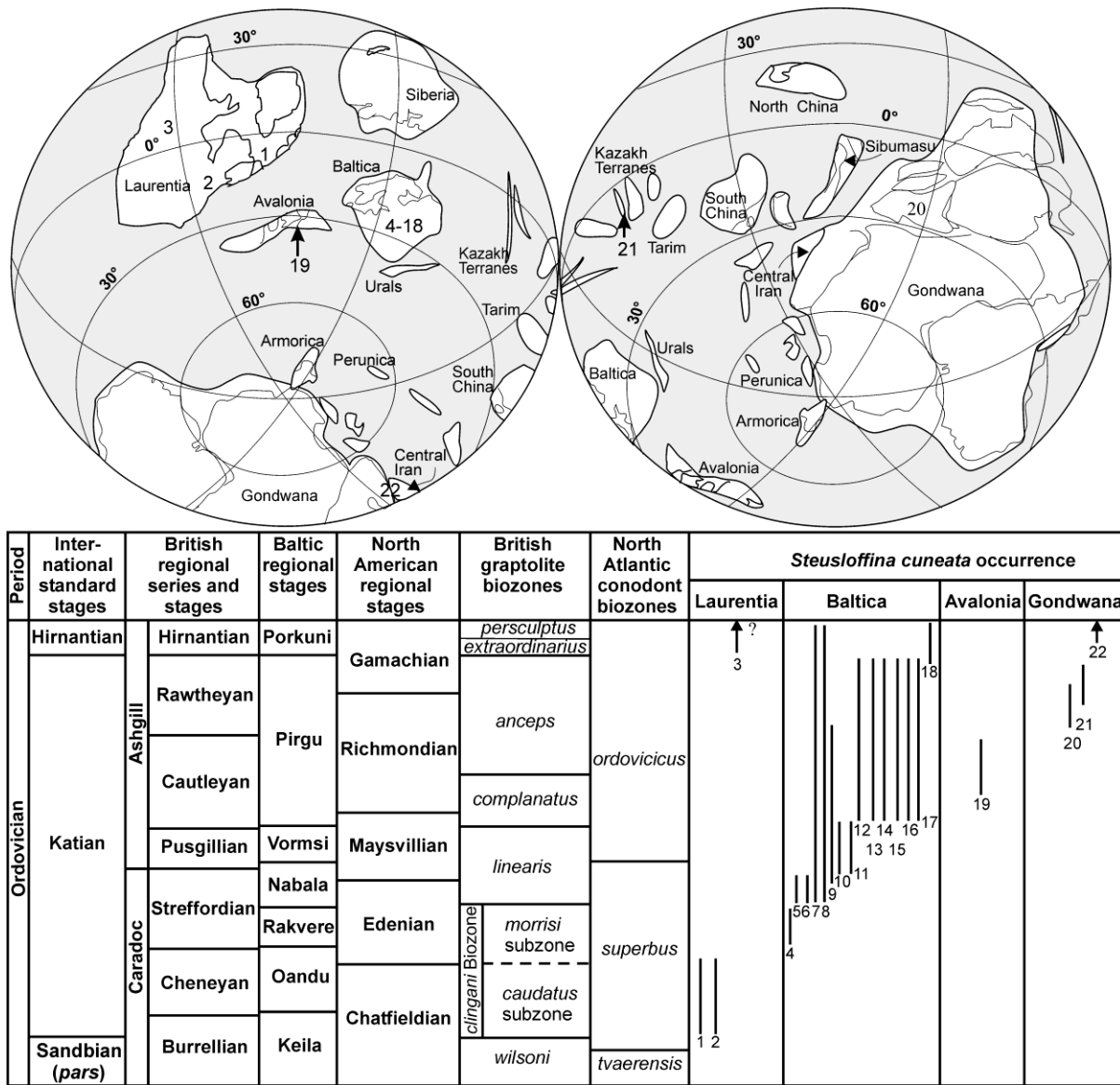


Figure 10. Temporal and geographical distribution of *Steusloffina cuneata*. Distribution indicates that this taxon originated in Laurentia, later migrated to Baltica, Avalonia and then Gondwana. Source references: Sarv (1960), Schallreuter (1968), Pranskevičius (1972) Hessland & Adamczak (1974), Siveter (1982), Copeland (1981, 1983), Meidla (1996), Williams *et al.* (2001b), Melnikova (1986), Schallreuter *et al.* (2008), Hairapetian *et al.* (2011). Numbers 1-22 indicate localities for *Steusloffina cuneata*: 1, Craighead Limestone Formation, Girvan, Scotland; 2, New York (Hessland & Adamczak 1974); 3, Silurian of Anticosti Island Quebec Canada (Copeland, 1981, 1983); 4, 5, 6, 10-18, early to latest Katian of Estonia (Meidla 1996); 7 early to latest Katian of Estonia (Sarv 1960; Pranskevičius 1972; Siveter 1982); 8, early to latest Katian of Latvia (Sarv 1960; Pranskevičius 1972; Siveter 1982); 9, Germany (Schallreuter 1968); 19, Northern England (Williams *et al.* 2001b); 20, India (Schallreuter *et al.* 2008); 21, late Katian of Kazakhstan (Melnikova 1999); 22, Silurian of central Iran.

### **Baltica affinities**

Many of the ostracod genera that occur in the Craighead Limestone Formation have a probable Baltica affinity (see Vannier *et al.* 1989; Meidla 1996; Williams *et al.* 2003) (Fig. 9). Thus, *Platybolbina*, *Oepikella*, and *Levisulculus* occur in the late Darriwilian strata of Baltica (Vannier *et al.* 1989; Williams *et al.* 2003) and congeneric species may have migrated to Laurentia during the late Sandbian-Katian (see Williams & Floyd 2000; Williams *et al.* 2003). In Laurentia these genera are present at a Sandbian-Katian (Mohawkian) horizon in the Bony Falls Limestone (Kesling 1960a, 1960b), the Lexington Limestone (Warshauer & Berdan 1982) and Edinburg Formation (Kraft 1962). *Kiesowia* species also first appear in the Darriwilian of Baltica (Vannier *et al.* 1989; Meidla 1996) and may have migrated to Laurentia in the early Katian. *Longiscula* first occurred in the Malopolska and Argentine Precordillera terranes during the Darriwilian and later appeared in Baltica and Laurentia (Sandbian; see Williams *et al.* 2003; Copeland 1977a). *Medianella longa* first appeared in the early Katian (Oandu stage of local Baltic usage) in Baltica (Meidla 1996), which is almost at the same horizon as the tentative occurrence of these taxa in the Craighead Limestone Formation. Species of *Medianella* have not been reported from other Ordovician successions of Laurentia. *Distobolbina* appears in Baltica first during the Sandbian (Vannier *et al.* 1989; Williams *et al.* 2003) and in Laurentia it occurs at almost the same horizon in Arctic Canada (Mohawkian; Copeland 1977a).

### **Laurentia affinities**

*Monoceratella* occurs first in the late Darriwilian of Laurentia and species of this genus might have migrated to Baltica where the genus appears in the latest Katian

(Williams *et al.* 2003). *Krausella* appeared first in Laurentia during the Darriwilian and species may have migrated to Baltica in the early Katian (Williams *et al.* 2003). *Steusloffina cuneata* is a cosmopolitan species with a long temporal range (early Katian to earliest Silurian), being reported from Laurentia (Hessland & Adamczak 1974; Copeland 1981, 1983), Baltica (Meidla 1996), Avalonia (Williams *et al.* 2001b) and Gondwana (Schallreuter *et al.* 2008) (Figs 9, 10). In Baltica *S. cuneata* first appears in the Katian at a level equivalent to the upper *clingani* graptolite Biozone (upper Rakvere) in the Rägavere Formation of Estonia (Meidla 1996). In Avalonia it has been reported from the late Katian (mid-Cautleyan, Ashgill) age strata of England (Williams *et al.* 2001b) and in Gondwana it is present in the late Katian strata of India (Schallreuter *et al.* 2008). The presence of *Steusloffina cuneata* in the early Katian Craighead Limestone Formation and Rysedorph Hill Conglomerate, New York are the oldest known possible occurrences, and suggest a Laurentian origin for the taxon. The migration of *Steusloffina cuneata* from low latitude Laurentia and Baltica to high latitude Gondwana (latitude 60° south, according to Cocks & Torsvik 2005) represents adaptation to a range of palaeoenvironments. Schallreuter *et al.* (2008) speculated that the migration of *Steusloffina cuneata* may have occurred as a result of dispersal via seaweed or algal mats, though there is no evidence to substantiate this.

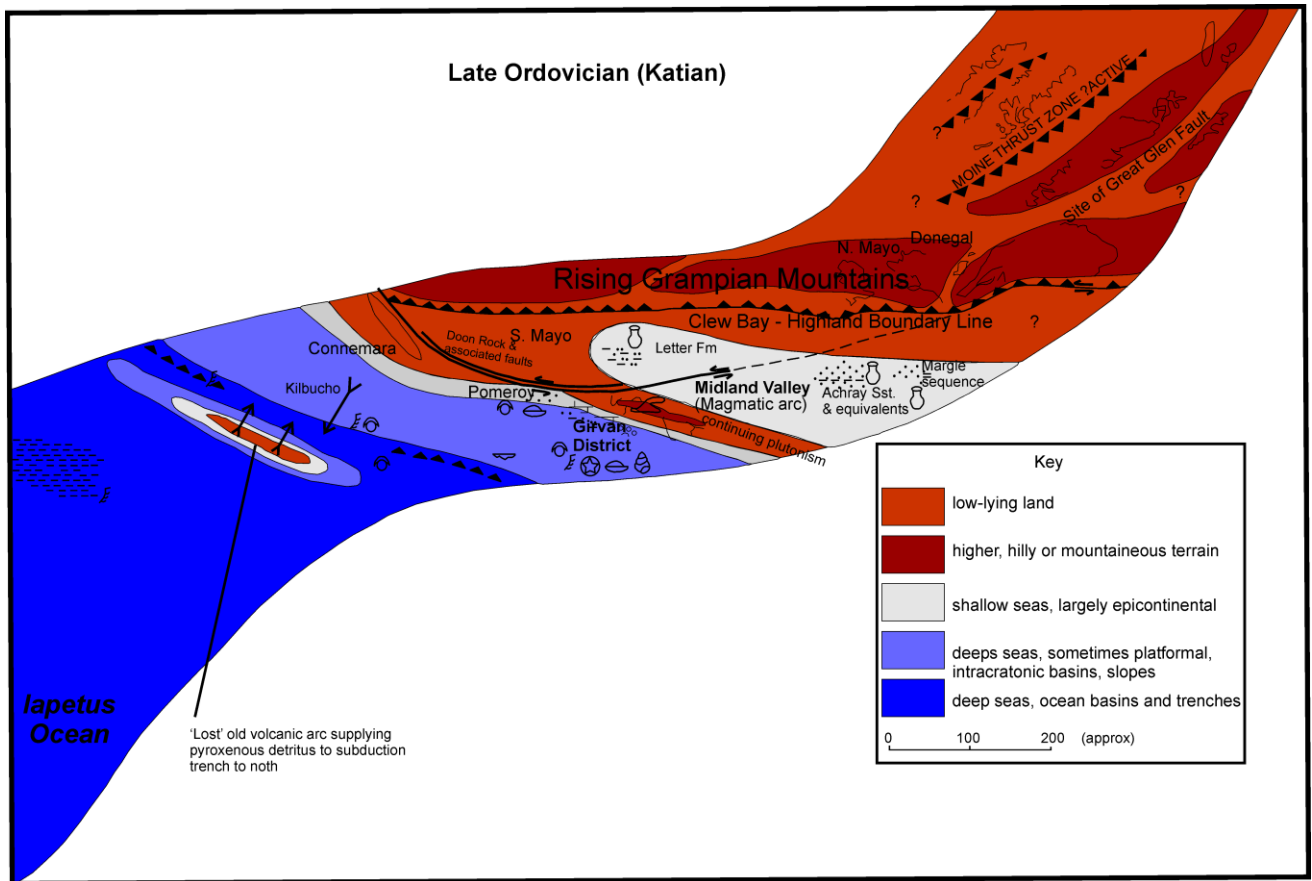


Figure 11. Regional palaeogeographic setting for the Girvan district in the Katian. Adapted from Bevens *et al.* (1992).

### Biogeographical evolution of the Craighead Limestone Formation fauna

Several authors have noticed the faunal similarity between the Late Ordovician ostracod faunas of North America and Scandinavia arguing that faunal migration between palaeocontinental Laurentia and Baltica was possible across the Iapetus Ocean by Late Ordovician time (e.g., Schallreuter & Siveter 1985; Vannier *et al.* 1989; Williams *et al.* 2001a, 2001b; Williams *et al.* 2003). This similarity progressively increased through the Sandbian and Katian marked by several common genera of trilobites, brachiopods (Cocks & Fortey 1990; Cocks *et al.* 1997) and ostracods (Williams *et al.* 2001b, 2003). Williams *et al.* (2003) discussed the broad patterns of Ordovician ostracod migrations between Laurentia, Avalonia and Baltica and demonstrated that the early peak of species migration from Baltica to

Laurentia was in the Sandbian-early Katian noting several genera common to these areas. The ostracods of the early Katian Craighead Limestone Formation confirm these links, suggesting strong migration of species from Baltica to Laurentia and some migrations towards Baltica (Fig. 9). Several of the ostracods in the Craighead Limestone Formation belong to genera whose species show tolerance to a wide range of environments from shallow to deep shelf: for example, *Platylolbina* (e.g., Kesling 1960a; Williams & Floyd 2000), *Kinnekullea* (e.g., Meidla 1996; Floyd *et al.* 1999; Williams *et al.* 2001b), *Krausella* (Copeland 1982), *Steusloffina* (e.g., Meidla 1996; Williams *et al.* 2001b; Schallreuter *et al.* 2008) and *Medianella* (Meidla 1996). The adaptation of ostracods to a wide range of shallow to deeper environments might have facilitated their migration between palaeocontinents, for example via island-hopping routes (see Fortey 1984; Schallreuter & Siveter 1985). Faunal migration may also have been influenced by climate, the northwards movement of Baltica and Avalonia into the tropics facilitating the migration of warm-water adapted taxa between these continental masses.

### Conclusions

The Upper Ordovician (Katian) ostracods of the Craighead Limestone Formation are characterized by two distinct ostracod assemblages: a shallow marine low diversity assemblage dominated by the palaeocope *Oepikella* with rare podocopes; and an open marine high diversity assemblage dominated by podocopes, especially *Steusloffina*, palaeocopes and binodicopes. The ostracod fauna contains species that facilitate broad correlation with Sandbian-early Katian age strata of North America. Biogeographically many of the ostracod taxa of the Craighead Limestone Formation have their probable origins in palaeocontinental Baltica and indicate the migration of Baltica species towards the tropics during the Late Ordovician. This is

consistent with supposed palaeogeographic changes as the Iapetus Ocean subducted, bringing Baltica and Avalonia within the tropics and in close geographical proximity to Laurentia.

## **Chapter 5: Marine Ostracod Provinciality in the Ordovician of Palaeocontinental Laurentia and its Environmental and Geographical Expression**

### **Abstract**

Analysis of the inter-regional distribution patterns of Ordovician Laurentian ostracods, focussing particularly on the diverse Late Ordovician Sandbian (ca 461 to 456 Ma) faunas, demonstrates strong endemism at the species-level. Local endemism is very pronounced, ranging from 25% (e.g. Foxe Basin) to 75% (e.g. Michigan basin) in each basin, a pattern that is also reflected in other benthic faunas such as brachiopods. Multivariate (ordination) analyses of the ostracod faunas allow demarcation of a Midcontinent Province and a southern Marginal Province in Laurentia. While these are most clearly differentiated at the stratigraphical level of the *bicornis* graptolite Biozone, analyses of the entire dataset suggest that these provinces remain distinct throughout the Sandbian interval. Differences in species composition between the provinces appear to have been controlled by changes in physical parameters (e.g. temperature and salinity) related to water depth and latitude and a possible regional geographic barrier, and these differences persist into the Katian and possibly the Hirnantian. Local environmental parameters, perhaps operating at the microhabitat scale, may have been significant in driving local speciation events from ancestor species in each region.

## Introduction

Ostracods are small bivalved crustaceans with a fossil record extending back to the Cambrian (Harvey *et al.* 2012). They are a diverse class of aquatic crustaceans (Schellenberg 2007), have a well-preserved fossil record (Pokorný 1978), and are known from more than 65,000 living and extinct species (Horne *et al.* 2002). Ostracods have adopted both benthic and pelagic lifestyles (Horne *et al.* 2002; Liebau 2005), but most ostracods in the fossil record are benthic: the weakly calcified shells of pelagic forms are not frequently preserved (Pokorný 1978). The earliest ostracods occupied shelf marine benthic environments during the Ordovician Tinn & Meidla 2004; Salas *et al.* 2007; Williams *et al.* 2008; Ghobadi Pour *et al.* 2011). Later, they colonised pelagic environments during the Silurian (Siveter *et al.* 1991) and radiated into non-marine aquatic environments during the Carboniferous (Bennett 2008; Bennett *et al.* 2011). Ordovician benthic ostracod distribution patterns have been used to identify biogeographical provinces (e.g. Vannier *et al.* 1989; Williams *et al.* 2003; Meidla *et al.* in press), to establish facies-dependent patterns (e.g. Vannier *et al.* 1989) and to track the relative movement of palaeocontinents (Schallreuter & Siveter 1985). As well as palaeogeographical controls on the distribution of benthic ostracods, environmental effects of temperature, substrate, food-supply and water depth are also influential (e.g. Vannier *et al.* 1989; Copeland 1982; Becker & Bless 1990; Cronin & Dowsett 1999; Williams & Siveter 1996; Wood & Whatley 1994). Discrete latitudinal (climatically) controlled biotopes have been identified in Cenozoic fossil ostracod faunas (Cronin & Dowsett 1990; Wood & Whatley 1994).

In this chapter I evaluate the distributional patterns of the Ordovician ostracods of palaeocontinental Laurentia (Cocks & Torsvik 2011) focussing particularly on the faunas of Sandbian age as these are amongst the most widely studied and best known of all Ordovician ostracod assemblages (Copeland 1965, 1982; Williams & Siveter 1996; Harris 1957; Swain 1957, 1962; Kraft 1962). Laurentian Ordovician ostracods spanned a palaeolatitudinal range from 13°N to 25°S, which encompassed tropical and sub-tropical climate zones (Vandenbroucke *et al.* 2010a, b); they occupied a range of marine environments from peri-tidal to deep shelf, and they occur in both carbonate and clastic sedimentary deposits. Therefore, potential latitudinal and depth-related changes in temperature, substrate, productivity, oxygenation-level and salinity may be expressed in the different spatial ranges of individual taxa and ostracod biotopes. Although such patterns have previously been discerned from evaluation of ostracod presence-absence data for individual formations (e.g. Copeland 1982; Williams & Siveter 1996), this is the first attempt to integrate data for the whole Laurentian palaeocontinent for specific time intervals using multivariate statistical techniques.

### Methodology

Unlike fossil Ordovician plankton, whose distribution patterns can be evaluated from global datasets (e.g. Vandenbroucke *et al.* 2009b, 2010a, b; Cooper *et al.* 1991), ostracods possessed no pelagic stage in their lifecycle and their primary distribution at the inter-continental scale was therefore largely controlled by geography and bathymetry (e.g. Vannier *et al.* 1989; Schallreuter & Siveter 1985). Nevertheless, distribution patterns analysed on a continent-by-continent

basis may still reflect latitudinal or environmental signatures. The research methodology used here is based on multivariate statistical assessment of presence-absence data for Laurentian species from well-defined time intervals within the Sandbian, specifically the *gracilis* and *bicornis* graptolite biozones (Cooper & Sadler 2004). The ‘time slab’ approach is a common method used to deal with large fossil datasets for environmental reconstruction (Dowsett 2007; Dowsett *et al.* 2010) and has recently been used for Late Ordovician zooplankton of Sandbian age (Vandenbroucke *et al.* 2009b, 2010a, b).

### Ostracod Database

A Sandbian dataset (for stratigraphical definition see following section) comprising 13 regions with 229 ostracod species from 88 genera was compiled from published literature (Table 1, Appendix 1). Taxonomic filtering of the original literature data was essential to minimise error as species nomenclature has evolved over the 80 years since the first descriptions of North American Ordovician ostracods (e.g. Williams & Siveter 1996; Ulrich 1894; Kay 1934, 1940; Harris 1931; Swain 1996; Swain *et al.* 1961; Kesling 1960a, b; Copeland 1977a, 1982; 2000; Warshauer & Berdan 1982; Williams *et al.* 2001a; Mohibullah *et al.* 2011; Chapter 3). Taxa described in open nomenclature or identified as “cf.” and “?” were examined and only those which closely resembled their holotype were included. Taxa described as “aff.” were excluded. And, taxa only identified to genus level were also excluded in order to avoid ‘noise’ in the analysis. All of the species are weighted from 1 to 4 using the following criteria, with 4 being the most reliable: 4, morphologically distinctive (lobation, marginal structures etc.), well described, stable

nomenclatorial history (e.g., *Monoceratella teres* Teichert, 1937); 3, most recent descriptions taxonomically sound, some history of misidentification (e.g., *Eoaquapulex socialis* (Levinson, 1961); 2, some history of misidentification and described in open nomenclature (e.g., *Krausella? spinosa* (Harris, 1957); and 1, simple morphology (i.e. carapace with few or no diagnostic characters, or morphological variation poorly defined or poorly described, long history of open nomenclature (e.g., *Eurychilina? aff. Chilobolbina hyposulcata* sensu Kraft, 1962. Most taxa fell into categories 4 and 1. Taxa with a weighting of '1' were excluded from the analysis. In our assessment of the ostracod assemblage dataset we have identified the primary sedimentary setting, taphonomy, lithology, palaeolatitude and sampling points (summarised in Table 1).

## Chapter 5: Marine Ostracod Provinciality in the Ordovician of Laurentia

Lithostratigraphy	Samples	Lithofacies	Depositional environment	Taphonomy	Palaeo-latitude	Location	Basin	No. of sampling points	No. of species	No. & % ge of endemic species in each basin	References
Lincolnshire Formation	1a	Limestone and chert	Mid to outer ramp	Apparently autochthonous	25°S	Virginia	Eastern basin Shenandoah valley basin	15+	22	Collectively 27 (57%) out of 47 species from Virginia are endemic	Kraft 1962
Edinburg Formation	1b	Argillaceous limestone & calcareous shales	Outer ramp	Apparently autochthonous	25°S	Virginia		20+	43		Kraft 1962
Crown Point Formation	2a	Limestone	Inner ramp	Apparently autochthonous	22°S	New York	Appalachian basin	10+	34	Collectively 24 out of 49 (49%) species from the Appalachian basin are endemic	Swain 1957, 1962
Valcour Formation	2b	Limestone & dolomite	Inner ramp	Apparently autochthonous	22°S	New York		5+	3		
Loysburg Formation	3a	Limestone & dolomite	Mid ramp	Apparently autochthonous	22°S	Pennsylvania		5+	12		
Hatter Formation	3b	Limestone	Peritidal	Apparently autochthonous	22°S	Pennsylvania		5+	14		
Benner Formation	3c	Limestone	Peritidal	Apparently autochthonous	22°S	Pennsylvania		5+	9		
Lexington Limestone	5	Limestone	Inner ramp	Apparently autochthonous	20°S	Kentucky		4	6		Warshauer & Berdan 1982
Balclatchie Formation	4a	Mudstones	Deep marine mudstones	Allochthonous	21°S	Girvan, Scotland	Girvan basin	?	2	0 (allochthonous, so no endemic species)	Williams et al. 2001
Ardwell Farm Formation	4b	Mudstones	Deep marine mudstones	Allochthonous	21°S	Girvan, Scotland		2+	5		Williams et al. 2001; Mohibullah et al. 2011
Bucke Formation	6	Limestone, dolomite and shales	Inner ramp	Apparently autochthonous	17°S	Ontario, Canada	Timiskaming outlier	20+	49	26 (53%)	Copeland 1965
Bony Falls Limestone	7	Limestone	Inner ramp	Apparently autochthonous	13°S	Michigan	Michigan basin	10+	12	9 (75%)	Kesling 1960a, b
Bromide Formation	8a, 8b	Limestone with few interbedded shales and sandstone	Peritidal to Mid ramp	Autochthonous	13°S	Oklahoma	Oklahoma Aulacogen	100+	53	29 (56%)	Williams & Siveter 1996
Hull Formation	9	Limestone & shales	Inner ramp	Apparently autochthonous	13°S	Ontario, Canada	Ottawa basin	?	17	5 (29%)	Kay 1934
Platteville Formation	10a	Limestone	Open marine shelf	Apparently autochthonous	11°S	Platteville, Minnesota	Illinois basin	?	18	16 (42%) out of 38 species from the Illinois basin are endemic	Swain 1996
Spechts Ferry Member Decorah Formation	10b	shales with few thin beds of Limestone	Open marine subtidal shelf	Apparently autochthonous	11°S	Minnesota NA		?	20		Swain et al. 1961
Glenwood Formation	10c	Shales	Outer shelf	Apparently autochthonous	10°S	Glenwood, Minnesota		?	5		Swain 1996
Silliman's Fossil Mount	12	Calcareous shales & Limestone	Mid to outer ramp	Apparently autochthonous	5°N	Franklin, Canada	Foxe basin	20+	30	8 out of 32 species (25%) are endemic	Copeland 1977a
Frobisher Bay Formation	11	limestone with some interbedded shales	Inner ramp	Apparently autochthonous	3°N	Baffin Island Nunavut, Canada		?	4		Copeland 2000
Lower Esbataottine Formation	13	Limestone	Inner to mid-ramp	Apparently autochthonous	13°N	Mackenzie, Canada	Root River basin	30	31	20 (65%)	Copeland 1982

Table 1. Sandbian ostracods of North America, Canada and southwest Scotland. Distribution shown by lithology, depositional setting, palaeolatitude, sampling points, taphonomy, total number of species in each Formation and basin and the number and percentage of endemic species in each depositional basin.

### Time Slab Definition

The Sandbian Stage of the Upper Ordovician has been selected as a time slab for this study. It represents an interval of rock deposited from approximately 461 to 456 million years ago (Cooper & Sadler 2004) and is well defined by the first appearance of the graptolite *Nemagraptus gracilis*. The graptolite *Ensigraptus caudatus* defines the base of the succeeding Katian Stage (Fig. 1). The Sandbian is thought to represent the onset of a cooling Ordovician climate, but there is no evidence for significant climate fluctuation within the interval itself (Vandenbroucke *et al.* 2009b, 2010a, b). Within the Sandbian interval some 229 ostracod taxa are described (from 13 regions; Fig. 2), of which 56 taxa are specifically limited to the *gracilis* Biozone (ca 3 million years duration) and 117 taxa to the *bicornis* Biozone (ca 2 million years duration; see Cooper & Sadler 2004 for chronology). We have analysed the distribution patterns of ostracods for the *gracilis* Biozone (5 regions) and the *bicornis* Biozone (11 regions). Analysis of the total (Sandbian) fauna (13 regions) was also undertaken.

Graptolites are the main biostratigraphic markers used for correlating our chosen rock successions together with the coeval conodont biozones (Bergström 1986). Here the upper *Pygodus anserinus* and lower *Amorphognathus tvaerensis* (*Prioniodus variabilis* Subzone) conodont Biozones are considered equivalent to the *gracilis* graptolite Biozone and the upper *A. tvaerensis* Biozone (*Prioniodus gerdæ* and *Prioniodus alobatus* subzones) as equivalent to the *bicornis* graptolite Biozone (Bergström 1986; Bergström *et al.* 2009). In some cases we have also used shelly fossils and chitinozoans for stratigraphic correlation (Mohibullah *et al.* 2011; Chapter 3).

Chronostratigraphy					Graptolites				Conodonts & chitinozoans				
System	Inter-national Series	Inter-national standard stages	British regional series and stages		North American regional stages	Scottish biozones	North American biozones	Welsh biozones	North Atlantic conodont biozones	North American midcontinent conodont biozones	North American chitinozoan biozone		
Ordovician ( <i>pars</i> )	Upper Ordovician	Katian ( <i>pars</i> )	Ashgill ( <i>pars</i> )	Pusgillian	Maysvillian	<i>linearis</i>	<i>pygmaeus</i>	<i>linearis</i>	<i>superbus</i>	<i>velicuspis</i>	<i>pygmaea/cristata spongiosa</i>		
				Streffordian		Edenian	<i>clingani</i>	<i>morrisi</i>		<i>spiniferus</i>		<i>clingingi</i>	<i>morrisi</i>
				Cheneyan	Chatfieldian			<i>caudatus</i>		<i>ruedemanni</i>	<i>caudatus</i>		
						<i>americanus</i>							
		Sandbian	Caradoc	Burrellian		<i>bicornis</i>	<i>bicornis</i>	<i>multidens</i>	<i>taerensis</i>	<i>alobatus</i>	<i>tenuis</i>	<i>gracqui multispinata/duplicitas primitiva</i>	
				Turinian	<i>undatus</i>								
	Middle Ordovician	Darriwilian	Llanvirn	Llandeilian			<i>teretiusculus</i>	<i>teretiusculus</i>	<i>anserinus</i>	<i>gerdae</i>	<i>compressa</i>	<i>S. sp. A</i>	
				Abereiddian			<i>murchisoni</i>	<i>murchisoni</i>		<i>quadrifidactylus</i>			
							<i>artus</i>	<i>artus</i>		<i>variabilis</i>	<i>aculeata</i>	<i>hirusta L.sp. A</i>	
										<i>seera</i>	<i>sweeti</i>	<i>friendsvillensis</i>	<i>jenkinsi</i>

Figure 1. 'Sandbian time-slab' (shaded). Between the first appearance of *N. gracilis* and the beginning of the *D. clingani* graptolite Biozone. The graptolite ranges follow Bergstrom *et al.* 1998; 2000; Williams *et al.* 2004; Loydell 2012; Zalasiewicz *et al.* 2009. The conodont data are from Bergstrom, 1986 and chitinozoans are after Achab 1989. The correlation between the graptolite, conodont, and chitinozoan biozones follows Webby *et al.* (2004).

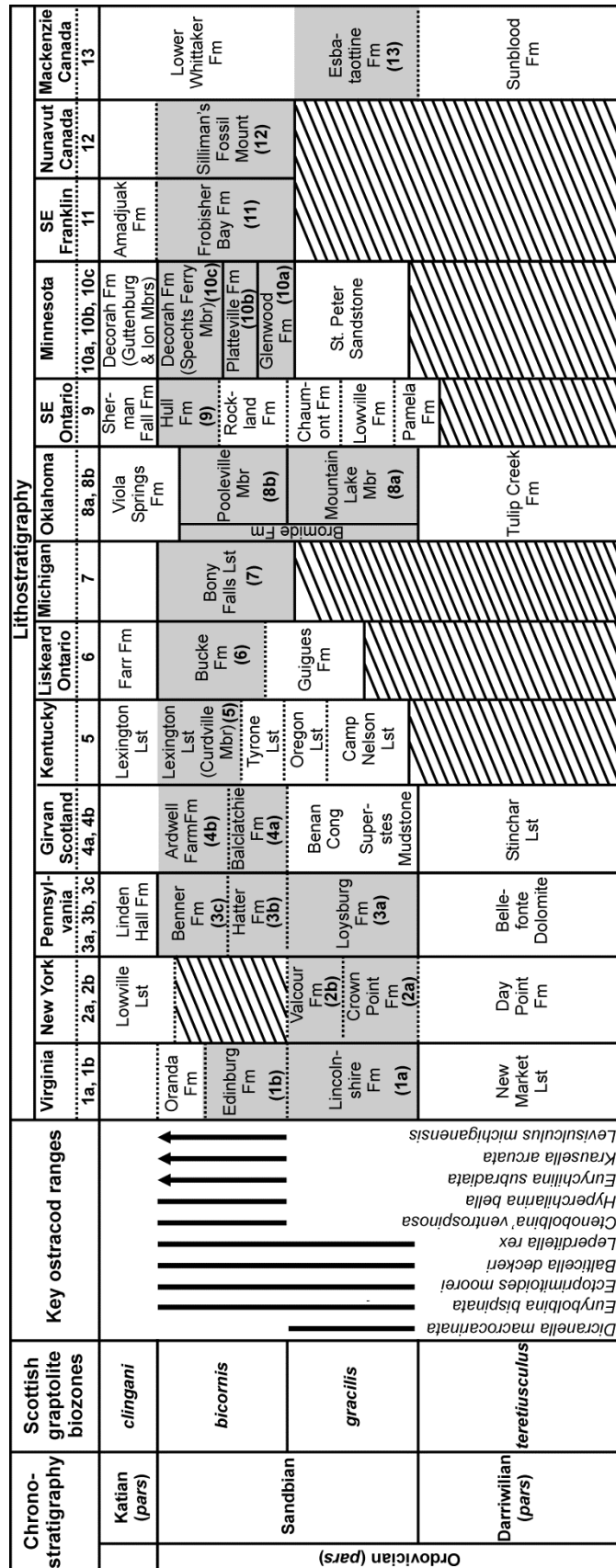


Figure 2. Ordovician chronostratigraphy and lithostratigraphy for North America, Canada, and the Girvan district, southwest Scotland. The North American stratigraphy follows Ross *et al.* 1982, Canadian stratigraphy follows Barnes *et al.* 1981 and Girvan is based on Williams *et al.* 2001a; Ingham, 2000. The Sandbian sections from which ostracods are documented and included in this study are highlighted grey.

## Geographical spread of data

Laurentia was selected for analysis because it yields one of the most diverse and geographically widespread ostracod faunas from the Late Ordovician (Sandbian) and because it includes a broad latitudinal range (greater than  $35^{\circ}$ ; Fig. 3) and a wide range of palaeoenvironments (Williams *et al.* 2003). We have also compared the Sandbian ostracod dataset from Laurentia with those of Avalonia (for the *gracilis* Biozone time slab) to show the relevant influence of inter-continental versus intra-continental environmental and geographical effects.

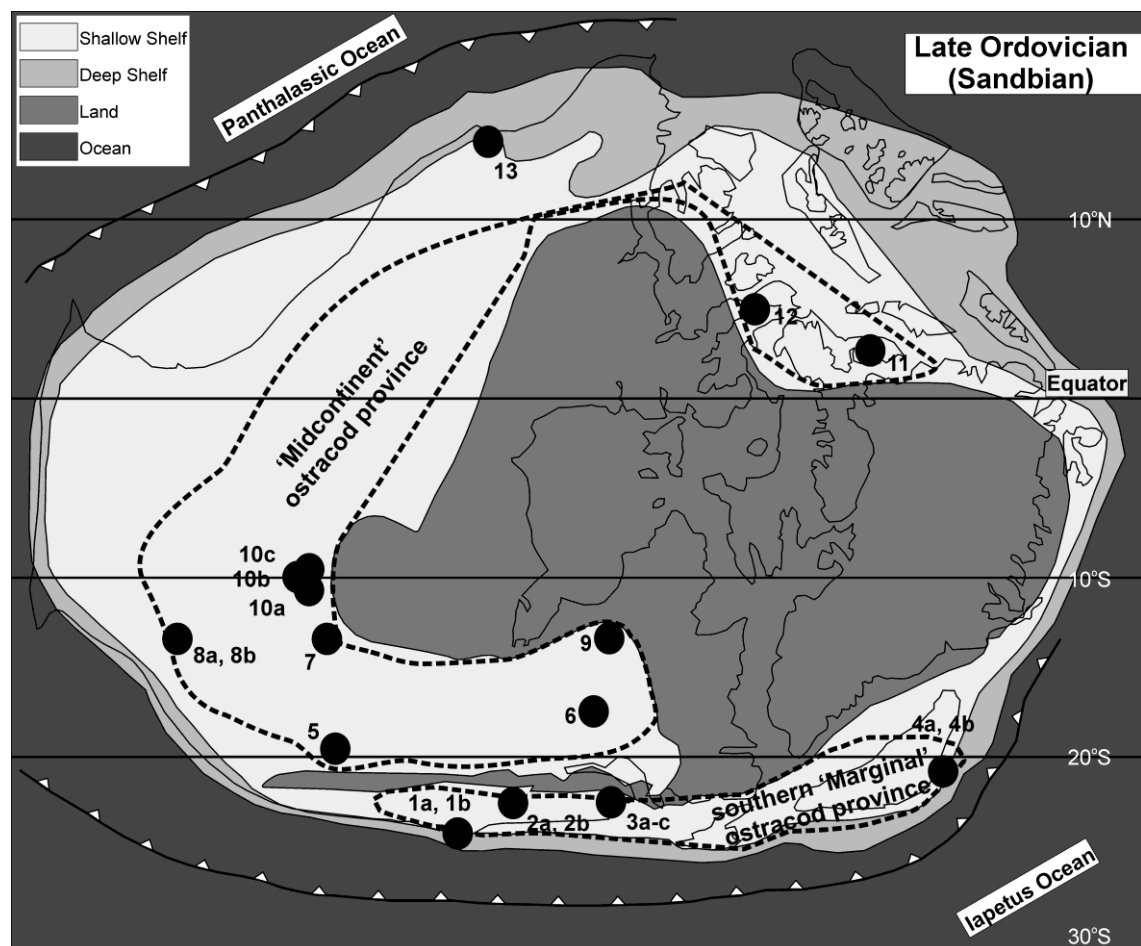


Figure 3. Late Ordovician (Sandbian) palaeogeography of Laurentia, the distribution of ostracod-bearing localities, and the two faunal provinces (map slightly modified after, Cocks and Torsvik, 2011).

### Ordination analysis

Ordination is a tool that allows the representation of complex multivariate datasets in simple diagrams in which the axes represent the main gradients in species composition in the original dataset. These ordination axes thus represent environmental gradients (ideally the gradient of an environmental variable, but mostly a combination of several variables) which drive the gradient in species composition. In ordination diagrams, samples (species) are ordered with respect to one another on the basis of their species composition (occurrence in the sample set) (Jongman *et al.* 1993). The samples that show more taxonomic resemblance are placed more closely to each other, whereas samples that show greater difference are placed apart. The ordination gives a better visual representation of the data (ordination diagrams) than does cluster analysis, because ordination diagrams are better at representing the distances (in CA chi-square distances) between all of the samples simultaneously. I chose CA (based on the assumption of underlying unimodal relationships between the species and the environmental gradients in the specific data set, as opposed to linear techniques such as Principal Components Analysis which are based on underlying linear relationships) because a preliminary DCA revealed a high degree of turnover in the data set (suggestive of unimodal relationships; length of gradient > 6 SD, cf. Jongman *et al.* 1995). I used CA (i.e. an analysis without explicitly introducing the environmental variables in the ordination model, as in CCA; see below), because I could then look at what the species data tell us regarding the similarities between the localities. To test whether we find a statistically significant relationship between the 'environmental' variables (in our case paleolatitude and stratigraphy) I then used CCA (canonical

correspondence analysis) because this allows one to explicitly statistically test the strength of relationships between species gradients (ordination axes) and 'environmental' gradients. I did not use multidimensional scaling (based on similarity tables) because this is more limited for hypothesis testing. The relationship between species and paleolatitude and stratigraphy (early versus late Sandbian) was tested, not that with substrate or water depth (as these data are not easily available). In interpretation, the observed differences are inferred and could be related different environmental variables e.g water depth.

Four datasets were analyzed. I first performed a test to assess the strength of the inter-continental geographical effect on the distribution of ostracods, selecting the early Sandbian *gracilis* Biozone interval (ca 3 million years duration from 461 Ma), with five localities from Avalonia and six localities from Laurentia. I then analysed the Laurentian dataset for three time intervals, the *gracilis* Biozone (ca 3 million years), the *bicornis* Biozone (ca 2 million years), and the entire Sandbian (ca 5 million years). In order to test whether a significant stratigraphical or latitudinal/geographic signal was present in the entire Sandbian dataset, we used the direct equivalent of CA, viz. Canonical Correspondence Analyses (CCA) with stratigraphy (dummy variables for *gracilis* and *bicornis*) and palaeolatitude (absolute values of degrees palaeolatitude) as the only variables respectively. CCA result with only latitude as environmental variable: trace 0,700, F-ratio 1,720, p-value 0,0002,; CCA with stratigraphy as environmental variable (so two dummy variables for early and late Sandbian): trace 0,477, F-ratio 1,133, p-value 0,1824. Significance was tested using Monte Carlo permutation tests (4999 unrestricted permutations,  $p < 0,001$ ).

## Discussion

### Inter-continental geographical analysis

For much of the Ordovician, Laurentia was separated by the Iapetus Ocean from the palaeocontinents of Baltica and Avalonia, though this ocean narrowed by the Late Ordovician (Cocks & Torsvik 2005). During the Sandbian no species are common between Laurentia and Avalonia and only a few genera are common: *Eridoncha* during the early Sandbian (*gracilis* Biozone), and *Ceratopsis* and *Easchmidtella* during the late Sandbian (*bicornis* Biozone; (Williams & Siveter 1996; Siveter 2009). Our results thus support the suggestion that palaeogeography exerted the strongest control over the global distribution of Ordovician ostracods (e.g. Schallreuter & Siveter 1985). Evidently, as there are no species in common, CA analysis for the early Sandbian (*gracilis* graptolite Biozone) shows Avalonian and Laurentian localities as two discrete clusters of samples (data not shown). Ostracod fauna from the early Katian (*clingani* Biozone) of Avalonia are sparse, only six species being documented and none of these are common to Laurentia (Siveter 2009). However, by the mid-late Katian and while the Iapetus Ocean was closing the Avalonian fauna became more similar to that of Laurentia at the generic level (Schallreuter & Siveter 1985) and by the late Katian included the earliest common species (see Williams *et al.* 2001b).

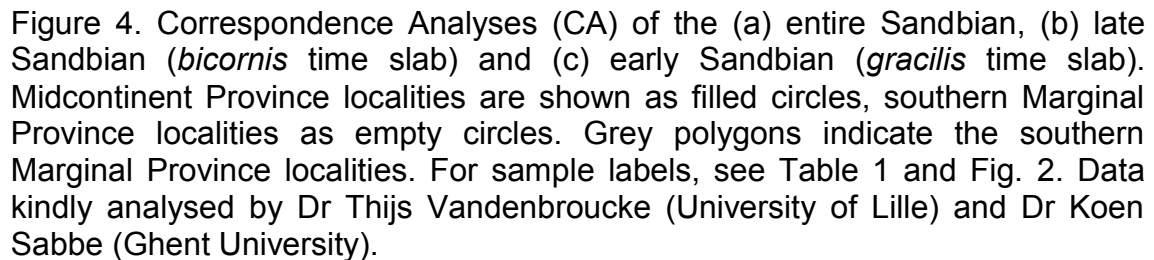
### Analysis of the Sandbian Laurentian dataset

A preliminary CA analysis (not shown) identified the samples from Kentucky (5), Michigan (7) and Mackenzie (13) as outliers. These three samples are characterized by the highest percentages (> 65 %) of endemic species in the

whole dataset, and were therefore omitted from further analyses. CA analysis of the entire Sandbian (*gracilis* and *bicornis* biozones) ostracod fauna revealed a clear latitudinal signal, with all southern marginal localities lying on the right side of the first CA axis, and most midcontinent localities on the left (Fig. 4a); this relation with latitude was highly significant (CCA,  $p < 0.001$ ). Thus, discrete Midcontinent and Marginal ostracod provinces can be recognised. The more or less intermediate position of Oklahoma is not surprising, as this was an aulacogen (Longman 1982) that straddled the shelf to basin and therefore contained elements that are both midcontinent and marginal. No significant stratigraphical signal was present (CCA,  $p > 0.05$ ). Indeed, samples from regions for which both *gracilis* and *bicornis* materials were available (Virginia, Pennsylvania and Oklahoma) consistently cluster together on the basis of region, not stratigraphy (Fig. 4a).

#### Analysis of the *bicornis* graptolite Biozone Laurentian dataset

As in the entire Sandbian dataset analysis (see 3.2), two ostracod provinces can be distinguished for the *bicornis* graptolite Biozone time slab (Fig. 4b). These are based on 173 species from 11 regions extending from Arctic Canada to Oklahoma (1b, 3b-c, 4a-b, 5, 6, 7, 8b, 9, 10a-c, 11 & 12 on Figs 2, 3; Table 1). The ostracod fauna at the geographical margins of Laurentia (1b, 3b-c, 4a-b on Figs 2, 3) shows considerable taxonomic difference from the midcontinent Laurentian fauna (Minnesota, Michigan, Kentucky, Ontario, Franklin District; 5, 6, 7, 9, 10a-c, 11 & 12 on Figs 2, 3). Oklahoma (8b on Figs 2, 3) represents the only midcontinent locality showing strong similarities with the marginal Laurentian assemblages (cf. 3.2). The Midcontinent Province comprises 48



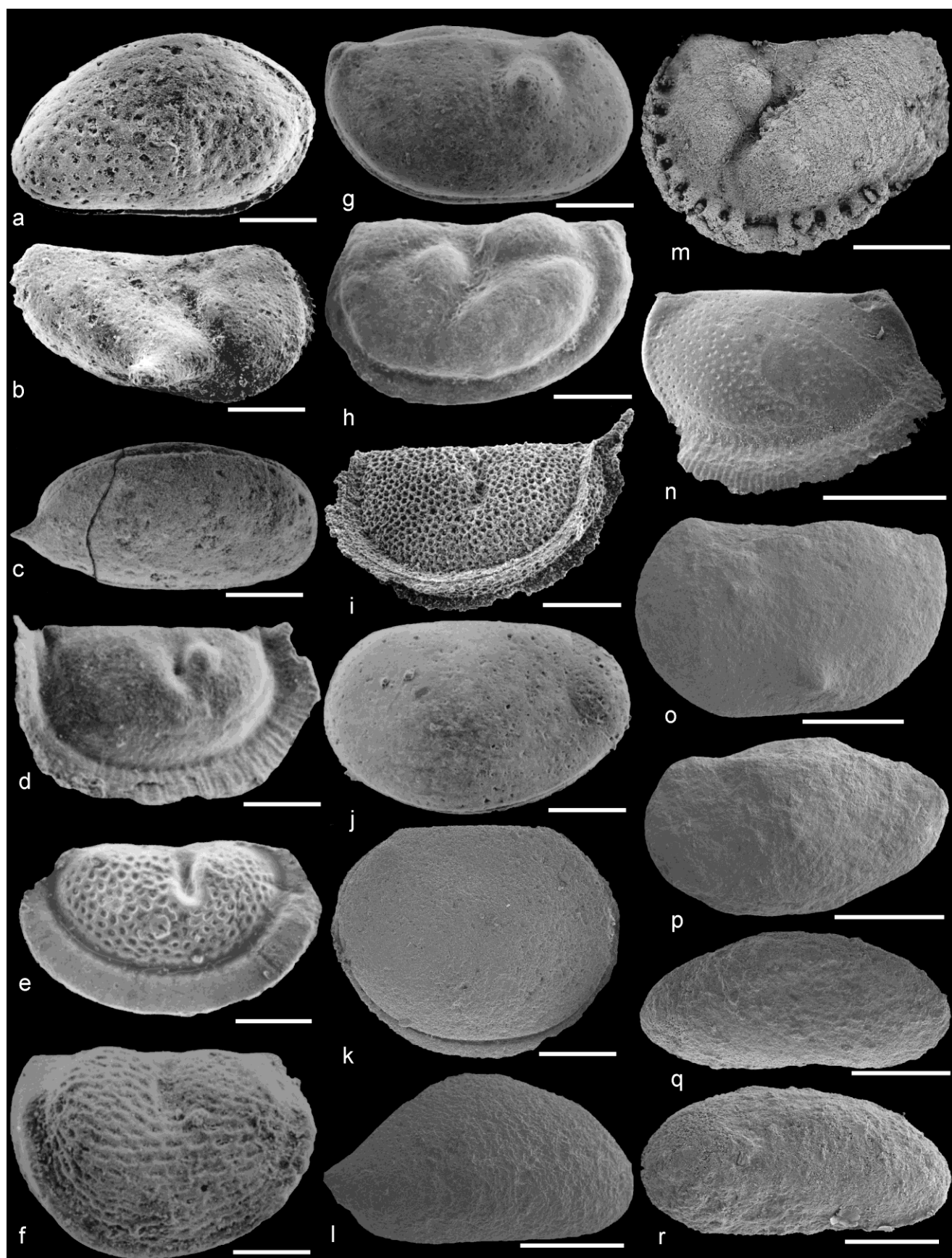


Figure 5. Late Ordovician ostracods of the Midcontinent and Marginal provinces and widespread (pandemic-Laurentian) assemblages of palaeocontinental Laurentia. (a-c) Sandbian Midcontinent Province assemblage; (d-l) Sandbian ostracod assemblage widespread in both the Midcontinent and south Marginal provinces; (m) Sandbian south Marginal Province assemblage; (n-r) Katian Marginal Province assemblage. (a) NMH UK OS13634 *Punctaparchites rugosus* (Jones, 1858), carapace, right lateral view. (b) NMH OS13479 *Winchellatla longispina* Kay, 1940, tecnomorphic right valve, lateral view. (c) MCZ4646 *Krausella calvini* (Kay, 1940), carapace right lateral view. (d) NMH OS13509 *Eurychilina indivisa* Levinson, 1961, juvenile tecnomorphic right valve, lateral view. (e) NHM UK I13216 *Eurychilina reticulata* Ulrich, 1889, heteromorphic right valve, lateral view. (f) NMH OS13535 *Hallatia labiosa* (Ulrich, 1894) tecnomorphic right valve, lateral view. (g) NMH OS13617 *Balticella deckeri* (Harris, 1931), carapace, right lateral view (h) MCZ 4599b *Eohollina depressa* (Kay, 1940), tecnomorphic carapace, right lateral view (i) NMH OS13538 *Eurybolbina bispinata* (Harris, 1957), juvenile tecnomorphic left valve, lateral view. (j) NMH OS13526 *Eoaquapulex socialis* (Levinson, 1961) tecnomorphic left valve, lateral view. (k) GSE 15387 *Baltonotella parsispinosa* (Kraft, 1962), carapace, left valve, lateral view (l) GSE 15385 *Krausella variata* Kraft, 1962, right valve, lateral view. (m) GSE 15384 *Hippula ventrospinosa* Kraft, 1962, heteromorphic, left valve, lateral view (n) BGS 16E1961 *Oepikella tunnicliffi* Williams & Floyd, 2000, heteromorphic right valve, lateral view. (o) MPA49672, *Balticella* sp., carapace, left lateral view. (p) GSE15354 *Steusloffina cuneata* (Steusloff, 1895), carapace, left lateral view. (q) GSE15360, *Longiscula* sp., carapace, left lateral view. (r) GSE15365, *Longiscula?* sp., carapace, right lateral view. Figs (a-d, f-h, j) are from the Bromide Formation of Oklahoma; (e) is from St. Paul's Minnesota; (l) is from the Edinburg Formation of Virginia; (k-m) are from the Ardwell Farm Formation, Girvan district, Scotland; (N-R) are from the Craighead Limestone Formation, Girvan district, Scotland. Scale bar (A) 0.2 mm; (b) 0.25 mm; (c) 0.294 mm; (d) 0.338 mm; (e) 0.32 mm; (f) 0.193 mm; (g) 0.205 mm; (h); 0.346 mm; (i) 0.346 mm; (j) 0.545 mm; (k-m, o, p) 0.5 mm; (n) 0.1 mm; (q, r) 0.2 mm. Repositories for specimens are: NHM UK, Natural History Museum, London; MCZ Museum of Comparative Zoology, Harvard University; GSE, British Geological Survey, Keyworth, Nottingham.

#### Analysis of the *gracilis* graptolite Biozone Laurentian dataset

The ostracod fauna from the *gracilis* graptolite Biozone of Laurentia includes materials from Virginia, New York, Pennsylvania, the Mackenzie District (Canada), and Oklahoma (1a, 2a-2b, 3a, 8a & 13 on Figs 2, 3). Out of 111 species 88 species are endemic to a single basin and only a few species (23) are common to several localities (appendix 3). CA analysis of this limited

*gracilis* dataset suggests the presence of a latitudinal signal (Fig. 4c), but more data are needed to confirm this.

### **‘Midcontinent’ and ‘Marginal’ ostracod provinces explored**

The midcontinent was characterised by carbonate platforms, whilst the margins were typically ramp settings characterised by carbonates and mudstones with a broader range of facies from peri-tidal to outer ramp settings. Studies of bryozoans, corals, conodonts and trilobites (Bergström 1973; Tuckey 1990; Fortey & Cocks 2003; Anstey *et al.* 2003; Webby *et al.* 2004) have distinguished discrete Laurentian provinces in the Ordovician, largely controlled by depth-related lithofacies, climate and sea level change. All the above mentioned faunal groups broadly show the same distribution pattern as the ostracods. Each displays distinct marginal faunas which differentiate them from the midcontinent faunas (Tuckey 1990). The ostracod distribution patterns can be closely correlated with those for brachiopods. The Middle and Late Ordovician brachiopod faunas show shallow benthic brachiopod assemblages in midcontinent Laurentia, whereas a broader range of brachiopod biofacies were developed in both eastern and western margins of the palaeocontinent (Potter & Boucot 1992).

The factors that may control the two ostracod provinces are those associated with geography, water depth (e.g. temperature, salinity), latitude (climatic), and substrate.

### Geography

The Palaeozoic geography of Laurentia has been reviewed and discussed in detail by Cocks and Torsvik (2011) by piecing together information from palaeomagnetic studies and faunal distribution patterns. They demonstrated that for most of the Ordovician the central part of the Laurentian craton was stable whereas the margins were tectonically active. Eperic seas also repeatedly flooded the Laurentian craton that resulted in thick successions of Ordovician carbonate platforms (Cocks & Torsvik 2011; Pruss *et al.* 2010). The distribution patterns of most of the fossil groups that show distinct assemblages in the marginal and midcontinent regions are widely regarded as differences between depositional environments (Cocks & Torsvik 2011; Fortey & Cocks 2003; Anstey *et al.* 2003; Zhen & Percival 2003). However, a peninsular land mass existed between the different regions and may, at least, have partly separated the southern margin from the midcontinent area (see Cocks & Torsvik 2011). This landmass might have formed a geographic barrier for exchange of ostracods and other benthic faunal groups.

### Substrate

Seabed substrate is recognised as an important factor in the distribution of Ordovician ostracods at a continental scale (Vannier *et al.* 1989). For example, the carbonate facies of Baltoscandia are dominated by palaecope-rich assemblages, whereas those from the Armorican Massif are dominantly mudstone lithofacies with binodicope-rich assemblages (Vannier *et al.* 1989). The dominance of binodicope is also noticed in the Ordovician mudstones of Saudi Arabia and southern Britain (Vannier *et al.* 1989). The Laurentian dataset

includes ostracods sourced from both clastic, carbonate and mixed carbonate-clastic lithologies (Table 1). Palaeocopes are the dominant group (see Appendix 1) in both the carbonates and mudstones. For example, the high diversity fauna of the shale unit of the Bucke Formation of Ontario is dominated by palaeocopes (Copeland 1965) as are the limestone facies of the Hatter and Benner formations of Pennsylvania (Swain 1962). Thus, the dominance at mid to high palaeolatitude (Armorican Massif, Saudi Arabia and southern Britain) by binodicopes, whilst low palaeolatitudes (Baltoscandia, Laurentia) are dominated by palaeocopes may also be related to latitudinal temperature change and not to substrate control alone. Therefore, while substrate may have affected ostracods at the very local level, perhaps indicated by the high degree of species-level endemism in each basin, it is not clearly expressed in the distribution patterns of binodicope-rich and palaeocope-rich ostracod assemblages at a provincial scale in Laurentia.

### Water depth

In previous studies of Late Ordovician ostracods water depth has been considered to have a strong influence on the distribution of ostracods (Copeland 1982; Williams & Siveter 1996; Mohibullah *et al.* 2010; Chapter 4). Copeland (1982) identified two biofacies in the lower Esbataottine Formation of the Mackenzie district, Canada, a distinct deeper platform biofacies and a shallow shelf biofacies that also has some elements extending into deeper shelf facies (Copeland 1982). Similarly, Williams and Siveter (1996) recognised a peri-tidal ostracod biofacies and an open-shelf biofacies in the carbonate ramp setting of the Bromide Formation of Oklahoma. However, the shallow and deep shelf

assemblages of the lower Esbataottine Formation are of questionable significance when the ostracod fauna is considered on the continental scale. Most of the supposed deeper platform taxa of the lower Esbataottine Formation are found in shallow marine facies elsewhere. These include species of the genera *Eohollina*, *Platyrhomboides*, *Dicranella*, *Cryptophyllus*, *Winchellatia*, *Baltonotella*, *Tetradella* and *Euprimitia*. The former six of these are found in shallow to deep shelf facies of the Bromide Formation of Oklahoma, whereas species of *Euprimitia* are found in shallow shelf facies of the Crown Point Formation of New York and species of *Tetradella* are present in the shallow shelf facies of the Hull Formation of Ontario (Williams & Siveter 1996; Swain 1962; Kay 1934). Copeland's (1982) water depth assemblages were based on generic-level assessments, which may be, at best, diagnostic only locally and cannot be traced on the pan-Laurentian scale (Copeland 1982). The Bromide Formation's shallow and deep shelf assemblages have only a few species that are widespread elsewhere. Some of the diagnostic deep shelf taxa of the Bromide Formation of Oklahoma such as *Baltonotella parsispinosa* are also present in the shallow shelf facies of the Crown Point Formation of New York and deep shelf facies of the Edinburg Formation of Virginia (Williams & Siveter 1996; Swain 1962; Kraft 1962). Similarly, *Eurybolbina bispinata* that occurs only in the deep shelf of the Bromide Formation is also present in the shallow to deep shelf facies of the lower Esbataottine Formation of the Mackenzie District and deep shelf facies of the Lincolnshire and Edinburg formations of Virginia (Copeland 1982; Williams & Siveter 1996; Kraft 1962). Nevertheless, analysis of the pan-Laurentian dataset does identify some diagnostic species that characterize shallow and deep shelf facies of the Bromide Formation in similar

settings elsewhere. *Leperditella rex* in peri-tidal and innermost shelf facies of the Bromide Formation is also present only in the peri-tidal facies of the Hatter and Benner formations of Pennsylvania and the inner shelf facies of the Bucke Formation of Ontario (Williams & Siveter 1996; Swain 1962; Copeland 1965). The distribution patterns of the Laurentian ostracod fauna may therefore reflect some depth-related physical parameters between the 'Marginal' and the 'Midcontinent' provinces.

### Latitude

Palaeoenvironmental change associated with palaeolatitude exerted a strong influence on the distribution of fossil marine organisms (Wood & Whatley 1994; Vandenbroucke *et al.* 2010a, b). The distribution patterns of zooplankton have already been shown to reflect climate zones in the Palaeozoic, Mesozoic and Cenozoic (Wood & Whatley 1994; Vandenbroucke *et al.* 2010a, b; Hart 2007; Kucera 2007; Dowsett & Robinson 2009). The distribution of Cenozoic benthic ostracods have also been demonstrated to be influenced by latitude (Wood & Whatley 1994; Cronin *et al.* 1993). The same pattern of latitudinal-restricted assemblages may also be reflected in Ordovician ostracods as the Laurentian ostracod provinces identified here are restricted to relatively narrow latitudinal ranges. The southern Marginal Province localities are restricted to latitudes 21-25°S whereas the Midcontinent Province is confined to 17°S-5°N and both of these are characterized by species with a restricted latitudinal range (Fig. 2). These include *Platybolbina punctata*, *Hippula ventrospinosa*, *Shenandoia acuminulata* and *Eurychilina strasburgensis* from the Marginal Province. Also, some 28 species (*Hyperchilarina bella*, *Tetradella ellipsira*, *T. Ulrichi* etc) are

restricted only to the Midcontinent Province (Appendix 2). This suggests that latitudinal temperature variation may have been a factor in the distribution of the Laurentian ostracod fauna, particularly as this is also reflected in the boundary between the tropical and subtropical climate zone determined at about 22°S from the analysis of zooplankton Vandenbroucke *et al.* 2010b.

### **Trans-lapetus ostracod connections between Laurentia and Baltica**

Schallreuter and Siveter (1985) demonstrated generic-links between Laurentia, Baltica and Avalonia commencing during the late Darriwilian (late Middle Ordovician). They argued that faunal similarity from the Middle to Late Ordovician was indicative of a narrowing lapetus Ocean and the ability of some species to migrate across this ocean. By Late Ordovician times, there were early species-level links between Laurentia, Baltica and Avalonia (Williams *et al.* 2001a,b; Mohibullah *et al.* 2010; Chapter 4).

The southern Marginal Province ostracod faunas of Laurentia established the earliest faunal links with the Baltic region during the early Darriwilian, as seen by the presence of species of *Rivillina* and *Laccochilina* in the Kanosh shale of Utah (Berdan 1988), species of these genera being also present in approximately contemporaneous deposits of the Baltic region (see Vannier *et al.* 1989). By the early Late Ordovician (*bicornis* Biozone) both the Marginal province faunas and the Midcontinent Province faunas possessed generic links with Baltica (Williams *et al.* 2003) and Avalonia (this study). Thereafter, the Marginal Province faunas produced the first species-level links with Baltica and Avalonia during the Late Ordovician (Floyd *et al.* 1999; Williams *et al.* 2001b; Mohibullah *et al.* 2010; Chapter 4). Many species (*Steusloffina cuneata*,

?*Medianella longa* and species of *Hemiaechminoides*, *Longiscula* and *Kinnekullea*) that are restricted to the Marginal Province of Laurentia are also present in the early Katian of the Baltic region (Fig. 5; Mohibullah *et al.* 2010; Chapter 4). Similar patterns of strong affinities between Laurentian marginal faunas across the Iapetus Ocean are also noticed in brachiopods, trilobites, conodonts and bryozoans (Cocks & Torsvik 2011; Cocks & Fortey 2003; Anstey *et al.* 2003; Harper & Stewart 2008).

### **Causes of intra-continental ostracod endemism in Laurentia**

At species-level, endemism amongst North American Sandbian-age ostracods is pronounced, and reflects patterns that were already firmly established in earlier Dapingian and Darriwilian ostracod faunas (Harris 1957; Berdan 1988). Of 229 Sandbian species documented here, only 65 species occur in more than one sedimentary basin. A few Sandbian taxa are truly pandemic to Laurentia and include *Baltonotella parsispinosa*, *Hallatia labiosa*, *Eoaquapulex socialis*, *Eurychilina subradiata*, *E. ventrosa*, *Macrocyproides trentonensis*, *Phelobythocypris cylindrica* and *Cryptophyllus oboloides* (Appendix 1). Endemism is most prominent in the successions of Oklahoma (Southern Oklahoma Aulacogen Basin), Virginia (East Shenandoah Valley Basin), the Mackenzie District (Root River Basin), Michigan and Lake Timiskaming, Ontario, Canada. All of these areas present more than 50% endemic species that are restricted to their particular depo-centre and are not found elsewhere (Table 1). Similar striking differences at species level persist into the Katian (*clingani* graptolite Biozone interval; for which see (Kay 1934, 1940; Mohibullah *et al.* 2010; Chapter 4).

The strong intra-continental endemism at the species-level in the Laurentian ostracod fauna suggests that rapid speciation was taking place from ancestor taxa in each basin. The comparative rate of speciation is different for different faunal groups (Sepkoski 1998). In marine benthic ostracods the rate of speciation can be completed in less than 0.5 million years (Cronin 1985, 1988; Whatley 1988). Speciation may have been driven by both biotic (competition) and abiotic factors such as geographic habitat, geographic isolation, climate, tectonics, and sea level change (Sepkoski 1998; Cronin 1988). Geographic isolation formed by barriers such as large deep-water bodies or islands may result in speciation from founder species as noticed across the Isthmus of Panama for ostracods (Cronin & Ikeya 1988; Butlin & Menozzi 2000). Notwithstanding the presence of a peninsula between the Midcontinent and Marginal ostracod provinces, that may have fostered allopatric speciation, the profound endemism of ostracod faunas between individual basins in both the Midcontinent and Marginal provinces suggests environmental factors operating at the micro-habitat scale in each depositional basin may have profoundly influenced the path of ostracod evolution.

Similar patterns of strong endemism at the species-level are reported from other Ordovician fossil groups. Hansen and Holmer (2010) reported a diverse brachiopod fauna from the Lower and Middle Ordovician (late-Floian to mid-Darriwilian) of Spitsbergen bearing strong generic affinities with faunas from the rest of Laurentia. However, at species-level the Spitsbergen fauna is dominated by local endemics, with only 13 from 60 species found elsewhere in North America. They also related endemism to local environmental effects influencing the evolution of taxa that had migrated from elsewhere.

## Conclusions

Analysis of the distribution patterns of Ordovician Laurentian ostracods demonstrates that:

- 1) Inter-continental geography exerts the strongest control on ostracod distribution, the faunas of Laurentia and Avalonia plotting as discrete entities for the early Sandbian, and supporting palaeogeographical reconstructions for this time interval;
- 2) Within Laurentia there is strong endemism at the species-level in each depositional basin, ranging from 25% (e.g. Foxe Basin) to 75% (e.g. Michigan Basin), with the exception of Girvan which is an allochthonous fauna;
- 3) Multivariate analyses of the entire Sandbian, *gracilis* and *bicornis* time slabs allows for demarcation of Midcontinent and southern Marginal ostracod provinces;
- 4) Midcontinent and southern Marginal ostracod provinces appear to persist from the Sandbian into the Katian, and faunal contacts with Baltica and Avalonia are strongest with the Marginal Province, including the first species-level links, possibly reflecting greater geographical proximity and water depth tolerance of these faunas;

5) The Midcontinent and southern Marginal provinces could, in part, reflect the Tropical and Subtropical climate belts, that have earlier been identified based on zooplankton distributions;

6) The strong regional endemicity of the Laurentian ostracod fauna at species-level is reflected in other faunas such as brachiopods. The strong endemicity suggests that local environmental parameters operating at the microhabitat scale may have been significant in driving local speciation events from ancestor species in each depositional basin.

## Chapter 6: Conclusions

The aims of this study were to determine the biostratigraphical, palaeoecological and biogeographical significance of the Late Ordovician ostracod fauna of Girvan; and to identify the broad distributional patterns of Ordovician Laurentian ostracods. These objectives produced the following results.

Taxonomic studies of the entire Late Ordovician succession of the Girvan district identified fifty-two species from twenty-six genera and fifteen families, including twenty-three species described in open nomenclature, and seventeen that are considered as *nomen dubia*. Two faunas in particular have been studied in detail, those of the Ardwell Farm Formation and those of the Craighead Limestone Formation.

The Ardwell Farm Formation of the Girvan district yields ostracods only from a single locality at Pinmerry. It has yielded a low diversity ostracod assemblage comprising of six species. The low diversity assemblage contains short-ranging taxa such as *Baltonotella parsispinosa* and *Hippula ventrospinosa* that allow correlation with Sandbian age strata of North America. The associated chitinozoans also suggest a Sandbian age, equivalent to either the *gracilis* or *bicornis* graptolite Biozone. The ostracod fauna is allochthonous, and may represent a deep shelf water low diversity assemblage or conversely may have been transported from the adjacent carbonate ramp.

The Late Ordovician (Katian) Craighead Limestone Formation was investigated for ostracods and a fauna comprising twenty-five species was recovered. Two distinct assemblages were identified: a shallow marine low diversity assemblage (7 species)

and an open marine higher diversity assemblage (25 species). The shallow marine assemblage is dominated by palaeocopes such as *Oepikella* and rare podocopes, whereas the open marine assemblage is dominated by podocopes especially *Steusloffina*, palaeocopes, leiocopes and rare binodicopes. This concurs with the Vannier *et al.* (1989) model of ostracod lithofacies distribution that associates palaeocope-rich assemblages with the carbonates of Baltoscandia. The ostracod fauna of the Craighead Limestone Formation has many taxa that allow broad correlation with the late Sandbian and early Katian strata of North America. Ostracods of the Craighead Limestone Formation show species level biogeographical links with faunas from North America but also contain many genera of Baltic origin. This supports the notion of close geographical proximity for Baltica and Laurentia by Katian times.

Analysis of the Girvan fauna in the context of the whole Laurentian Ordovician ostracod fauna have been evaluated using multivariate statistical analysis. The analysis supports the notion that inter-continental geography exerted the strongest control over the global distribution of Ordovician ostracod, plotting Laurentia and Avalonia as discrete entities for the early Sandbian, thus supporting palaeogeographical reconstructions for this time interval. The ostracod fauna of Laurentia shows strong intra-continental endemism at species-level, ranging from 25% (e.g. Foxe basin) to 75% (e.g. Michigan Basin). Similar patterns of endemism are reflected in other benthic faunas such as brachiopods. The strong endemism indicates that local environmental parameters operating at the microhabitat scale may have been influential in driving local speciation events from ancestor species in each region. The Sandbian age fauna of Laurentia also shows notable differences between the marginal and midcontinent assemblages. Multivariate analyses allow

the demarcation of Midcontinent and southern Marginal ostracod provinces for the Sandbian time and these provinces appear to persist into the Katian. The Marginal province appears to have had the strongest faunal contacts with Baltica and Avalonia, forming the first species-level links by the early Katian, possibly reflecting greater geographical proximity and broad ecological tolerance of these faunas. The Midcontinent and southern Marginal provinces may also possibly reflect the Tropical and Subtropical climate belts that have earlier been tracked by zooplankton distributions.

- Achab, A. 1984. Chitinozoaires de l'Ordovicien moyen de subsurface de l'île Anticosti. *Review of Palaeobotany and Palynology*, **43**, 123-43.
- Achab, A. 1988. Mise en évidence d'un provincialisme chez les Chitinozoaires ordoviciens. *Canadian Journal of Earth Sciences*, **25**, 635-638.
- Achab, A. 1989. Ordovician chitinozoan zonation of Quebec and western Newfoundland. *Journal of Paleontology*, **63**, 14-24.
- Achab, A., Bertrand, R. & Van Grootel, G. 1992. Chitinozoan Contribution to the Ordovician and Lower Silurian Paleobiogeography. *The Journal of Geology*, **100**, 621-629.
- Anderson, F.W. & Pringle, J. 1946. On a section of the Balclatchie Beds at Craighead Quarry, near Girvan, Ayrshire. *Geological Magazine*, **83**, 172-176.
- Anstey, R.L., Pachut, J.F. & Tuckey, M.E. 2003. Patterns of bryozoan endemism through the Ordovician–Silurian transition. *Paleobiology*, **29**, 305–328.
- Barnes, C.R., Norford, B.S. & Skevington, D. 1981. The Ordovician System in Canada. Correlation chart and explanatory notes. *International Union of Geological Sciences, Publication No. 8*. 26 p.
- Barrande, J. 1872. Système silurien du centre de la Bohême. Supplement au Vol. **1**. Trilobites, Crustacés divers et Poisson, Praha. 30, 647pp.
- Bassler, R.S. & Kellet, B. 1934. Bibliographic index of Paleozoic Ostracoda. *Geological Society of America, special paper*, **1**, p. 500.
- Bauer, J.A. 1994. Conodonts from the Bromide Formation (Middle Ordovician), south-central Oklahoma. *Journal of Paleontology*, **68**, 358-376.

- Becker, G. & Bless, M.J.M. 1990. Biotope indicative features in Palaeozoic ostracods: a global phenomenon. *In: Whatley, R. & Maybury, C. (eds) Ostracoda and global events*. British Micropalaeontological Society Publication Series, London (Chapman and Hill), 422–436.
- Bennett, C.E. 2008. A review of the Carboniferous colonisation of non-marine environments by ostracods. *Senckenbergiana Lethaea*, **88**, 37–46.
- Bennett, C.E., Siveter, D.J., Davies, S.J., Williams, M., Wilkinson, I.P., Browne, M. & Miller, C.G. in press. Ostracods from freshwater and brackish environments of the Carboniferous of the Midland Valley of Scotland: the early colonisation of terrestrial water bodies. *Geological Magazine*.
- Berdan, J. 1961. ?Family Krausellidae Berdan, n. fam. *In: Moore, R.C. (ed.) Treatise on Invertebrate Paleontology, Part Q (Arthropoda)*, Lawrence, Kansas, Q371-373.
- Berdan, J.M. 1988. Middle Ordovician (Whiterockian) palaeocopid and podocopid ostracodes from the Ibex Area, Millard County, Western Utah. *New Mexico Bureau of Geology and Mineral Resources Memoir*, **44**, 273–301.
- Bergström, S.M. 1971. Conodont biostratigraphy of the Middle and Upper Ordovician of Europe and eastern North America. *In: Sweet, W.C. & Bergström, S.M. (eds) Symposium on Conodont Biostratigraphy*. Geological Society of America, Memoir **127**, 83-161.
- Bergström, S.M. 1973. Ordovician conodonts. *In: Hallam A. (ed.) Atlas of Palaeobiogeography*. Elsevier, Amsterdam, 45-58.

- Bergström, S.M. 1986. Biostratigraphic integration of Ordovician graptolite and conodont zones-a regional review. *In*: Hughes, C.P. & Rickards, R.B. (eds) *Palaeoecology and biostratigraphy of graptolites*. Special Publication of the Geological Society of London, **20**, 61–78.
- Bergström, S.M. 1990. Biostratigraphic and biogeographic significance of Middle and Upper Ordovician conodonts in the Girvan succession, southwest Scotland. *Courier Forschungsinstitut Senckenberg*, **118**, 1–43.
- Bergström, S.M., Chen, X.u., Gutiérrez-Marco, J.C. & Dronov, A. 2009. The new chronostratigraphic classification of the Ordovician System and its relations to major regional series and stages and to  $\delta^{13}\text{C}$  chemostratigraphy. *Lethaia*, **42**, 97–107.
- Bergström, S.M., Finney, S.C., Chen, X. & Wang, Z.H. 1998. The base of the Nemagraptus gracilis Zone as the base of the global Upper Ordovician Series: three potential stratotypes. *In*: Gutierrez Marco, J.C. & Rabano, I. (eds) *Proceedings of the 6th International Graptolite Conference (GWG-IPA) and Field Meeting of the IUGS Subcommittee on Silurian Stratigraphy*. Temas Geológico - Mineros ITGE, **23**, 148–151.
- Bergström, S.M., Finney, S.C., Chen, X., Pålsson, C., Wang, Z.H. & Grahn, Y. 2000. A proposed global boundary stratotype for the base of the Upper Series of the Ordovician System: the Fågelsång section, Scania, southern Sweden. *Episodes*, **23**, 102–109.
- Bevins R.E., Bluck B.J., Brenchley P.J., Fortey R.A., Hughes C.P., Ingham J.K., Rushton A.W.A. 1992. Ordovician. *In*: Cope, J.C.W., Ingham, J.K. & Rawson,

- P.F. (eds) Atlas of Palaeogeography and Lithofacies Geological Society, London, Memoirs, **13**, 19–36.
- Bluck, B.J. 1985. The Scottish paratectonic Caledonides. *Scottish Journal of Geology*, **21**, 437–464.
- Bonnema, J.H. 1909. Beitrag zur Kenntnis der Ostrakoden der liuckerschen Schicht (C<sub>2</sub>). *Mitteilungen aus dem Mineralogischen-Geologischen Institut der Reichs-Universität zu Groningen*, **2**, 1–81, 8 pls.
- 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*: Park, L.E. & Smith, A (eds) *Bridging the Gap: Trends in the Ostracode Biological and Geological Sciences*. The Paleontological Society, Papers, 9: pp. 153–179.
- Bulman, O.M.B. 1944–1947. A monograph of the Caradoc (Balclatchie) graptolites from limestones in Laggan Burn, Ayrshire. *Monograph of the Palaeontographical Society, London* (1) 1945, 1–42, pls 1–3; (2) 1946, 43–58, pls 4–6; (3) 1947, i–xi, 59–78, pls 7–10.
- Butlin, R.K. & Menozzi, P. 2000. Open questions in evolutionary ecology: do ostracods have the answers? *Hydrobiologia*, **419**, 1–14.
- Carter, B., Miller, P. & Smosna, R. 1988. Environmental aspects of Middle Ordovician Limestones in the central Appalachians. *Sedimentary Geology*, **58**, 23–36.
- Cocks, L.R.M. & Fortey, R.A. 1982. Faunal evidence for oceanic separations in the Palaeozoic of Britain. *Journal of the Geological Society, London*, **139**, 465–78.

- Cocks, L.R.M. & Fortey, R.A. 1990. Biogeography of Ordovician and Silurian faunas. *In: Mckerrow, W.S. & Scotese, C.F. (eds) Palaeozoic Palaeogeography and Biogeography*. Geological Society of London Memoir, no. **12**, 97-104.
- Cocks, L.R.M. & Torsvik, T.H. 2002. Earth geography from 500 to 400 million years ago: a faunal and palaeomagnetic review. *Journal of the Geological Society of London*, **159**, 631–644.
- Cocks, L.R.M. & Torsvik, T.H. 2005. Baltica from late Precambrian to mid-Palaeozoic times: the gain and loss of a terrane's identity. *Earth-Science Reviews*, **72**, 39–66.
- Cocks, L.R.M. & Torsvik, T.H. 2006. European geography in a global context from the Vendian to the end of the Palaeozoic. *In: Gee, D.G. & Stephenson, R.A. (eds) European Lithosphere Dynamics*. Geological Society, London, Memoirs, **32**, 83–95.
- Cocks, L.R.M. & Torsvik, T.H. 2011. The Palaeozoic geography of Laurentia and western Laurussia: A stable craton with mobile margins. *Earth-Science Reviews*, **106**, 1–51.
- Cocks, L.R.M. 2000. The Early Palaeozoic geography of Europe. *Journal of the Geological Society, London*, **157**, 1–10.
- Cocks, L.R.M., McKerrow, W.S. & Van staal, C.R. 1997. The margins of Avalonia. *Geological Magazine*, **134**, 627–636.
- Coimbra, J.C., Pinto, I.D., Würdig, N.L. & Do Carmo D.A. 1999. Zoogeography of Holocene Podocopina (Ostracoda) from the Brazilian Equatorial shelf. *Marine Micropaleontology*, **37**, 365-379.

- Cooper, B.N. & Cooper, G.A. 1946. Lower Middle Ordovician stratigraphy of the Shenandoah Valley, Virginia. *Bulletin of the Geological Society of America*, **57**, 35-114.
- Cooper, R.A. & Sadler, P.M. 2004. Ordovician System. *In*: Gradstein, F.M., Ogg, J.G. & Smith, A.G. (eds) *A Geologic Time Scale*. Cambridge University Press, Cambridge, 165–187.
- Cooper, R.A., Fortey, R.A. & Lindholm, K. 1991. Latitudinal and depth zonation of Early Ordovician graptolites. *Lethaia*, **24**, 199–218.
- Copeland, M.J. 1965. Ordovician Ostracoda from Lake Timiskaming, Ontario. *Bulletin of the Geological Survey of Canada*, **127**, 1-52.
- Copeland, M.J. 1974. Middle Ordovician Ostracoda from southwestern district of Mackenzie. *Geological Survey of Canada, Bulletin*, **244**, 1-55.
- Copeland, M.J. 1977a. Ordovician Ostracoda, southeastern District of Franklin. *In*: Bolton, T.E., Sanford, B.V., Copeland, M.J., Barnes, C.E. & Rigby, J.K. (eds) *Geology of Ordovician rocks, Melville Peninsula and region, southeastern District of Franklin*. *Bulletin of the Geological Survey of Canada*, **269**, 77-97.
- Copeland, M.J. 1977b. Early Paleozoic Ostracoda from southwestern District of Mackenzie and Yukon Territory. *Bulletin of the Geological Survey of Canada*, **275**, 1-88.
- Copeland, M.J. 1981. Latest Ordovician and Silurian ostracode faunas from Anticosti Island, Québec. *In*: Lespérance, P.J. (ed.) *Field Meeting, Subcommittee on Silurian stratigraphy, Ordovician – Silurian Boundary Working Group, Anticosti – Gaspé, Quebec 1981, II: Stratigraphy and Paleontology*, 185-195.

- Copeland, M.J. 1982. Bathymetry of early Middle Ordovician (Chazy) ostracodes, Lower Esbataottine Formation, District of Mackenzie. *Bulletin of the Geological Survey of Canada*, **347**, 1-39.
- Copeland, M.J. 1983. *Steusloffina cuneata* (Steusloff), 1895, from Anticosti Island, Quebec. *Geological Survey of Canada, Paper*, **83-1B**, 201-204.
- Copeland, M.J. 1989. Silicified Upper Ordovician–Lower Silurian ostracodes from the Avalanche Lake area southwestern District of Mackenzie. *Bulletin of the Geological Survey of Canada*, **341**, 1–100.
- Copeland, M.J. 2000. Ordovician Ostracoda from southern Baffin Island, Nunavut. In *Geology and Paleontology of the southeast Arctic Platform and southern Baffin Island, Nunavut. Bulletin of the Geological Survey of Canada*, **557**, 217–36.
- Cronin, T.M. & Ikeya, N. 1988. Tectonic Events and Climate Change: Opportunities for Speciation in Marine Ostracoda. In: Warren, D.A. (ed.) *Causes of evolution: a paleontological perspective*, 210–230.
- Cronin, T.M. 1985. Speciation and stasis in marine Ostracoda: Climatic modulation of evolution. *Science*, **227**, 60–63.
- Cronin, T.M. 1988. Geographical isolation in marine species: Evolution and speciation in Ostracoda. In: Hanai, T., Ikeya, N. & Ishizaki, K. (eds) *Evolutionary Biology of Ostracoda*. Elsevier, Oxford, 871–889.
- Cronin, T.M., Whatley, R., Wood, A., Tsukagoshi, A., Ikeya, N., Brouwers, E.M. & Briggs, W.M.Jr., 1993. Microfaunal evidence for elevated Pliocene temperatures in the Arctic Ocean. *Paleoceanography*, **8**, 161–173.

- Cronin, T.M. & Dowsett, H.J. 1990. A quantitative micropaleontological method for shallow marine paleoclimatology: Application to Pliocene deposits of western North Atlantic Ocean. *Marine Micropaleontology*, **16**, 117–148.
- Decker, C.E. 1935. The graptolites of the Simpson group of Oklahoma. *National Academy of Sciences Proceedings*, **21**, 239-243.
- Decker, C.E. 1941. Simpson Group of Arbuckle and Wichita Mountains of Oklahoma. *American Association of Petroleum Geologists Bulletin*, **25**, 650-667.
- Dowsett, H.J. & Robinson, M.M. 2009. Mid-Pliocene equatorial Pacific sea surface temperature reconstruction: a multi-proxy perspective. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, **367**, 109–125.
- Dowsett, H.J. 2007. The PRISM palaeoclimate reconstruction and Pliocene sea-surface temperature. In: Williams, M., Haywood, A.M., Gregory, F.J. & Schmidt, D.N. (eds) *Deep-Time Perspectives on Climate Change: Marrying the Signal from Computer Models and Biological Proxies*. Special Publications of the Micropalaeontological Society. The Geological Society, London, 459–480.
- Dowsett, H.J., Robinson, M., Haywood, A., Salzmann, U., Hill, D., Sohl, L., Chandler, M., Williams, M., Foley, K. & Stoll, D. 2010. The PRISM3D Paleoenvironmental Reconstruction. *Stratigraphy*, **7**, 123-139.
- Ebbestad, J.O.R. 2008. The Tergomyan mollusc *Carcassonnella* from the Upper Ordovician of Girvan, Scotland. *Palaeontology*, **51**, 663-675.

- Eisenack, A. 1959. Neotypen Baltischer Silur-Chitinozoen und neue Arten. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **108**, 1-20.
- Finney, S. 2005. Global series and stages for the Ordovician System: A progress report. *Geologica Acta*, **3**, 309–316.
- Finney, S.C. 1986. Graptolite biofacies and correlation of eustatic, subsidence, and tectonic events in the Middle to Upper Ordovician of North America. *Palaaios*, **1**, 435-461.
- Floyd, J.D. & Williams, M. 2003. A revised lithostratigraphy for the Silurian of the Girvan district. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **93**, 383-392.
- Floyd, J.D. 1999. Geology of the Carrick-Loch Doon district. *Memoir for 1:50,000 Geological Sheets 8W and 8E (Scotland)*. London: The Stationery Office, BGS.
- Floyd, J.D., Williams, M. & Rushton, A.W.A. 1999. Late Ordovician (Ashgill) ostracodes from the Drummuck Group, Craighead Inlier, Girvan district, southwest Scotland. *Scottish Journal of Geology*, **35**, 15-24.
- Fortey, R.A. & Cocks, L.R.M. 2003. Palaeontological evidence bearing on global Ordovician–Silurian continental reconstructions. *Earth Science Reviews*, **61**, 245–307.
- Fortey, R.A. 1984. Global earlier Ordovician transgressions and regressions and their biological implications. In: Bruton, D.L. (ed.) *Aspects of the Ordovician System*. Contributions from the University of Oslo, no. 295, Universitetsforlaget, 37–50.

- Ghobadi Pour, M., Mohibullah, M., Williams, M., Popov, L.E. & Tolmacheva, T.Yu. 2011. New, early ostracods from the Ordovician (Tremadocian) of Iran: systematic, biogeographical and palaeoecological significance. *Alcheringa*, **35**, 517–529.
- Ghobadi Pour, M., Williams, M., Vannier, J., Meidla, T. & Popov, L.E. 2006. Ordovician ostracods from east central Iran. *Acta Palaeontologica Polonica*, **51**, 551–560.
- Grahn, Y. & Nölvak, J. 2010. Swedish Ordovician Chitinozoa and biostratigraphy: a review and new data. *Palaeontographica, Abteilung B: Palaeobotany-Palaeophytology*, **283**, 5-71.
- Hairapetain, V., Mohibullah, M., Tilley, L.J., Williams, M., Miller, C.G., Afzal, J., Ghobadi Pour, M. & Hejazi, S.H. 2011. Early Silurian carbonate platform ostracods from Iran: A peri-Gondwanan fauna with strong Laurentian affinities. *Gondwana Research*, **20**, 645-653.
- Hansen, J. & Holmer, L.E. 2010. Diversity fluctuations and biogeography of Ordovician brachiopod faunas in northeastern Spitsbergen. *Bulletin of Geosciences*, **85**, 497–504.
- Harper, D.A.T. & Owen, A.W. 1986. A shelly biofacies from the graptolitic mudstones of the lower Balclatchie Group (lower Caradoc) near Laggan, Girvan district. *Scottish Journal of Geology*, **22**, 271-83.
- Harper, D.A.T. & Stewart, S.E. 2008. Brachiopod biofacies in the Barr and Ardmillan groups, Girvan: Ordovician biodiversity trends on the edge of Laurentia. *Earth*

- and Environmental Science: Transactions of the Royal Society of Edinburgh*, **98**, 281–289.
- Harper, D.A.T. 1979. The environmental significance of some faunal changes in the Upper Ardmillan succession (upper Ordovician), Girvan, Scotland. *In*: Harris, A.L., Holland, C.H. & Leake, B.E. (eds) *The Caledonides of the British Isles – reviewed. Geological Society, London, Special Publication*, **8**, 439–45.
- Harper, D.A.T. 1981. The stratigraphy and faunas of the Upper Ordovician High Mains Formation of the Girvan district. *Scottish Journal of Geology*, **17**, 247–55.
- Harper, D.A.T. 1982. The stratigraphy of the Drummuck Group (Ashgill), Girvan. *Geological Journal*, **17**, 251–7.
- Harper, D.A.T. 1984. Brachiopods from the Upper Ardmillan Succession (Ordovician) of the Girvan district, Scotland. *Palaeontographical Society Monograph, Part 1*, **136**, 1–78, pls 1–11.
- Harper, D.A.T. 1988. Ordovician–Silurian junctions in the Girvan district, S.W. Scotland. *Bulletin of the British Museum of Natural History (Geology)*, **43**, 45–52.
- Harper, D.A.T. 1989. Brachiopods from the Upper Ardmillan succession (Ordovician) of the Girvan district, Scotland. *Palaeontographical Society Monograph, Part 2*, **142**, 78–128, pls 12–22.
- Harper, D.A.T. 2001. Late Ordovician brachiopod biofacies of the Girvan district, SW Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **91** (for 2000), 471–7.

- Harper, D.A.T. 2006. Brachiopods from the Upper Ardmillan succession (Ordovician) of the Girvan district, Scotland. *Palaeontographical Society Monograph*, Part 3, **159**, 129–87, pls 23–33.
- Harris, R.W. 1931. Description of Microfauna. *In*: Decker, C. E. & Merritt, C. A. (eds) *The stratigraphy and physical characteristics of the Simpson Group*. Bulletin of the Oklahoma Geological Survey, **55**, 87-95.
- Harris, R.W. 1957. Ostracoda from the Simpson Group. *Oklahoma Geological Survey Bulletin*, **75**, 1-333.
- Hart, M.B. 2007. Late Cretaceous climate and foraminiferid distributions. *In*: Williams, M., Haywood, A.M., Gregory, F.J. & Schmidt, D.N. (ed.) *Deep-Time Perspectives on Climate Change: Marrying the Signal from Computer Models and Biological Proxies*. Special Publications of the Micropalaeontological Society. The Geological Society, London, 235–250.
- Harvey, T.H.P., Vélez, M.I. & Butterfield, N.J. 2012. in press. Exceptionally preserved crustaceans from western Canada reveal a Cryptic Cambrian radiation. *Proceedings of the National Academy of Sciences of the United States of America*.
- Henningsmoen, G. 1948. The Tretaspis Series of the Kullatorp Core. *Bulletin of the geological Institutions of the University of Uppsala*, **32**, 374-432.
- Henningsmoen, G. 1953. Classification of Paleozoic straight-hinged ostracods. *Norsk geologisk Tidsskrift*, 31, 185-288.
- Henningsmoen, G. 1954. Upper Ordovician ostracods from the Oslo Region, Norway. *Norsk geologisk Tidsskrift*, **33**, 69-108.

- Hessland, I. & Adamczak, F. 1974. On the taxonomic position of *Steusloffina* Teichert (Ostracoda). *Geoscience and Man*, **6**, 59–64.
- Hessland, I. 1949. Investigations of the Lower Ordovician of the Siljan District, Sweden I. Lower Ordovician ostracods of the Siljan District, Sweden. *Bulletin of the Geological Institution of the University of Upsala*, **33**, 97–408.
- Horne, D.J., Cohen, A.C. & Martens, K. 2002. Taxonomy, morphology and biology of Quaternary and living Ostracoda. *In*: Holmes, J.A. & Chivas, A.R. (eds) *The Ostracoda: Applications in Quaternary Research*. Washington DC, American Geophysical Union, Geophysical Monographs, **131**, 5–36.
- Ingham J.K. & Tripp R.P. 1991. The trilobite fauna of the Middle Ordovician Doularg Formation of the Girvan district, Scotland, and its palaeoenvironmental significance. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **82**, 27–54.
- Ingham, J.K. 1992a. Girvan foreshore. *In*: Lawson, J.D. & Weedon, D.S. (eds) *Geological excursions around Glasgow and Girvan*. The Geological Society of Glasgow, 396–416.
- Ingham, J.K. 1992b. The Craighead Inlier. *In*: Lawson, J.D. & Weedon, D.S. (eds) *Geological Excursions around Glasgow and Girvan*. Geological Society of Glasgow, 417–35.
- Ingham, J.K. 2000. Scotland: the Midland Valley Terrane-Girvan. *In*: Fortey, R.A., Harper, D.A.T., Ingham, J.K., Owen, A.W, Parkes, M.A, Rushton A.W.A. & Woodcock, N. (eds) *A revised correlation of Ordovician Rocks in the British Isles*. Geological Society, London, Special Report, **24**, 43–7.

- Jaanusson, V. 1957. Middle Ordovician ostracodes of Central and Southern Sweden. *Bulletin of the Geological Institution of the University of Uppsala*, **37**, 173-442.
- Jansonius, J. 1964. Morphology and classification of some Chitinozoa. *Bulletin of Canadian Petroleum Geology*, **12**, 901-918.
- Jones, C.R. 1986. Ordovician (Llandeilo and Caradoc) Beyrichiocyte Ostracoda from England and Wales, Part 1. *Monograph of the Palaeontographical Society, London*, pp. 1–76. (Publ. No. 569, part of Vol. 138 for 1984.)
- Jones, C.R. 1987. Ordovician (Llandeilo and Caradoc) Beyrichiocyte Ostracoda from England and Wales, Part 2. *Monograph of the Palaeontographical Society, London*, pp. 77–114. (Publ. No. 571, part of Vol. 139 for 1985.)
- Jones, T.R. & Holl, H.B. 1868. Notes on the Palaeozoic bivalved Entomostraca. No. 8. Some Lower Silurian species from the Chair of Kildare, Ireland. *Annals and Magazine of Natural History*, Series 4, **2** (7), 54-62.
- Jones, T.R. & Holl, H.B. 1886. Notes on the Palaeozoic bivalved Entomostraca. No. 20. On the Genus *Beyrichia* and some new species. *Annals and Magazine of Natural History* Series 5, **17**, 337-63.
- Jones, T.R. 1858. Notes on the Palaeozoic Bivalved Entomostraca, No. 4. Some North American species. *Annals and Magazine of Natural History*, series, **3**, 1 (4), 241–257, pls. 9, 10.
- Jones, T.R. 1879. Order Ostracoda. In: Nicholson, H.A. & Etheridge, R. (eds) *A monograph of the Silurian fossils of the Girvan district in Ayrshire with special*

- reference to those contained in the "Gray collection". Fasciculus II. William Blackwood and Sons, Edinburgh and London, 1, 216-223.*
- Jones, T.R. 1889. Notes on the Palaeozoic bivalved Entomostraca. No. 28: *Annals and Magazine of Natural History*, **4**, 267-273.
- Jones, T.R. 1893. On some Palaeozoic Ostracoda from the district of Girvan, Ayrshire. *Quarterly Journal of the Geological Society, London*, **49**, 296-307.
- Jones, T.R. 1901. Jones, T.R. in Chapman, F. 1901. On some Fossils of Wenlock Age from Mulde, near Klinteberg, Gotland. *Annals and Magazine of Natural History*, Series 7, **7**, 141–160, pl. 3.
- Jongman, R.H.G., ter Braak, C.J.F. & Van Tongeren, O.F.R. 1995. Data analysis in community and landscape ecology. *Cambridge University Press, Cambridge UK*.
- Kay, G.M. 1934. Mohawkian Ostracoda: species common to Trenton faunules from the Hull and Decorah formations. *Journal of Paleontology*, **8**, 328-343.
- Kay, G.M. 1940. Ordovician Mohawkian ostracoda: Lower Trenton Decorah fauna. *Journal of Paleontology*, **14**, 234-269.
- Kesling, R.V. 1960a. Middle Ordovician Black River ostracods from Michigan, Part III, *Platybolbina*. *Contributions from the Museum of Paleontology, University of Michigan*, **15**, 365-385.
- Kesling, R.V. 1960b. Middle Ordovician Black River ostracods from Michigan, Part II, *Levisulculus* and *Eurychilina*. *Contributions from the Museum of Paleontology, University of Michigan*, **15**, 349-363.

- Kraft, J.C. 1962. *Morphologic and systematic relationships of some Middle Ordovician ostracoda*. Memoir of the Geological Society of America, **86**, viii + 104 pp., 19 pls.
- Krandievski, V.S. 1960. Nekotorye zamečaniya po povodu Korreljacji llandoverskich otloženij Estonii i Podolii (Na osnove izučenija ostracod) Einige Bemerkungen über die Korrelation des Llandovery Estland und podoliens (auf Grund der Untersuchung der Ostrakoden) – Eesti NSV Teaduste Akad. Geol. Inst. Uurimused (*Tr. Instituta geologii Akademii nauk Éstonsko, SSR*, **5**, 171-180.
- Krause, A. 1889. Über Beyrichien und verwandte Ostracoden in untersilurischen Geschieben. *Zeitschrift der Deutschen Geologischen Gesellschaft*, **41**, 1-26, Pls. 1-2.
- Krause, A. 1892. Neue Ostrakoden aus märkischen Silurgeschieben. *Zeitschrift der Deutschen Geologischen Gesellschaft*, **44**, 383-399.
- Kruizinga, P. 1918. Bijdrage tot de kennis der sedimentaire zwerfsteen in Nederland (zwerfsteen van Baltischen oorsprong, uitgezonderd, die welke in en bij di stad Groningen en bij Maarn zijn gevonden). — Verh. Geol.-Mijnbouwk. Genootschap Nederland Kolonien., Geol. Ser., **4**, 1-271.
- Kucera, M. 2007. Planktonic foraminifera as traces of past oceanic environments. *In*: Hillaire-Marcel, C. & De Vernal, A. (eds) *Proxies in Late Cenozoic palaeoceanography*. Developments in Marine Geology, Elsevier, Amsterdam, **1**, 213–262.

- Kummerow, E. 1924. Beiträge zur Kenntnis der Ostracoden und Phyllocariden aus nordischen Diluvialgeschieben. *Jahrbuch der Preußischen Geologischen Landesanstalt*, **44**, 405-448.
- Latreille, P.A. 1802. *Histoire naturelle, générale et particulière, des crustacés et des insectes*, 3rd ed. Paris, Dufart, 468.
- Laufeld, S. 1967. Caradocian Chitinozoans from Dalarna, Sweden. *Geologiska Föreningens i Stockholm Förhandlingar*, **89**, 275-349.
- Leslie, S.P. & Bergström, S.M. 1995. Revision of the North American late middle Ordovician standard stage classification and timing of the Trenton transgression based on K-bentonite bed correlation. In: Cooper, J.D., Droser M.L & Finney, S.C. (eds) *Ordovician Odyssey: short papers from the Seventh International Symposium on the Ordovician System*. Society for Sedimentary Geology (SEPM), Fullerton, California, 49–54.
- Levinson, S.A. 1961. New genera and species of Bromide (Middle Ordovician) ostracodes of Oklahoma. *Micropaleontology*, **7**, 359–364.
- Levinson, S.A. 1968. *Eoaquapulex*, new name for *Diploopsis* Levinson, 1961. *Micropalaeontology*, **14**, 248.
- Liebau, A. 2005. A revised classification of the higher taxa of the Ostracoda (Crustacea). *Hydrobiologia*, **538**, 115–137.
- Longman, M.W. 1982. Depositional environments. In: Sprinkle J. (ed.) *Echinoderm faunas from the Bromide Formation (middle Ordovician) of Oklahoma*. University of Kansas Paleontological contributions Monograph 1, 17–30.

- Loydell, D.K. 2012. Graptolite biozone correlation charts. *Geological Magazine*, **149**, 124–132.
- M'Coy, F. 1851. On some new Cambro-Silurian fossils. *Annals and Magazine of Natural History*, Series 2, **8**, 387-409.
- Männil, R. 1963. On the correlation of Ordovician strata of Estonia and Leningrad region. *Tr. Instituta geologii Akademii nauk Éstonskoj, SSR*, **13**, 3-40 (in Russian).
- Martinsson, A. 1960. The primitiopsid ostracodes from the Ordovician of Oklahoma and the systematics of the Family Primitiopsidae. *Bulletin of the Geological Institution of the University of Uppsala*, **36**, 79-105.
- McKerrow, W.S., Dewey, J.F. & Scotese, C.R. 1991. The Ordovician and Silurian development of the Iapetus Ocean. *Special Papers in Palaeontology*, **44**, 165-178.
- Meidla, T. & Tinn, O., Salas, M.J., Williams, M., Siveter, D.J., Vandenbroucke, T.R.A. & Sabbe, K., in press. Biogeographical patterns of Ordovician ostracods.
- Meidla, T. 1986. New ostracodes from the Ordovician of the Baltic area. *Proceedings of the Estonian SSR. Geology*, **35**, 10-19.
- Meidla, T. 1993. The ostracode genus *Longiscula* Neckaja, 1958 in the Ordovician of East Baltic. *Neues Jahrbuch für Geologie and Paläontologie, Abhandlungen*, **188**, 289-303.
- Meidla, T. 1996. Late Ordovician ostracodes of Estonia. *Fossilia Baltica*, **2**. Tartu University Press, 222p.

- Melchin, M.J. & Legault, J.A. 1985. Evolutionary lineages in some Ordovician Chitinozoa. *Palynology*, **9**, 199-210.
- Melnikova, L.M. & Michailova, E.D. 1999. Late Ashgill–Early Llandovery ostracodes from the Zeravshan–Gissar mountainous region (Shakhriomon-II reference section): Platycopida, Metacopida and Podocopida. *Paleontological Journal*, **33**, 392–402.
- Melnikova, L.M. 1986. The Ordovician ostracods of Kazakhstan. *Transactions of the Paleontological Institute, Academy, Nauk, USSR*, **218**, 1-103.
- Melnikova, L.M. 2010. Some Ostracodes from the Gur'yanovka Formation (Upper Ordovician) of Northeastern Gorny Altai. *Paleontological Journal*, **44**, 399–408.
- Mohibullah, M., Afzal, J., Williams, M., Meidla, T., Siveter, D.J. & Zalasiewicz, J.A. 2010. Ostracods from Upper Ordovician (Katian) carbonate lithofacies in southwest Scotland. *Geological Magazine*, **147**, 919-939.
- Mohibullah, M., Vandenbroucke, T.R.A., Williams, M., Floyd, J., Meidla, T., Zalasiewicz, J.A. & Siveter, D.J. 2011. Late Ordovician (Sandbian) ostracods from the Ardwell Farm Formation, southwest Scotland. *Scottish Journal of Geology*, **47**, 57-66.
- Morris, W.E. & Hill, A.L. 1952. New Ostracoda from the Middle Silurian Newson shale of Tennessee. *Bulletins of American Paleontology*, **34**, 1-22.
- Neckaja, A.I. 1958. New species and genera of ostracodes of the Ordovician and Silurian of the Russian platform. *Trudy VNIGRI*, **115**, 349–373 [in Russian].

- Neckaja, A.I. 1966. Ordovician and Silurian Ostracods of the USSR (families Schmidtellidae, Longisculidae and some new species from other families). *Trudy VNIGRI*, **251**, 1–103 (in Russian).
- Nõlvak, J. & Grahn, Y. 1993. Ordovician chitinozoan zones from Baltoscandia. *Review of Palaeobotany and Palynology*, **79**, 245-69.
- Nõlvak, J., Meidla, T. & Hints, L. 1989. The Taucionys Formation (Holorhynchus Beds) in the Iljinskoje boring (Pskov District). *Proceedings of the Academy of Sciences of the Estonian SSR Geology*, **38**, 88-93.
- Olempska, E. 1994. Ostracods of the Mojca Limestone. *In*: Dzik, J., Olempska, E & Pisera, A. Ordovician carbonate platform ecosystem of the Holy Cross Mountains, Poland . *Palaeontologia Polonica*, **53** , 129- 212, pls. 25-50.
- Õpik, A. 1937. Ostracoda from the Ordovician Uhaku and Kukruse formations of Estonia. *Loodusuurijate Seltsi Aruanded*, **43**, 65-138, 15 pls (reprinted as *Tartu Ülikool Geoloogia-Instituudi Toimetused*, **50**, 74 pp., 15 pls).
- Orr, R.J. 1987. Upper Ordovician ostracodes from Portrane, eastern Ireland. Queen's University of Belfast, PhD thesis (unpublished).
- Owen, A.W. & Rushton, A.W.A. 1999. Scotland: Ordovician of the Midland Valley Terrane. *In*: Owen, A.W., Rushton, A.W.A., Owens, R.M. & Prigmore, J.K. (eds) *British Cambrian to Ordovician Stratigraphy*. Joint Nature Conservation Committee, Monkstone House, City road, Peterborough, 325-347.
- Ozawa, H. & Kamiya, T. 2005. Ecological analysis of benthic ostracods in the northern Japan Sea, based on water properties of modern habitats and late Cenozoic fossil records. *Marine Micropaleontology*, **55**, 255-276.

- Paris, F. 1981. Les chitinozoaires dans le Paléozoïque du sud-ouest de l'Europe (cadre géologique—étude systématique—biostratigraphie). *Mémoire de la Société géologique et minéralogique de Bretagne, Rennes*, **26**, 1-496.
- Peach, B.N. & Horne, J. 1899. The Silurian rocks of Britain. Scotland. *Memoirs of the Geological Survey of the United Kingdom*. HMSO, Glasgow, **1**, 749 pp, 27 pls.
- Pennant, T. 1777. Crustacea, Mollusca, Testacea, *British Zoology*, edition 4, B. White, London, i-viii + 154pp, 93pls.
- Pickering, K.T., Bassett, M.G. & Siveter, D.J. 1988. Late Ordovician-early Silurian Destruction of the Iapetus Ocean: Newfoundland, British Isles and Scandinavia - a discussion. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **79**, 361-382.
- Pokorný, V. 1954. A contribution to the taxonomy of the Paleozoic ostracods. *Sborník ústředního ústavu geologického (oddíl paleontologický)*, **20** (for 1953), 213 – 232.
- Pokorný, V. 1978. Ostracodes. In: Haq, B.L. & Boersma, A. (eds) *Introduction to Marine Micropaleontology*. Elsevier: New York, 109–149.
- Potter, A.W. & Boucot, A.J. 1992. Middle and late Ordovician brachiopod benthic assemblages of North America. In: Webby, B.D. & Laurie, J.R. (eds) *Global Perspectives on Ordovician geology*. Balkema, Rotterdam, 307–323.
- Pranskevičius, A. 1972. South Baltic Silurian Ostracoda. *Department of Geology under the council of Ministers of Lithuanian SSR, Lithuanian Scientific-Research Geological Survey Institute, Transactions*, **15**, 1-280.

- Příbyl, A. 1988. Ostracodes from the Silurian of central Bohemia. *Palaeontologie*, **29**, 49-143.
- Pruss, S.B., Finnegan, S., Fischer, W.W. & Knoll, A.H. 2010. Carbonates in skeleton-poor seas: new insights from Cambrian and Ordovician strata of Laurentia. *Palaios*, **25**, 73-84.
- Purnell, M.A. 2003. Casting, replication, and anaglyph stereo imaging of microscopic detail in fossils, with examples from conodonts and other jawless vertebrates. *Palaeontologia Electronica*, **6**(2), 1-11.
- Ross, R.J., Adler, F.J., Amsden, T.W., Bergström, D., Bergström, S.M., et al. 1982. The Ordovician System in the United States, Correlation chart and explanatory notes. *International Union of Geological Sciences, Publication No.* 12.
- Rushton, A.W.A. 2001. The graptolite fauna of the Superstes Mudstone Formation in the Ordovician of the Girvan Cover Sequence. *Scottish Journal of Geology*, **37**, 45–52.
- Rushton, A.W.A. 2003. An addition to the graptolite fauna of the Superstes Mudstone Formation, Girvan district. *Scottish Journal of Geology*, **39**, 87–8.
- Rushton, A.W.A., Owen, A.W., Owens, R.M. & Prigmore, J.K. 1999. *British Cambrian to Ordovician Stratigraphy*. Geological Conservation Review Series no. **18**. xxi+1-435 pp. Peterborough, UK.
- Rushton, A.W.A., Tunnicliff, S. P. & Tripp, R.P. 1996. The faunas of the Albany Group in the Girvan area, and their palaeogeographical implications. *Scottish Journal of Geology*, **32**, 23-32.

- Salas, M.J. 2002. Podocope ostracods from the Ordovician of the Precordillera of San Juan, Argentina. *Ameghiniana*, **39**, 129-149.
- Salas, M.J., Vannier, J. & Williams, M. 2007. Early Ordovician ostracods from Argentina: their bearing on the origin of the binodicope and palaeocope clades. *Journal of Paleontology*, **81**, 1384 – 1395.
- Salter, J.W. & Etheridge, R. 1881. On the fossils of North Wales. *In*: Ramsay, A.C. (ed.) *The Geology of North Wales*. Memoirs of the Geological Survey of Great Britain and of the Museum of Practical Geology. HMSO, London, 331-611.
- Sars, G.O. 1866. Oversight af Norges marine ostracoder. *Forhandlinger i Videnskabs-Selskabet i Christiania*, **1865**, 1-30.
- Sarv, L.I. & Meidla, T. 1984. Ostracod distribution pattern in the Ordovician-Silurian boundary beds of the North East Baltic. *VINITI, No. 3813-3814 Department Tallinn*, pp. 1-21.
- Sarv, L.I. 1959. Ostracody Ordovika SSR Estonskoy (Ordovician Ostracods in the Estonian SSR). *Ibid.*, **4**, 210pp., 32pls.
- Sarv, L.I. 1960. On the stratigraphic distribution of ostracods in the Estonian S.S.R. *Ensv Teaduste Akadeemia Geologia Instituudi Uurimused*, **5**, 237-244.
- Sarv, L.I. 1962. Ostrakody porkuniskogo gorizonta i llandovery v Estonii (Ostracods from the Porkuni Stage and Llandovery of Estonia). *Eesti NSV Teaduste Akadeemia Geoloogia Instituudi Uurimused*, **9**, 95-141.

- Schallreuter, R.E.L. & Krüta, M. 1991. The Baltoscandian ostracode genus *Levisulculus* in the Bohemian Ordovician. *Archiv für Geschiebekunde*, **1**, 235–236.
- Schallreuter, R.E.L. & Siveter, D.J. 1985. Ostracodes across the Iapetus Ocean. *Palaeontology*, **28**, 577-598.
- Schallreuter, R.E.L. 1964. Neue Ostrakoden der Überfamilie Hollinacea.- *Berichte der Geologischen Gesellschaft in der Deutschen Demokratischen Republik Sonderheft*, **2**, 87-93, 142-147.
- Schallreuter, R.E.L. 1966. Zur Taxonomie und Phylogenie der Ostrakodenfamilie Tetradellidae Swartz, 1936 (Palaeocopina, Hollinacea) und eine neue Familie der Hollinacea. *Geologie*, **15**, 846–875.
- Schallreuter, R.E.L. 1967. Neue Ostracoden aus ordovizischen Geschieben (New Ostracods from Ordovician Boulders). *Geologie*, **16**, 615-631.
- Schallreuter, R.E.L. 1968. Ordovizische ostracoden mit geradem Schlossrand und konkavem Ventraland; Wissenschaftliche Zeitschrift der Ernst Moritz-Arndt-Universität Greifswald, Jahrgang XVII, 1968; *Mathematisch-naturwissenschaftliche Reihe NR*, **1/2**, 127-152.
- Schallreuter, R.E.L. 1971. Asymmetrische ordovizische Ostrakoden. *Neues Jahrbuch für Geologie und Paläontologie, Monatsheft*, **4**, 249-260.
- Schallreuter, R.E.L. 1972. Drepanellacea (Ostracoda, Beyrichicopida) aus mittelordovizischen Backsteinkalkgeschieben IV. *Laterophores hystrix* sp. n., *Pedomphalella germanica* sp. n. und *Easchmidtella fragosa* (Neckaja) [Drepanellacea (Ostracoda, Beyrichicopida) from Middle Ordovician

- Backsteinkalk Boulders IV. *Laterophores hystrix* sp.n., *Pedomphalella germanica* sp.n. and *Easchmidtella fragosa* (Neckaja)]. *Berichte der Deutschen Gesellschaft für Geologische Wissenschaften A*, 17 (1): **5**, 139-145, 2 pls.
- Schallreuter, R.E.L. 1973. Die Ostracodengattung *Hyperchilarina* und das *Aparchites*-Problem. *Geologiska Foreningens i Stockholm Forhandlingar*, **95**, 37-49.
- Schallreuter, R.E.L. 1975. Palaeocopine Ostrakoden aus Backsteinkalk-Geschieben (Mittelordoviz) Norddeutschlands (mit Ausnahme der *Tvaerenellidae*, *Ctenonotellidae* und *Tetradellidae*). *Palaeontographica A*, **149**, 139-192.
- Schallreuter, R.E.L. 1979. Ordovician podocope ostracodes. In Proceedings of the 7th International symposium on ostracodes, Beograd (Taxonomy, biostratigraphy and distribution of ostracodes), 25-28.
- Schallreuter, R.E.L. 1983. Glossomorphitinae und Sylthinae (*Tetradellidae*, *Palaeocopa*, *Ostracoda*) aus Backsteinkalk-Geschieben (Mittelordoviz) Norddeutschlands. *Palaeontographica A*, **180**, 126-191.
- Schallreuter, R.E.L. 1984. Geschiebe-Ostrakoden I. (Ostracodes from erratic boulders I). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **169**, 1-40.
- Schallreuter, R.E.L. 1985. Homeomorphy, phylogeny and natural classification: case studies involving Palaeozoic ostracodes. 9th international symposium on ostracoda (Evolutionary biology of ostracoda, its fundamentals and applications. Programs and abstracts, Shizuoka, 1985, 94-95.

- Schallreuter, R.E.L., Hinz-Schallreuter, I. & Suttner, T. 2008. New Ordovician ostracodes from Himalaya and their palaeobiological and palaeogeographical implications. *Revue de Micropaleontologie*, **51**, 191-204.
- Schallreuter, R.E.L., Suttner, T.J. & Hinz-Schallreuter, I.C.U. 2005. Late Ordovician ostracodes from Himalaya and their palaeobiogeographic relations. *Berliner Paläobiologische Abhandlungen*, **6**, 107–108.
- Schellenberg, S.A. 2007. Marine Ostracods. *Paleolimnology*, 2046-2062.
- Scott, H.W. 1959. Type species of Paraparchites Ulrich and Bassler. *Journal of Paleontology*, **33**, 670-674.
- Sepkoski, J.J.Jr. 1998. Rates of speciation in the fossil record. *Philosophical Transactions of the Royal Society Series B*, **353**, 315–326.
- Sidaravičiencė, N. 1992. Ordovician ostracodes of Lithuania. Vilnius, pp. 1-252.
- Siebold, C.T.E. Von & Stannius, H. 1845. *Lehrbuch der Vergleichenden Anatomie*. Von Veit, Berlin.
- Siveter, D.J. & Curry, G.B. 1984. Lower Ordovician (Arenig) ostracods from the Highland Border Complex. *In*: Curry, G.B., Bluck, B.J., Burton, C.J., Ingham, J. K., Siveter, D.J. & Williams, A. (eds) *Age, evolution and tectonic history of the Highland Border Complex, Scotland*. Transactions of the Royal Society of Edinburgh: Earth Sciences, **75**, 113-133.
- Siveter, D.J. 1978. The Ordovician. *In*: Bate, R.H. & Robinson, E. (eds) *A stratigraphical index of British Ostracoda*. Geological Journal Special Issue, **8**, 41-56.

- Siveter, D.J. 1982. Late Ordovician and Early Silurian ostracodes from the Oslo Region, Norway, *In: Worsley, D. (ed.) IUGS Subcommittee on Silurian Stratigraphy, Field Meeting, Oslo Region 1982*. Palaeontological contributions from the University of Oslo, **278**, 121-128.
- Siveter, D.J. 1984a. Casts illustrating fine ornament of a Silurian ostracod. *In: Donovan, D.T., Bate, R.H., Robinson, E. & Sheppard, L.M. (eds) Fossil and Recent Ostracods*. Ellis Horwood, Chichester, 105-122.
- Siveter, D.J. 1984b. Habitats and modes of life of Silurian Ostracodes, *In: Basset, M.G. (ed.) The Autecology of Silurian organisms*. Special papers in Palaeontology, **32**, 71-85.
- Siveter, D.J. 2009. Ordovician. *In: Whittaker, J.E. & Hart, M.B. (eds) Ostracods in British Stratigraphy*. The Micropalaeontological Society, Special Publications, 15-44.
- 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.
- Smith, J. 1892. English upper Silurian Ostracoda. *Proceedings and Transactions of the Natural History Society of Glasgow*, 3 (new series), 134-58.
- Sohn, I.G. 1961. Paleozoic species of Bairdia and related genera. U.S. Geological Survey Professional Paper, **330-A**, 1-105, Plates 1-6.
- Stepanova, A., Taldenkova, E., Simstich, J. & Bauch, H.A. 2007. Comparison study of the modern ostracod associations in the Kara and Laptev Sea: Ecological aspects. *Marine Micropaleontology*, **63**, 111-142.

- Steusloff, A. 1895. Neue Ostrakoden aus Diluviageschieben von Neu-Brandenburg. *Zeitschrift der Deutschen Geologischen Gesellschaft*, **46**, 775-787.
- Stewart, S.E. and Owen, A.W. 2008: Probing the deep shelf: a Lagerstätte from the Upper Ordovician of Girvan, southwestern Scotland. *Lethaia* , **41**, 139–146.
- Stumbur, H. 1956. About the ostracode fauna of Porkuni stage of Estonia. *Tartu Riikliku Ülikooli Toimetised*, **42**, 176–185 (in Russian).
- Swain, F.M. 1957. Early Middle Ordovician ostracoda of the eastern United States. Part I. Stratigraphic data and description of Leperditiidae, Aparchitidae and Leperditellidae. *Journal of Paleontology*, **31**, 528-570.
- Swain, F.M. 1962. Early middle Ordovician ostracoda of the eastern United States; Part 2. Leperditiidae, (part), Hollinacea, Kloedenellacea. *Journal of Paleontology*, **36**, 719-744.
- Swain, F.M. 1996. Ostracoda speciation following Middle Ordovician extinction events, north central United States. In: Hart, M.B. (ed.) *Biotic recovery from Extinction Events*. Geological Society, London, Special Publications, **102**, 97-104.
- Swain, F.M., Cornell, J.R. & Hansen, D.L. 1961. Ostracoda of the families Aparchitidae, Aechminidae, Leperditellidae, Drepanellidae, Eurychilinidae and Punctaparchitidae from the Decorah shale of Minnesota. *Journal of Paleontology*, **35**, 345-372.
- Swartz, F.M. 1936. Revision of Primitidae and Beyrichiidae, with new ostracoda from the Lower Devonian of Pennsylvania. *Journal of Paleontology*, **10**, 541-586.

- Sweet, W.C. & Bergström, S.M. 1976. Conodont biostratigraphy of the Middle and Upper Ordovician of the United States Mid-continent. *In* Bassett, M.G. (ed.) *The Ordovician System*. Proceedings of a Palaeontological Association Symposium, Birmingham, September 1974. University of Wales Press and National Museum of Wales, Cardiff, 121-151.
- Sweet, W.C. 1983. Conodont biostratigraphy of Fite Formation and Viola Group. *In*: Amsden, T.W. & Sweet, W.C. (eds) *Upper Bromide Formation and Viola Group (Middle and Upper Ordovician) in eastern Oklahoma*. *Oklahoma Geological Survey Bulletin*, **132**, 23-36.
- Sweet, W.C. 1984. Graphic correlation of upper Middle and Upper Ordovician rocks, North American Mid-continent Province, U.S.A. *In* Bruton, D.L. (ed.) *Aspects of the Ordovician System*. Palaeontological Contributions from the University of Oslo, Universitetsforlaget, **295**, 23-35.
- Sylvester-Bradley, P.C. 1961. Suborder Metacopina Sylvester-Bradley, n. suborder. *In*: Moore, R.C. (ed.) *Treatise on Invertebrate Paleontology, Part Q (Arthropoda)*. Lawrence, Kansas, Q358-Q359.
- Sylvester-Bradley, P.C. 1971. The reaction of Systematics to the revolution in Micropalaeontology. *In*: Heywood, V.H. (ed.) *Scanning Electron Microscopy, Systematic and Evolutionary Application* London: Academic press for the Systematics Association, 95-111.
- Teichert, C. 1937. Ordovician and Silurian faunas from Arctic Canada. *Report of the Fifth Thule Expedition 1921-24*. 169 pp., 24 pls. Gyldendalske Boghandel, Nordisk Forlag, Copenhagen.

- ter Braak, C.J.F. & Smilauer, P. 1998. Canoco reference Manual and User's Guide to Canoco for Windows: software for canonical community ordination (Version 4). *Ithaca, New York*: Microcomputer Power.
- Thorslund P. & Westergård A.H. 1938. Deep Boring Through the Cambro-Silurian at File Haidar, Gotland. *Sveriges Geologiska Undersökning C*, 415 = Årsbok, **32**, 57 pp.
- Thorslund, P. 1940. On the Chasmop series of Jemtland and Sodermanland (Tvaren. *Sveriges Geologiska Undersoenkning, Series C*, **436**, 1-191.
- Tinn, O. & Meidla, T. 2004. Phylogenetic relationships of Early Middle Ordovician ostracods of Baltoscandia. *Palaeontology*, **47**, 199–221.
- Tripp, R.P. 1980a. Trilobites from the Ordovician Ardwell Group of the Craighead Inlier, Girvan district, Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **71**, 147-157.
- Tripp, R.P. 1980b. Trilobites from the Ordovician Balclatchie and lower Ardwell groups of the Girvan district, Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **84**, 87-102.
- Tripp, R.P. 1993. Review of the trilobites from the Middle Ordovician Barr Group, Girvan district, Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **71**, 123-145.
- Tromelin, G. de & Lebesconte, P. 1876. Essai d'un catalogue raisonné des fossiles siluriens des départements de Maine-et-Loire, de la Loire-inférieure et du Morbihan, avec des observations sus les terrains paléozoïques de l'Ouest de

- la France. *Association Française pour l'Avancement de la Sciences*, Comptes Rendus de la 4.session (Nantes 1875), 601–661.
- Tuckey, M. 1990. Biogeography of Ordovician bryozoans. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **77**, 91–126.
- Ulrich, E.O. & Bassler, R.S. 1908. New American Paleozoic Ostracoda. Preliminary revision of the Beyrichiidae, with descriptions of new genera. *Ibid.*, **35**, (1646), 277-340, pls. 37-44.
- Ulrich, E.O. & Bassler, R.S. 1923. Paleozoic Ostracoda: their morphology, classification and occurrence. *Maryland Geological Survey, Silurian*, pp. 271-391.
- Ulrich, E.O. 1889. Contributions to the micro-palaeontology of the Cambro-Silurian rocks of Canada, pt. 2. *Geological and Natural Survey of Canada*, 48–57, pl. 9, figs. 4–14.
- Ulrich, E.O. 1892. New Lower Silurian Ostracoda, No 1. *American Geologist*, **10**, 263-270.
- Ulrich, E.O. 1894. The Lower Silurian Ostracoda of Minnesota. *Report of the Geological and Natural History Survey of Minnesota*. **3**, pt. 2, *Paleontology*, 629-693, pls. 43-47.
- Ulst, R.Zh., Gailite, L.K & Yakovlvea, V.I. 1982. Ordovik Lattvii. *Zinatne, Riga*. 294p.
- Vandenbroucke, T., Verniers, R. & Clarkson, E.N.K. 2003. A chitinozoan biostratigraphy of the Upper Ordovician and lower Silurian strata of the Girvan

- area, Midland Valley, Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **93**, 111-134.
- Vandenbroucke, T.R.A., Armstrong, H.A., Williams, M., Paris, F., Sabbe K., Zalasiewicz J.A., Nölvak, J. & Verniers, J. 2010b. Epipelagic chitinozoan biotopes map a steep latitudinal temperature gradient for earliest Late Ordovician seas: Implications for a cooling Late Ordovician climate. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **294**, 202–219.
- Vandenbroucke, T.R.A., Armstrong, H.A., Williams, M., Zalasiewicz J.A., Paris, F., Sabbe K., Nölvak, J., Jallands, T.J., Verniers, J. & Servais, T. 2010a. Polar front shift and atmospheric CO<sub>2</sub> during the glacial maximum of the Early Paleozoic Icehouse. *PNAS*, **107**, 14983–14986.
- Vandenbroucke, T.R.A. 2004. Chitinozoan biostratigraphy of the Upper Ordovician Fågelsång GSSP, Scania, southern Sweden. *Review of Palaeobotany and Palynology*, **130**, 217-238.
- Vandenbroucke, T.R.A. 2008a. Upper Ordovician chitinozoans from the historical type area in the UK. *Monograph of the Palaeontographical Society*, London. no. 628, Vol. **161** (for 2007), 113 pp.
- Vandenbroucke, T.R.A. 2008b. An Upper Ordovician Chitinozoan Biozonation in British Avalonia (England & Wales). *Lethaia*, **41**, 275–294.
- Vandenbroucke, T.R.A., Ancilletta, A., Fortey, R.A. & Verniers, J. 2009a. A modern assessment of Ordovician chitinozoans from the Shelve and Caradoc areas, Shropshire, and their significance for correlation. *Geological Magazine*, **146**, 216-236.

- Vandenbroucke, T.R.A., Armstrong, H.A., Williams, M., Zalasiewicz, J.A. & Sabbe, K. 2009b. Ground-truthing Late Ordovician climate models using the paleobiogeography of graptolites. *Paleoceanography*, **24**, PA4202.
- Vannier, J.M.C., Siveter, D.J. & Schallreuter, R.E.L. 1989. The composition and palaeogeographical significance of the Ordovician ostracode faunas of southern Britain, Baltoscandia, and Ibero-Armorica. *Palaeontology*, **32**, 163–222.
- Warshauer, S.M. & Berdan, J.M. 1982. Palaeocopid and podocopid ostracoda from the Lexington Limestone and Clays Ferry Formation (Middle and Upper Ordovician) of Central Kentucky. *Professional Paper United States Geological Survey*, **1066-H**, 1-80.
- Webby, B.D., Paris, F., Droser, M.L., & Percival, I.G. (eds), 2004. *The Great Ordovician Biodiversification Event*. Columbia University Press, New York, 484pp.
- Whatley, R.C. 1988. Patterns and rates of evolution among Mesozoic Ostracoda. In: Hanai, T., Ikeya, N. & Ishizaki, K. (eds) *Evolutionary Biology of Ostracoda*. Elsevier, Oxford, 1021–1040.
- Williams, A. 1962. The Barr and Lower Ardmillan Series (Caradoc) of the Girvan district, south-west Ayrshire, with descriptions of the Brachiopoda. *Memoir of the Geological Society of London*, **3**, 1-267.
- Williams, A., Strachan, I., Bassett, D.A., Dean, W.T., Ingham, J.K., Wright, A.D. & Whittington, H.B. 1972. A correlation of Ordovician rocks in the British Isles. *Geological Society Special Report No. 3*, 74pp.

- Williams, M. & Floyd, J.D. 2000. Mid-Caradoc (Ordovician) ostracodes from the Craighead Limestone Formation, Girvan district, southwest Scotland. *Scottish Journal of Geology*, **36**, 51-60.
- 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. & Vannier, J.M.C. 1995. Middle Ordovician Aparchitidae and Schmidtellidae: the significance of 'featureless' ostracodes. *Journal of Micropalaeontology*, **14**, 7-24.
- Williams, M., Floyd, J.D., Miller, C.G., Siveter, D.J. & Stone, P. 2000. *Kinnekullea comma* (Jones, 1879), a trans-lapetus ostracod locum for the late Ordovician *Dicellograptus anceps* graptolite Biozone. *Journal of Micropalaeontology*, **19**, 163-164.
- Williams, M., Floyd, J.D., 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., Floyd, J.D., Siveter, D.J. & Miller, C.G. 2001a. Scottish Ordovician Ostracodes: a review of their palaeoenvironmental, biostratigraphical and palaeobiogeographical significance. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **91**, 499-508.

- Williams, M., Rushton, A.W.A., Wood, B., Floyd, J.D., Smith, R. & Wheatley, C. 2004. A revised graptolite biostratigraphy for the lower Caradoc (Upper Ordovician) of southern Scotland. *Scottish Journal of Geology*, **40**, 97-114.
- 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*, **88**, 1-11.
- Williams, M., Stone, P., Siveter, D.J. & Taylor, P. 2001b. Upper Ordovician ostracods from the Cautley district, northern England: Baltic and Laurentian affinities. *Geological Magazine*, **138**, 589-607.
- Williams, S.H. 1987. Upper Ordovician graptolites from the *D. complanatus* Zone of the Moffat and Girvan districts and their significance for correlation. *Scottish Journal of Geology*, **23**, 65–92.
- Wood, A.M. & Whatley, R.C. 1994. Northeast Atlantic and Arctic faunal provinces based on the distribution of recent ostracod genera. *The Holocene*, **4**, 2, 174-192.
- Zalasiewicz, J.A., Taylor, L., Rushton, A.W.A., Loydell, D.K., Rickards, R.B. & Williams, M. 2009. Graptolites in British stratigraphy. *Graptolites in British Stratigraphy. Geological Magazine*, **146**, 785-850.
- Zhen, Y-Yi. & Percival, I. 2003. Ordovician conodont biogeography – reconsidered. *Lethaia*, **36**, 357–369.