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Distribution and palaeoecology of Ordovician bivalves and gastropods from Girvan, SW Scotland

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ABSTRACT: Molluscs from the Middle and Upper Ordovician succession of Girvan, SW Scotland are common and diverse in some localities. The mollusc fauna consists mainly of gastropods, bivalves and various univalved molluscs (mimospirids and tergomyans), along with scarcer polyplacophorans, rostroconchs and cephalopods. The present study gives an overview of the distribution and palaeoecology of bivalves, gastropods and univalved molluscs and compares them with mollusc faunas worldwide. Gastropods, mimospirids and tergomyans are present from the Darriwilian (mid Llanvirn) onwards in both siliciclastic and carbonate facies, and increase in diversity through the Sandbian (Caradoc) and into the Katian (Ashgill). Bivalves first appeared in Girvan in the late Darriwilian (early Caradoc) in deep water siliciclastic facies; where they continued to be more abundant and diverse than in equivalent carbonate facies. Molluscs are initially Laurentian in aspect, though peri-Gondwanan faunal elements occur, particularly during the Sandbian. The pattern of bivalve and gastropod diversity found in the Ordovician of Girvan generally follows that of the known global diversity for these groups.

KEY WORDS: bivalvia, gastropoda, Laurentia, mollusca

The Ordovician succession of Girvan (Fig. 1) consists of marine siliciclastic (mudstones, conglomerates and sandstones) and carbonate facies deposited on an active tectonic margin (Ingham 2000), at or near the eastern edge of Laurentia. There are distinct North American affinities to many of the faunal groups (Ingham 2000); though Baltic and Avalonian faunal elements appear in the deepest waters from the late Darriwilian onwards. There has been a long history of collecting in the Girvan area; the Gray Collection in particular (largely held in the Natural History Museum (NHM), London) contains very comprehensive collections of well localised taxa (see Cleevely *et al.* 1989 for overview). The stratigraphy is well constrained (Ingham 2000), though many of the faunas have been transported downslope to some degree, resulting in the mixing of some shallow and deeper water faunas. Although groups such as trilobites and brachiopods are well known, there have been few recent studies on Girvan molluscs; particularly relating to the diversity and palaeoecology of pre-Ashgill faunas, and on comparing these on a more global scale.

The mollusc fauna consists mainly of gastropods, bivalves and various univalved molluscs (mimospirids and tergomyans), along with scarcer polyplacophorans, rostroconchs, and cephalopods. Molluscs are present in most localities (Fig. 2) and substrate types, but vary in number between only a few specimens known from some localities to several hundred specimens, as in the Balclatchie Formation, Balclatchie and the Katian Farden Member ('Starfish beds') of the Drummuck subgroup.

1. Methods and material

1.1. Multivariate analysis

The statistical package PAST version 2.08 (Hammer *et al.* 2001) was used to determine likely palaeoenvironmental distribution patterns for the Girvan molluscs. Included were trilobites and brachiopods, for which the palaeoecology is much better known. The ordination method of detrended correspondence analysis (DCA), based on presence/absence in a locality (see Hammer & Harper 2006 for discussion), was used to determine likely environmental preferences.

Data were compiled from historical collections, including the Hunterian Museum, Glasgow (GLAHM), the Gray Collection, Natural History Museum, London (NHM), the British Geological Survey (Murchison House), Edinburgh (BGS) and National Museums Scotland, Edinburgh (NMS), and from literature reviews and field work. Several 'classic' sites in Girvan are now overgrown and difficult to access, though limited sampling (collecting a sample and recording all fossils found) was still possible at, or near, some of these localities. New localities at Dalfask and Byne Hill were also investigated as part of the present study.

Bivalves and gastropods (listed in Tables 1–3) were identified as accurately as possible. Gastropods were originally described by Donald (1902, 1906), Longstaff (1924), Lamont (1935, 1946a) and Peel (1975); bellerophontoid gastropods and tergomyans by Reed (1920, 1921) and updated by Wagner (2002, 2008). Some indeterminate gastropods were simply identified according to shell type; e.g. 'planispiral', 'high-spired' etc., which may give an indication of preferred environment (see Peel 1977, 1978, 1984 and references therein for discussion).

Bivalve taxonomy was taken from Hind (1910), Lamont (1935, 1946b), Reed (1944, 1946), Tunnicliff (1982) and Cope (1996). Most bivalves belonging to the Nuculoidea were classed simply as 'nuculoids' because of widely recognised problems with their taxonomy (see Pojeta 1971; Cope 2004).

Brachiopod data were complied mainly from Williams (1962), Harper (2001) and Harper & Stewart (2008) and

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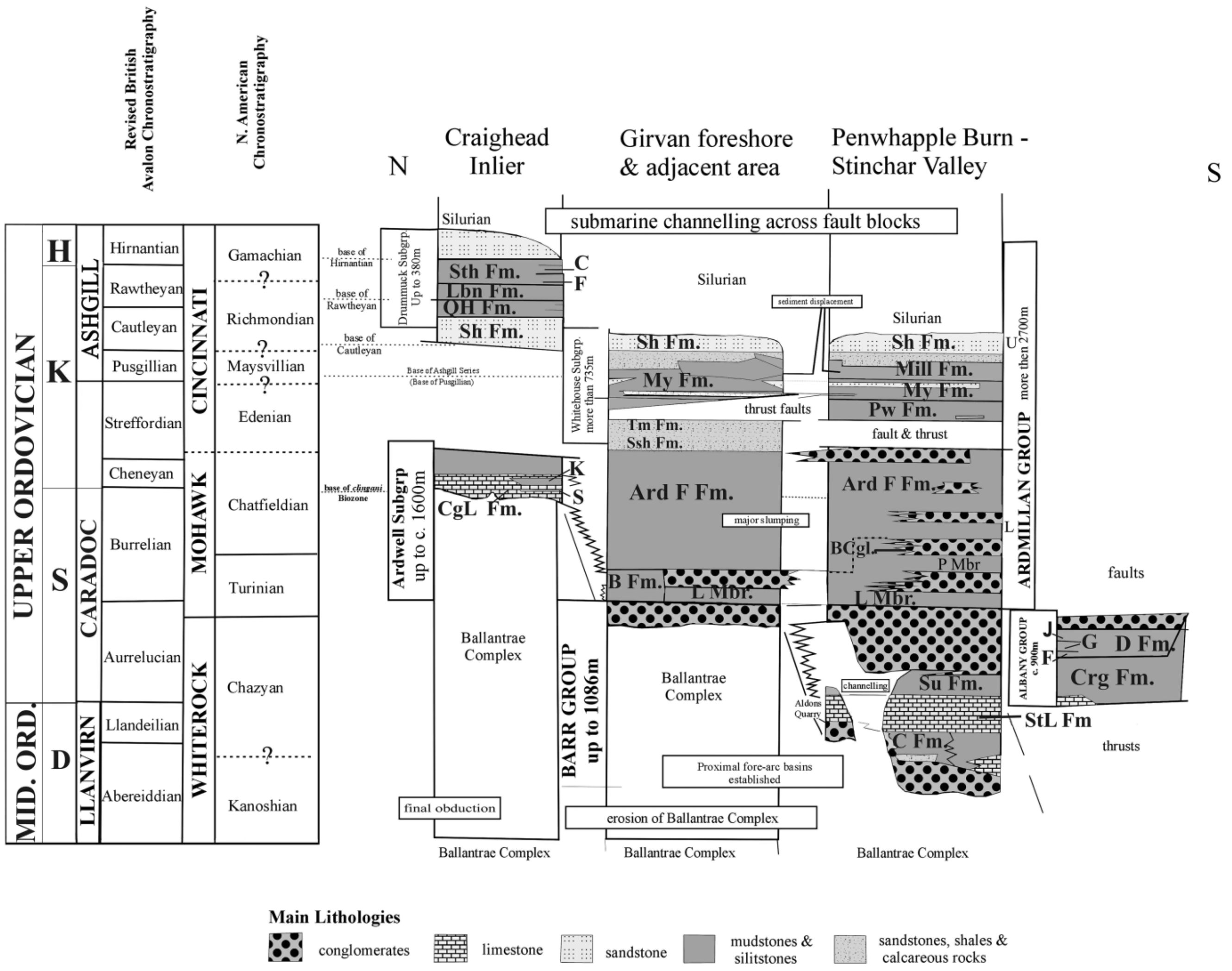

Stratigraphy

Albany Group
Crg Fm. Craigmalloch Formation
D Fm. Doularg Formation
F Fence Member
G Gorse Member
J Jubilation Member

Barr Group
StL Fm Stinchar Limestone Formation
C Fm. Confinis Formation
Su Fm. Superstes Formation

Ardmillan Group
B Fm Balclatchie Formation
Ard F Fm. Ardwell Farm Formation
L Mbr. Laggan Member
P Mbr. Pumphouse Member
B Cgl Burnside Conglomerate Member
CgL Fm. Craighead Limestone Formation
K Kiln Member
S Sericoidea Member

Whitehouse Subgroup
Pw Fm. Penwhapple Formation
Tm Fm. Three Mile Formation
Ssh Fm. South Shore Formation
My Fm. Myoch Formation
Sh Fm. Shalloch Formation

Drummuck Subgroup
QH Fm. Quarrel Hill Formation
Lbn Fm. Lady Burn Formation
Sth Fm. South Threave Formation
F Farden Member
C Cliff Member

H Hirnantian
K Katian
S Sandbian
D Darriwilian

Figure 1 Girvan Ordovician stratigraphy showing major lithologies and formations. Adapted from Ingham (2000) with data from Bergström *et al.* (2009).

updated where possible. Trilobites were compiled from a database of Ordovician fossils held at the University of Glasgow (McCormick & Owen 1999; Owen & McCormick 1999).

1.2. Barr and Albany groups

The Darriwilian/Sandbian (Llanvirn and earliest Caradoc) in Girvan is represented by the Barr and Albany groups, located mainly in the Stinchar Valley, south of Girvan. The Barr

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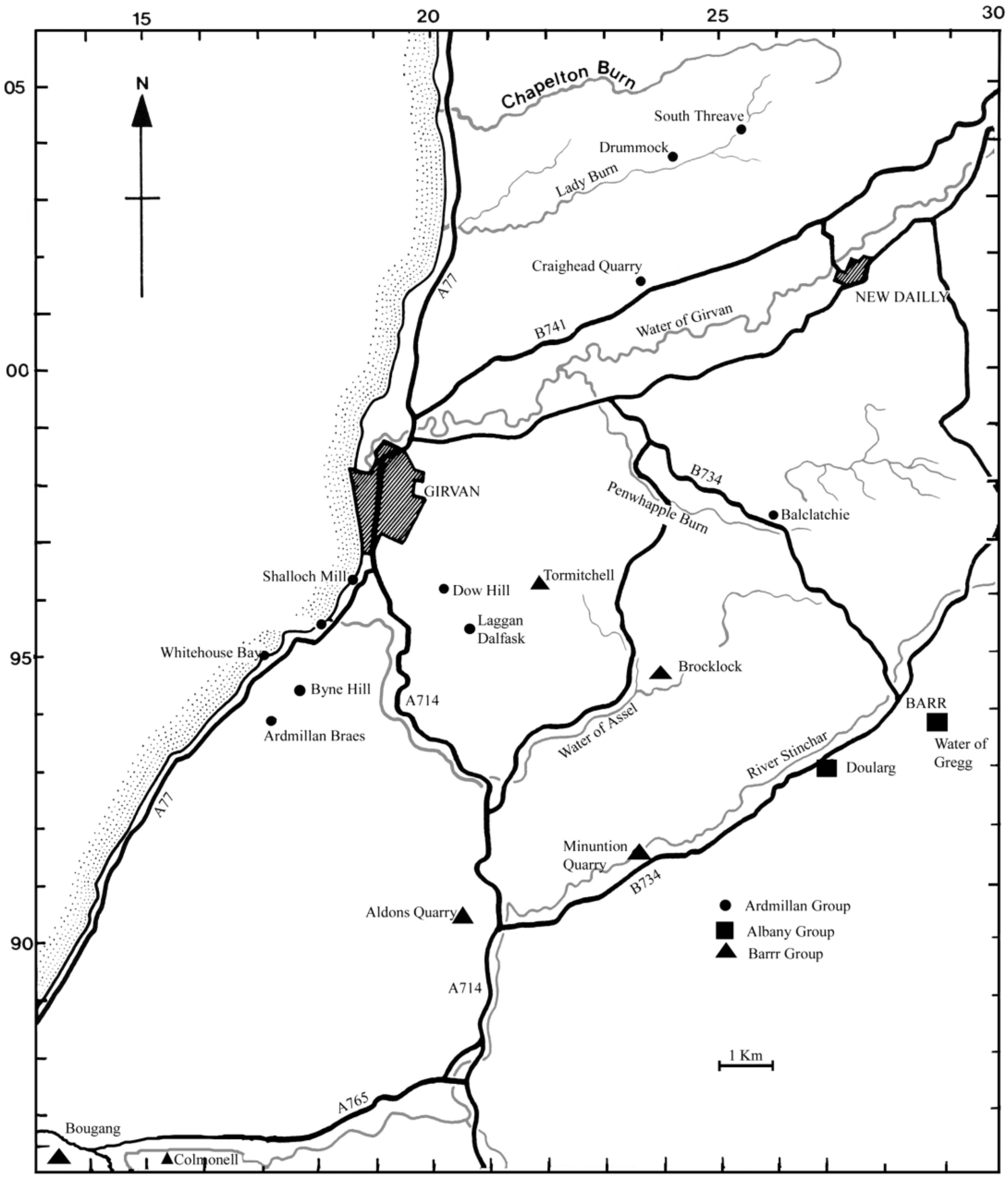

Figure 2 Localities of Ordovician faunas with mollusc faunas. Adapted from Tripp 1980a.

Group comprises a fan delta succession with repeated cycles of deposition of mainly shallow water carbonates, conglomerates, sandstones and mudstones (Ince 1984; Ingham 1992a). Deeper water siliciclastic facies are found in the laterally equivalent Albany Group, which crops out near the village of Barr (Ingham & Tripp 1991; Ingham 1992a; Tripp 1993; Rushton *et al*. 1996).

When the faunas from the Barr and Albany groups are analysed using detrended correspondence analysis (DCA) (Fig. 3), the majority of the gastropods cluster together in a distinct group, suggesting distinct environmental preferences; e.g., shallow, possibly hypersaline or brackish water which trilobites and brachiopods could not tolerate. This occurs next to a cluster of trilobites known from only carbonate substrates.

The most diverse gastropod fauna (Fig. 4a, d, e) is found in the Stinchar Limestone Formation at Minuntion. Here, *Maclurina* is common in the *Girvanella* limestones, along with *Ectomaria* and *Lophospira*. However, they are generally poorly preserved and can be difficult to identify to species level. Decalcified limestone from near the top of the Stinchar Limestone Formation at Minuntion, described by Tripp (1979), does not contain the large gastropods and *Maclurina* known from the lower, massive limestone and may reflect a slightly different environment. Ince (1984) suggested Minuntion represents a nearshore intertidal environment. According to Tripp (1979), the decalcified limestone at Minuntion represents shallow illaenid–cheiruid trilobite facies, with the Stinchar Limestone at Aldons representing slightly deeper water than Minuntion. The top of the Stinchar Limestone Formation exposed at Aldons Quarry preserves a less diverse gastropod fauna with *Maclurina* and bellerophontoid gastropods.

Gastropods are much less common in the deeper water siliciclastic facies of the Barr and the Albany groups, where only a few specimens have been recorded. In the Superstes Formation at Craigneil, Colmonell, Tripp *et al*. (1981) recorded just four gastropods, compared to 158 (Tripp 1979) in the Stinchar Limestone Formation at Minuntion. The graptolite-dominated Craigmalloch Formation at the Water of Gregg (Rushton *et al*. 1996) contains specimens of *Archinacella* (BGS Collections).

The scarce bivalves cluster beside trilobites including *Nileus* from the deep water facies of the Superstes Formation and Albany Group. The oldest known Girvan bivalve occurs in the deeper water siliciclastic facies of the Superstes Formation of

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Table 1 Gastropods, univalved molluscs and bivalves from the Barr and Albany Groups.

	Albany Group			Barr Group								
	Jubilation Mbr, Doularg Fm	Gorse Mbr, Doularg Fm	Water of Gregg, Craigmalloch Fm	Colmonell, Superstes Fm	Aldons, Stin. Lst. Fm	Brockloch, Stin. Lst. Fm	Tormitchell, Stin. Lst. Fm	Minuntion, decalcified Stin. Lst. Fm	Minuntion massive Stin. Lst. Fm	Water Gregg Stin. Lst. Fm	Bougang, Stin. Lst. Fm	Bougaang Stin. Lst. Fm
Gastropods and univalved molluscs												
Archinacella sp.			x									
Ectomaria prisca									x			
eotomarioid indet.							x		x		x	
Eccyliomphalus bucklandi?							x					
high spired gastropod				x				x	x			
indeterminate gastropod								x	x			
?*Liospira* sp.					x							
Lophospira modesta								x	x			
Maclurina sp.					x	x	x		x			x
'*Metoptoma*'				x					x			
murchisonioid indet.								x	x		x	
planispiral gastropod				x								
bellerophontoid indet.					x						x	
?*Alaskadiscus hunteri*					x	x						
Groomodiscus buccinoideum									x			
Bivalves												
modilolopsid?		x										
actinodontoid?				x								

the Barr Group, at Craigneil, Colmonell (Tripp *et al*. 1981; Ingham & Tripp 1991). A single poorly preserved specimen, from Tripp's bulk collection in the Hunterian Museum, is tentatively assigned to the actinodontoids (Fig. 5a). A modiomorphoid bivalve possibly *Goniophora*? sp., or a form close to it, (Fig. 5b) occurs in the mudstones of the slightly younger Gorse Member of the Doularg Formation, Doularg near Barr.

Tripp (1979) recorded bivalves in decalcified limestone of the Darriwilian Stinchar Limestone Formation at Minuntion Quarry, but examination of his material (kept in the Hunterian Museum, Glasgow) did not reveal any unambiguous bivalves. Some of the specimens he ascribed to this group are probably rostroconchs; however the material is now very friable and fossils are difficult to identify.

1.3. Ardmillan Group

The Sandbian/Katian (Caradoc–Ashgill) Ardmillan Group comprises mainly mudstones and conglomerates with some carbonate facies (Ingham 1992a). The deepest water facies are preserved in the Laggan Member (Stewart & Owen 2008) and the Whitehouse Subgroup (Ingham 1992b), which contain trilobites of the cyclopygid–atheloptic biofacies and brachiopods of the *Foliomena* Fauna.

Detrended correspondence analysis of the Ardmillan Group faunas (Ardwell and Whitehouse subgroups) produced plots with few obvious clusters, probably due to the transported nature and subsequent mixing of many of the faunas. Figure 6 does show the spread of molluscs across the shelf, and the influence of water depth and substrate on mollusc distribution. Gastropods and bivalves are more diverse in the shallower water facies, with few occurring in the deepest waters. Brachiopods are more diverse than bivalves and are distributed across shallow and deep waters, though diversity decreases with depth.

The mollusc fauna preserved in the mudstones of the Bellmoor Member of the Balclatchie Formation at Dow Hill is dominated by planispiral and wide, low-spired gastropods, particularly *Liospira* (Fig. 4j), with few trochiform and high-spired forms present. The widely expanded bellerophontoid *Carinaropsis* is found here (Fig. 4c), along with some species of bivalve (Fig. 5g, i), consisting of *Edmondia* and *Paracyclas* of Hind (1910) and infaunal nuculoids. An unusual fauna with scarce bivalves and gastropods but abundant polyplacophoran sclerites is present in the laterally equivalent Laggan Member at Dalfask (Stewart & Owen 2008).

The highest diversity and abundance of molluscs is preserved at Balclatchie in the mudstones of the Pumphouse and overlying Burnside Conglomerate members of the Balclatchie Formation. Bivalves are diverse, with *Paracyclas* (Fig. 5h), *Gosseletia*, *Leptodesma*, infaunal nuculoids (Fig. 5f) and modiolopsids. Most common are the epibyssate ambonychiids *Ambonychia* (Fig. 5c) and *Byssonychia*.

The diverse gastropod (Fig. 4g, i, k) fauna of the Pumphouse and Burnside Conglomerate members includes species of *Ecculiomphalus* (Fig. 4b), *Ectomaria*, *Eotomaria* and *Lophospira*. The cap-shaped mollusc *Archinacella* is common. Scarce mimospirids (Fig. 4g) appear in Girvan for the first time in the Pumphouse Member (Frýda & Rohr 1999). Bellerophontoid gastropods become more diverse and are represented in the Pumphouse Member by *Grandostoma*, *Tetranota*, *Kokenospira*, *Bucania* and *Pterotheca*, with *Sinuites* as the most abundant genus.

The Ardwell Farm Formation, which crops out at Ardmillan Braes, contains the nuculoid bivalves *Ambonychia* and *Leptodesma*, gastropods, including *Liospira* and *Ecculiomphalus*, and bellerophontoids, including *Sinuites*, *Pterotheca* and *Carinaropsis*. A described quarry on Byne Hill contains allochthonous faunas with two genera of bivalve (Fig. 5j) and

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Table 2 Gastropods, univalved molluscs and bivalves from the Ardmillan Group.

ARDMILLAN GROUP	Whitehouse Subgroup			Craighead Farm (Craighead Quarry)			Arwell Farm		Balclatchie Farm			
	Mill Fm	Myoch Fm	Gully Mbr., Penwhapple Fm	Kiln Mbr	Sericoidea Mbr	Craighead Lst. Fm	Ardmillan Braes	Byne Hill	Burnside Congl. Mbr	Pumphouse Mbr	Dalfask Quarry, Laggan Mbr	Dowhill, Bell. Mbr
Gastropods and univalved molluscs												
Alaskadiscus hunteri									x	x		
Alaskadiscus sp.	x					x			x	x		
Archinacella? *porifera*							x					
Archinacella sp.		x								x	x	x
Arjamannia bellicarinata	x											
bellerophontoid indet.	x		x			x	x			x		x
Boucotspira ordovicus							x		x	x		
Bucania playfairi	x											
Bucaniopsis forbesi Reed 1921 (*nomen vanum*according to Wagner 2008)	x											
Carinaropsis gracilis							x			x		x
Carinaropsis sp.		x										x
Catozone striatula										x		
Clathrospira trochiformis							x					
Cyclonema longstaffe of Lamont 1946a	x											
Cymbularia youngi	x											
Cyrtolites craigensis						x						
Ecculiomphalus? *coincinnus*	x											
Ecculiomphalus? *macroomphalus*						x			x			
Ecculiomphalus? sp. nov. of Lamont (1946a)	x											
Eccyliomphalus balclatchiensis										x		
Eccyliomphalus scotica									x			
Eotomaria subplana									x			
eotomarioid indet.										x		
euomphaloid gastropod indet.							x	x	x	x		
Donaldiella filosa	x											
Groomodiscus buccinoidem									x			
Gyronema sp.	x											
high spired gastropod	x				x	x						x
Hormotoma nigra	x											
Hormotoma nitida										x		
Hormotoma ordovix	x											
Hormotoma polita	x											
indeterminate gastropod	x					x				x		
Isospira huttoni	x											
Joleaudella transiens							x			x		x
Kokenospira maccullochi									x			
Kokenospira nicholsoni						x						
Laeogyra sp.							x			x		
Liospira disciformis									x			x
Liospira striatula									x			
Liospra aequalis									x			
Lophospira ferruginea							x					
Lophospira gyrogonia	x											
Lophospira modesta	x											
Lophospira perangulata										x		
Lophospira shallockensis	x											
Lophospira subglobosa						x						
Loxobucania evoluta									x			
Loxobucania gravida						x				x		
Maclurina sp.						x			x	x		
Mestoronema sp.									x			
Mimospira balclatchiensis							x			x		

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Table 2 *Continued.*

ARDMILLAN GROUP	Whitehouse Subgroup			Craighead Farm (Craighead Quarry)			Arwell Farm		Balclatchie Farm			
	Mill Fm	Myoch Fm	Gully Mbr., Penwhapple Fm	Kiln Mbr	Sericoidea Mbr	Craighead Lst. Fm	Ardmillan Braes	Byne Hill	Burnside Congl. Mbr	Pumphouse Mbr	Dalfask Quarry, Laggan Mbr	Dowhill, Bell. Mbr
Naticopsis sp.	x											
Pachystophia balclatchiensis									x			
Palaeoschisma girvanensis							x					
Phragmolites girvanensis	x											
planispiral gastropod						x				x		x
Plethospira? *caledonensis*									x			
Pterotheca girvanensis							x			x		
Pterotheca simplex										x		
Raphistoma sp.						x				x		
Rhabdostropha primitivia	x											
Rhabdostropha? *latisinuata*	x											
Salpingostoma etheridgei						x						
Salpingostoma shallochensis												
Scalites depressa										x		
Sinuites? *separatus*									x			
Sinuites discoides							x		x	x		x
Sinuites maccallumi							x			x		
Sinuites sp.						x	x			x		x
Sinuites sphaeroidalis									x			
Sinuitopsis congruens										x		
Spiroecus excavata	x											
Strangulites balcltchiensis										x		
Tetranota carrickensis						x	x			x		
trochiform gastropod						x		x	x	x		
Trochonema? *shallochense*	x											
Valattotheca sp.								x				
Zonidiscus grayi	x											
Bivalves												
Ambonychia sp.						x	x		x	x		
?*Byssonychia angusta*	x											
Ambonychiopsis? sp.										x		
Cleionychia undata							x					
Clidophorus planulatus	x				x	x				x		
Cypricardinia lineata							x					
Edmondia sp.						x	x			x		x
Goniophora antiqua							x					
Gosseletia sp.										x		
indeterminate bivalve			x	x	x		x					
Leptodesma ardmillanensis							x			x		
Modilolopsis sp.						x	x			x		
Myalinia prisca						x				x		
nuculoid bivalve	x					x	x	x	x	x		x
Orthonota sp.												x
Paracyclas minor	x									x		x
Posidinomya antiqua	x											
Similodonta sp.			x							x		x
Sphenolium richmondense						x						
Vanuxemia distans						x				x		x

euomphaloid? gastropods from the Ardwell Farm Formation; though the fauna is in need of thorough sampling.

The Craighead Limestone Formation, exposed at Craighead Quarry contains gastropods, including *Liospira* and *Grandostoma*. Bivalves are present in the limestones of the Craighead Formation, but are less common and diverse than in equivalent siliciclastic facies, with only four species (*Ambonychia*, *Myalinia*, *Clidophorus* and '*Nucula*') recorded in the Gray Collection. In contrast, brachiopods are diverse (Williams 1962), with over 48 type species known from here. The

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Table 3 Gastropods, univalved molluscs and bivalves from the Drummuck Subgroup.

	HIGH MAINS FORMATION High Mains	LADY BURN FORMATION Farden Member, South Threave	QUARREL HILL FORMATION Quarrel Hill
Gastropods & univalved molluscs			
Archinacella cf. *prendigasti*		x	
Archinacella sp.			x
Arjamnnia thraivensis		x	
Boucotspira sp.		x	
Bucaniopsis nicoli		x	x
Cataschima convexa		x	
Clisospira reticulata		x	
Cymbularia drummockensis		x	
Cyrtolites thraivensis		x	
Eccyliomphalus quarrelensis			x
Ectomaria orientalis		x	
Euomphalid gen et. sp. indet. Lamont (1946a)			x
Grandostoma grande		x	
Helicotoma patula		x	x
Hormotoma polita		x	x
Indeterminate gastropod	x		
Kokenospira girvanensis		x	x
Liospira praedo		x	x
Lophospira modesta		x	
Palaeoschisma globosa		x	
Palaeoschisma thraivensis		x	
Phragmolites cf. *fimbriata*		x	
Platyceras rete			x
Pterotheca drummockensis		x	
Sinuites subrectangularis		x	x
Spiroecus girvanensis		x	
Straparollus drumuckensis		x	
Straparollus inferus			x
Subulites grayarum		x	
Tetranota carrickensis		x	
Threavia gulosa		x	
Zonidiscus grayi		x	x
Bivalves			
Indeterminate bivalve	x	x	x
Ambonychia arundinea		x	x
Clidophorus sp.			x
Ctenodonta sp.		x	x
Cyrtodonta transversa		x	x
Goniophora sp.		x	
Goniophorina sp. of Reed (1920)			x
Gosseletia ponderossa		x	
Gramyssia undata		x	
Modiolopsis scotica		x	
Nuculoid indet.		x	
Orthodesma sp.		x	
Orthonota inornata		x	
Parcyclas minor		x	
Pterinea reticulata		x	x
Similodonta sp.		x	
Vanuxemia sp.			x
Whitella cf. *brycei* of Lamont (1946b)			x

Craighead Limestone Formation contains two siliciclastic units, namely the Sericoidea and Kiln Members, which represent deeper water incursions. The graptolite-bearing Sericoidea Member is thought to be a deeper water facies than the Kiln Member (Williams & Floyd 2000). Tripp (1980b) recorded bivalves and gastropods from both (36 specimens in the Sericoidea Member and 77 specimens in the Kiln Member). Bivalves numbered 20 specimens in the Sericoidea Member and 59 in the Kiln Member, compared with 432 brachiopods in the Sericoidea Member and 368 in the Kiln Member.

The Whitehouse Subgroup, exposed inland and on the foreshore south of Girvan (Ingham 1992b), contains derived

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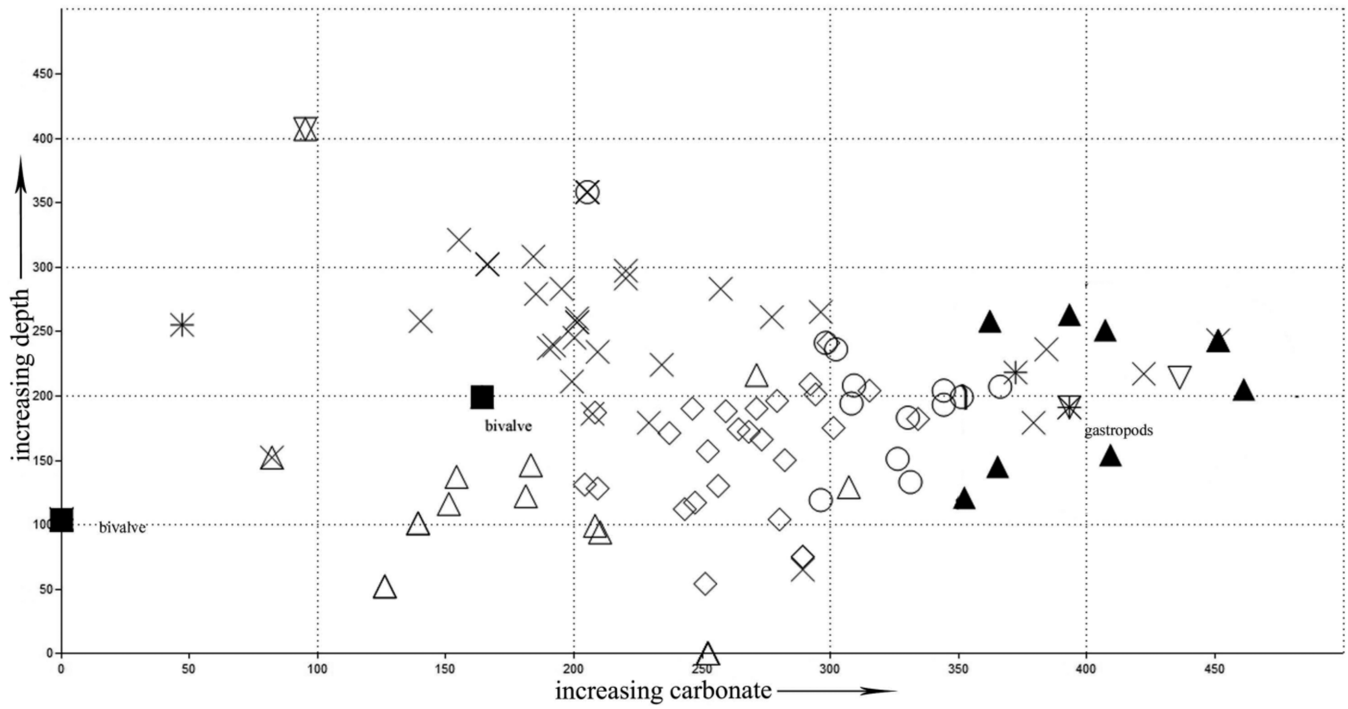

Figure 3 Detrended correspondence graph of Darriwilian and Sandbian (Llanvirn–Caradoc) faunas of the Barr and Albany Groups. Gastropods are largely confined to an area interpreted as carbonate facies in shallow waters. Scarce bivalves are confined to deeper water siliciclastic facies containing cyclopygid trilobites. Symbols: ■ = bivalves; X = brachiopods; ▲ = gastropods; ◇ = trilobites; ○ = trilobites from carbonate facies only; △ = trilobites from siliciclastic facies only; ▽ = other molluscs; ✳ = other fauna. Eigenvalue: axis 1, 0·6; axis 2, 0·4.

faunas as well as *in situ* deep water taxa. Few bivalves are preserved in these deeper water rocks. *Ambonychia*, *Paracyclas*, *Leptodesma* and some nuculoids are present in the Gray Collection (NHM) from the Mill Formation, but these may have been transported from a shallower water setting. Gastropods (Fig. 4f, h, n) from the Mill Formation include *Liospira* and *Spireoecus*. The bellerophontoids *Carinaropsis* and *Pterotheca* are present in the red mudstones of the Myoch Formation, which are thought to represent deep water channel fill deposits from submarine fans (Ingham 1992b). Ebbestad (2008) also recorded *Carcassonnella* from the Whitehouse Subgroup. Inland, the Gully Member, Penwhapple Formation at Penwhapple contains a few derived bivalves and bellerophontoids.

1.4. Drummuck Subgroup

The Katian (Ashgill) Drummuck Subgroup contains the most widely known of all the Girvan faunas, as it contains the famous obrution deposits (‘Starfish Beds’) of the Farden Member of the South Threave Formation, South Threave. The stratigraphy of the subgroup has been described in detail by Lamont (1935) and Harper (1981, 1982). Several units show signs of mass movement and many of the fossils are allochthonous. Lamont (1935) described molluscs from the Quarrel Hill Formation, including species of *Ecculiomphalus, Lophospira*, *Platyceras* and *Sinuites*. Bivalves included *Similodonta* and *Whitella*.

The bivalve fauna of the Farden Member is dominated by epibyssate ambonychiids (Fig. 4e); of which there is a large number in all collections examined (e.g. >100 specimens in the Gray Collection, NHM). Their presence suggests sampling from shallow waters. Infaunal nuculoids, such as *Orthonota* and *Cleoinychia*, together with the nuculoid *Similodonta*, are also present.

Gastropods and univalved molluscs are diverse (Fig. 4m) with species of *Arjamannia*, *Cyrtolites*, *Ectomaria*, *Helicotoma*, *Hormotoma* and *Lophospira*. Bellerophontoids include *Grandostoma* and *Kokenospira*, with *Sinuites* the most common genus (>200 specimens in the Gray Collection, NHM).

Molluscs are scarce in the overlying Cliff Member and in the following High Mains Formation, which records the Hirnantian glaciation event (Harper 1982; Owen 1986).

2. Wider comparison

The pattern of bivalve and gastropod distribution and diversity in the Ordovician is currently less well known than for other fossil groups due to lack of collecting, scarcity and, for bivalves in particular, outdated taxonomy (see Babin 2000; Novack-Gottshall & Miller 2003a, b; Cope 2004; Frýda & Rohr 2004; Ebbestad *et al.* in press). The distribution of Girvan molluscs generally follows that of those known worldwide.

Cambrian bivalves are known worldwide, but are not known in the Ordovician from Laurentia until the latest Darriwilian–earliest Sandbian (Babin 2000; Cope 2002, 2004 and references therein), apparently being confined to Gondwana in the early Ordovician. Girvan bivalves are similar to North American species (Hind 1910) and also to those from Norway (Soot-Ryen & Soot-Ryen 1960). At Girvan, the earliest unambiguous bivalves occur in the late Darriwilian Superstes Formation of the Barr Group and in the relatively deep water siliciclastic facies of the Doularg Formation of the Albany Group. The Doularg Formation represents quiet water conditions (Ingham & Tripp 1991); though transport from shallower waters is a possibility. The trilobites from the Doularg Formation (Jubilation Member) recorded by Ingham & Trip (1991) and the Superstes Formation (Tripp *et al.* 1981; Tripp 1993) are representative of the deep water *Nileus* biofacies of Fortey (1975). Some genera, like *Microparia*, are peri-Gondwanan in origin (Rushton *et al.* 1996) and provide evidence for migration of faunal elements to Laurentia. The

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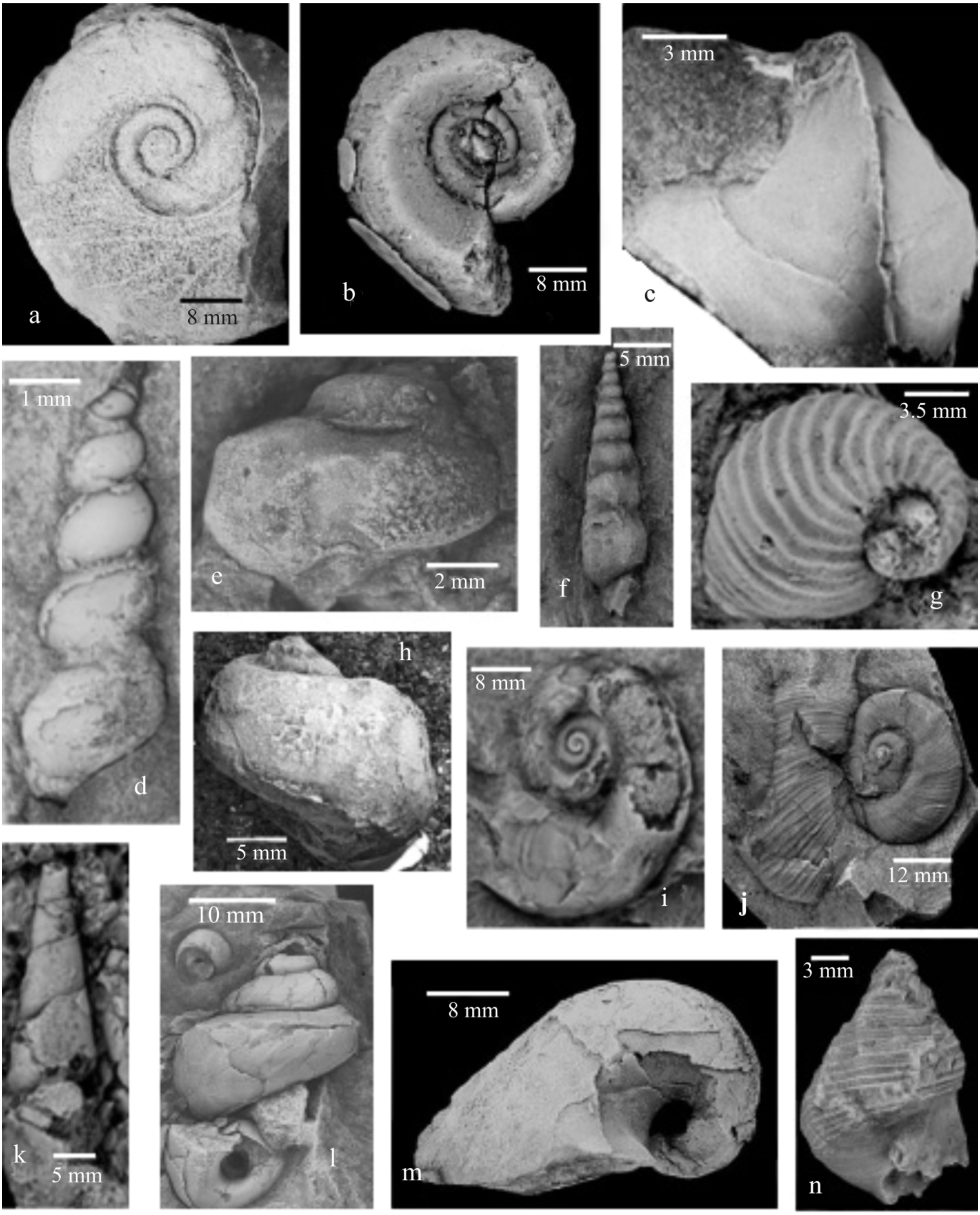

Figure 4 Girvan gastropods tergomyans and mimospirids: (a) *Maclurina* sp., Stinchar Limestone Formation, Minuntion, NMS.G. 1964.30.223; (b) *Ecculiomphalus scotica*, Burnside Conglomerate Member, Balclatchie Formation, Balclatchie, NHM G25378; (c) *Carinaropsis* sp., Balclatchie Formation, Dow Hill, BGS JS17818; (d) *Hormotoma*? sp., Stinchar Limestone Formation, Minuntion, BGS JS15901; (e) *Cyclonema*?, Stinchar Limestone Formation, Aldons GLAHM 131526; (f) *Spiroecus excavata* Mill Formation, Whitehouse Foreshore, NHM G44554; (g) *Laeogyra* sp. Pumphouse Member, Balclatchie Formation, Balclatchie, NHM G47702; (h) *Naticopsis*? sp., Mill Formation, Whitehouse Foreshore, GLAHM s19356a; (i) *Liospira* sp.?, Pumphouse Member, Balclatchie Formation, Balclatchie, NHM G47590; (j) *Liospira disciformis*, Pumphouse Member, Balclatchie Formation, Balclatchie, NHM G25328; (k) *Subulites* sp., NHM G44192, Burnside Conglomerate Member, Balclatchie Formation, Balclatchie; (l) *Lophospira* sp., GLAHM s9703, Farden Member, Lady Burn Formation, South Threave; (m) *Cyrtolites thraivensis*, GLAHM 21619, Farden Member, Lady Burn Formation; (n) *Gyronema* sp?, NHM G 47919, Whitehouse Subgroup. All coated with ammonium chloride sublimate. Images b, f, g, i, j and n courtesy NHM photography.

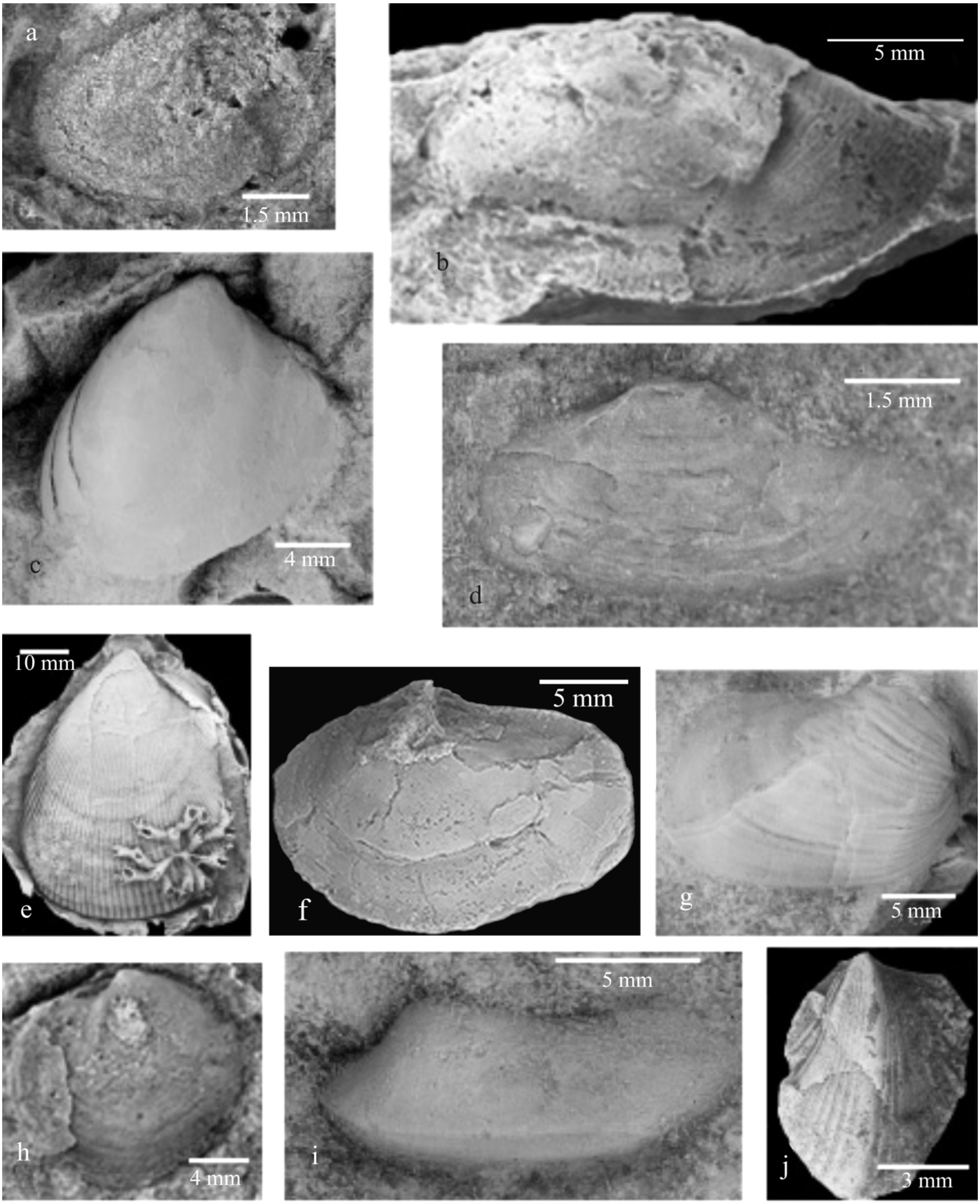

Figure 5 Girvan bivalves: (a) actinodontoid? bivalve, Superstes Formation, Barr Group, Colmonell, Hunterian Tripp collection, GLAHM 131528; (b) modiolopsid? bivalve, Albany Group, Craigneil, GLAHM 131529; (c) *Ambonychia* sp. Pumphouse Member, Balclatchie Formation, Balclatchie, NMS.G.1976.71.74; (d) nuculoid bivalve?, Ardwell Farm Formation, Byne Hill, GLAHM 131776; (e) *Ambonychia* sp., Farden Member, Lady Burn Formation, South Threave, GLAHM 146892 latex; (f) nuculoid bivalve, Pumphouse Member, Balclatchie Formation, Balclatchie, GLAHM s30628; (g) modiolopsid? bivalve, Balclatchie Formation, Dow Hill, BGS JS17801; (h) *Paracyclas* sp?, Pumphouse Member, Balclatchie Formation, Balclatchie, NHM L50060; (i) Nuculoid bivalve?, Balclatchie Formation, Dow Hill, BGS JS 17802; (j) *Ambonychia* sp., Burnside Conglomerate Member, Balclatchie Formation, Balclatchie, GLAMH 131777. All coated with ammonium chloride sublimate. Image h courtesy NHM photography.

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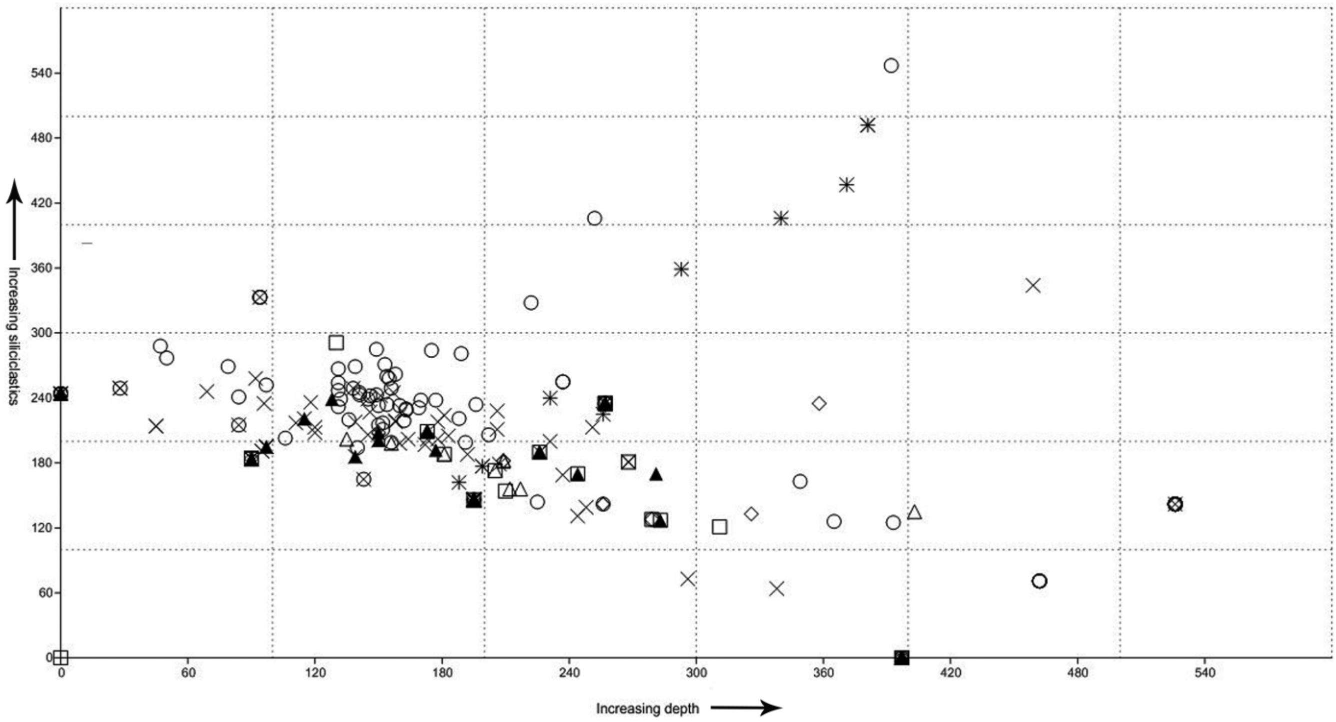

Figure 6 Detrended correspondence graph of Sandbian–Katian faunas (Albany Group–Whitehouse Subgroup). Axis 1 is interpreted as water depth. Most species are located in shallower waters, with only a few occurring in the deepest water settings of the *Foliomena* brachiopod associations. Molluscs are spread across the shelf, but occur mainly in the shallower waters. Brachiopods and trilobites are spread across the shelf. Axis 2 may reflect the amount of siliciclastics. Symbols: △ = bellerophontoids; □ = bivalves; X = brachiopods; ▲ = gastropods; ◇ = other molluscs; ○ = trilobites; ✳ = other fauna. Eigenvalue: axis 1, 0·77; axis 2, 0·6.

presence of bivalves in this deeper water facies reflects bivalve distribution, noted by Novack-Gotshall & Miller (2003a, b), in the Cincinnati Arch of Laurentia. Harper *et al.* (1988) recorded bivalves in a marginal deep water mudstone facies with a *Nileus* trilobite fauna in the *D. bifidus–D. murchisoni* zone (middle Llanvirn) of the Partry Mountains, Lough Shee, Ireland.

Conversely, bivalves recorded in rocks of similar age in North American occur in the shallower water of the St. Stephens Sandstones, Minnesota (see Cope & Babin 1999), and Ethington (2008) recorded bivalves from the North Esk Inlier Margie Limestone of the Highland Border Complex, along with Arenig–Tremadoc conodonts. Studies by Cherns *et al.* (2010 and references therein) suggest that taphonomic loss of molluscs is important in Lower Palaeozoic carbonate facies, so the pattern of bivalve distribution seen in the Ordovician may be distorted, with an incomplete record of true distribution preserved.

Bivalves continued to be more diverse and abundant in siliciclastic facies than in carbonate facies at Girvan throughout the Ordovician. Novack-Gottshall & Miller (2003a, b) also recorded a higher abundance and diversity of bivalves in deeper water, particularly siliciclastic, faunas in the Cincinnati Arch and Mississippi Valley areas in Laurentia than in carbonate settings. Frey (1987) noted that bivalves tended to be scarcer than brachiopods in the carbonate facies of the Cincinnatian Series, where ambonychiids and other epibyssate and endobyssate forms were the most common bivalves.

Hurst (1979) similarly reported that bivalves were more common in deep water siliciclastic settings in the Caradoc of Wales, with *Similodonta* present in deeper waters. Novack-Gottshall & Miller (2003a, b) have suggested that the Taconic Orogeny was an important factor in the radiation of bivalves in the Darriwilian–Sandbian in Laurentia, by producing an influx of clastic sediments to the shelves which would favour their environmental preferences. Therefore, the periodic subsidence and influx of sediment may have been important for the spread of bivalves in the Girvan area.

Near and onshore facies are dominated by ambonychiids in North America (Pojeta 1971; Frey 1987); and in Girvan in the Balclatchie Formation at Balclatchie and the Farden Member, South Threave Formation, where they are most abundant.

Gastropods originated in the Cambrian and are known globally. They are known to have diversified worldwide in the Ordovician; first in the Floian and then in the Sandbian (Frýda & Rohr 2004; Frýda *et al.* 2008). Globally, gastropods are more diverse in shallower (particularly carbonate rich facies) waters than in deeper waters (Novack-Gottshall & Miller 2003a, b). The macluritoid–*Girvanella* association seen in the massive Stinchar Limestone Formation at Girvan is known worldwide from warm water environments during the Darriwilian (Banks & Johnson 1957; Rohr 1979).

Bretsky (1970) reported murchisonioids to be confined to carbonate substrates and clear waters in the Upper Ordovician of Tennessee. High-spired murchisoniids and loxonematids occur mainly in soft substrates (Peel 1977, 1978), which may account for the difference in gastropod distribution in the massive and decalcified limestones at Minuntion.

North American Laurentian faunas from carbonate facies are characterised by *Maclurina*, *Omospira*, *Lophospira*, *Hormotoma* and *Holopea* (see Stanley 1977; Holland & Patzkowsky 2009) all of which (or closely related genera) are present in Girvan in similar facies.

An increase in gastropod diversity in the Sandbian–Katian Ardmillan Group is consistent with the global pattern in gastropod diversity seen at this time (Frýda & Rohr 2004; Frýda *et al.* 2008), though some groups declined in diversity at this time and became extinct during the Katian. Shallow-water Girvan faunas were still mainly Laurentian in origin, with many genera shared with eastern North America (Ebbestad

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et. al in press) and also Baltica. However, Ebbestad (2008) noted increasing deep water peri-Gondwanan influences in Girvan gastropod faunas. The presence of the genera *Laeogyra*, *Carcassonella* and *Grandostoma* in Girvan may reflect a marine transgression known as the *Linearis* 2 drowning event in Baltica (Nielsen 2004). A corresponding rise in sea level in North America was noted by Ross & Ross (1995) at this time. The deep water mudstones of the Bellmoor Member at Dowhill contain few murchisoniid gastropods and have a mollusc fauna dominated by low-spired and planispiral gastropods, which may have preferred a deposit-feeding mode of life in soft sediment.

Bellerophontoid gastropods are distributed across the shelf in Girvan, but appear to be more common in siliciclastic facies; a pattern similar to that described by Hurst (1979) for the Upper Ordovician Welsh Borderland, where *Sinuites* and *Carinaropsis* are present in the deep water facies. Pickerill & Brenchley (1979), Brenchley & Cocks (1982) and Horný & Vonka (2002) also record *Sinuites* in deeper waters. Horný (1963, 1995) recorded bellerophontoids in offshore siliciclastic facies of Bohemia; principally in silty and muddy substrates. Shallow-water facies, possibly with a firm substrate, are characterised by the presence of trilobed and explanate forms, including *Phragmolites*, *Bucania* and *Groomodiscus* (Peel 1977; Wahlman 1992).

Wahlman (1992) suggested that bellerophontoids had a wide environmental distribution. *Pterotheca*, known from deep water deposits in Girvan, is also known from shallow water settings in the Silurian of the Pentland Hills (Clarkson *et al.* 1985), so may have had a broader environmental range, or changed environmental preferences through time.

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