

Earliest Silurian faunal survival and recovery after the end Ordovician glaciation: evidence from the brachiopods

L. Robin M. Cocks¹ and Rong Jia-yu²

¹ Department of Palaeontology, The Natural History Museum, London SW7 5BD, UK

² Institute of Geology and Palaeontology, Academia Sinica, 39 East Beijing Road, Nanjing, 210008 China

ABSTRACT: Earliest Silurian (basal Llandovery) brachiopod faunas are surveyed and listed from around the globe, and divided between Lower Rhuddanian and Upper Rhuddanian occurrences. 60 genera are known from the Lower Rhuddanian within 20 superfamilies and there are 87 genera in 25 superfamilies in the Upper Rhuddanian. The 29 areas surveyed span the globe, both latitudinally and longitudinally. Only six superfamilies are Lazarus taxa which are known both from the Ordovician and Middle Llandovery (Aeronian) and later rocks but have not been recorded from the Rhuddanian. These are surprising results, since many previous studies have inferred that the Rhuddanian was a time of very sparse faunas. The global warming that followed the latest Ordovician (Hirnantian) ice age did not proceed quickly, with an ice-cap probably present through at least the Llandovery. There is a marked absence of Lower Rhuddanian bioherms even at low palaeolatitudes; however, the ecological recovery rate was far faster than that following the end-Permian mass extinction event. The partitioning of the Rhuddanian shelf faunas into well-defined benthic assemblages progressed slowly over the interval.

KEY WORDS: Llandovery, post-glacial recovery, Rhuddanian

The latest Ordovician Hirnantian Stage saw one of only three Phanerozoic glacial intervals (the other two being the Carboniferous-Permian and the Oligocene-Recent), which is now well-documented globally (Brenchley *et al.* 1994). The top of the Hirnantian is defined by the base of the Silurian. Because of the large volume of water locked up in the polar ice-caps, there was widespread regression during the Hirnantian. The ice melted during the early Silurian and there were consequent global transgressions: as a result, the Ordovician–Silurian boundary is marked in most regions of the world by unconformities of various sizes, many of them substantial. The melting was apparently fairly fast during the Rhuddanian, but nevertheless it is probable that ice caps were present at both poles during most of the Llandovery.

The global cooling associated with the glaciation also triggered one of the most substantial Phanerozoic faunal extinction events in two or more phases, which are also well documented (see references in Sheehan 2001). However, the recovery of the various invertebrate groups during the subsequent early Silurian has received less attention, and it is the purpose of this paper to evaluate how one of the most abundant marine invertebrate groups, the brachiopods, reacted to the changing conditions after the peak of the glacial interval. The topic has been treated for the important South China region by Rong & Harper (1999), but this present paper discusses it in a wider context. It is in some ways complementary to the paper on Lazarus taxa across the Ordovician–Silurian boundary by Rong *et al.* (2006), but differs fundamentally from it in (a) going back to the source papers for the brachiopod distributions (and thus ignoring the time distribution data in the *Treatise on Invertebrate Paleontology*); (b) in dividing the Rhuddanian occurrences into upper and lower; and (c) in confining the age range considered to the Rhuddanian, rather than extending further upwards into the



Aeronian and higher parts of the Llandovery. Preliminary surveys by Cocks (1988) and Sheehan & Coorough (1990) of the earliest Silurian brachiopod faunas did not clearly assess which of the then limited number of faunas known were of Late or Early Rhuddanian age: many more Rhuddanian brachiopod faunas have become known since then.

The paper commences with a review, terrane by terrane, of the recorded occurrences of brachiopods in the lowest Silurian stage, the Rhuddanian Stage of the Llandovery Series, following the terranes depicted in Cocks & Torsvik (2002). The actual length of time involved is difficult to assess in detail; however, the outlines are now clearer. The Ordovician–Silurian boundary was at 443 Ma, and the top of the Silurian at 418 Ma, but, although there are three further series (the Wenlock, Ludlow and Pridoli) above the Llandovery within the Silurian, the Llandovery is now known to have extended for more than half of Silurian time, about 12 million years. The Llandovery is divided into three stages, the Rhuddanian, Aeronian and Telychian; however, their relative ages are not precisely known. Nevertheless, the Rhuddanian may by interpolation be approximately estimated as having lasted for about four million years. Within the Rhuddanian, correlation is best made through graptolites, of which there are four zones, in ascending order the *ascensus*, *acuminatus*, *vesiculosus* and *cyphus* Biozones; however, it is unfortunate that many of the occurrences of shelly fauna outlined below do not have associated graptolites, and thus can only be dated here as ‘Early’ or ‘Late’ Rhuddanian, but graptolite control has been indicated where knowledge of the age is more precise. Some major terranes, notably Sibumasu, Lhasa (part of Tibet) and Perunica (Bohemia), have no Rhuddanian brachiopod faunas recorded from them, and it is noteworthy that the vast superterrane of Gondwana has relatively few when its size is considered. The faunas are numbered 1 to 31 and their

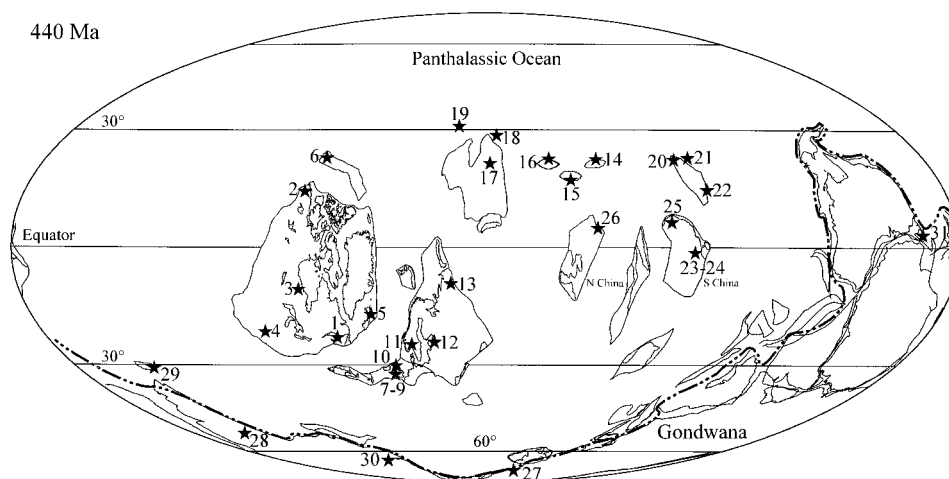


Figure 1 Rhuddanian brachiopod localities plotted on the 440 Ma global reconstruction of Cocks & Torsvik (2002, fig. 7). 1–5, Laurentia; 6, Kolyma; 7–13, Avalonia-Baltica; 14–16, Kazakh terranes; 17–19, Siberia and peri-Siberia; 20–22, Tien-Shan and Tarim; 23–25, South China; 26, North China; 27–31, Gondwana. The Kazakh terranes are shown as plotted by Fortey & Cocks (2003, fig 15).

locations (Fig. 1) are plotted on the 440 Ma global reconstruction modified from that published by Cocks & Torsvik (2002). Some faunas are from a number of localities within the numbered areas; that is particularly true of Siberia.

This review has been conducted at the generic and family level: although species are often critically important, not enough extensive systematic work has yet been published on most of the areas to list them with confidence. Taxa which are not determined generically are not included, and thus a few families which have been recorded from the Rhuddanian, but without identified genera, may have been omitted from this review. Where the generic identification has been altered from that originally published, it is marked with an asterisk*, but basic revision of the systematics, whilst needed in many cases, is outside the scope of this paper. For example, a specific change is that the present authors have not yet positively identified the abundant pentameroid *Clorinda* (which has carinae) from rocks older than Aeronian in age, and have thus changed its identification to **Clorinda*: that Rhuddanian form may in fact be a close relative of *Brevilammulella*. A further unresolved problem is whether or not the meristelloid genera *Hindella* and *Cryptothyrella* are synonyms, and so here the original authors in their records have largely been followed. There are comparable problems in unravelling the relationships of the orthotetoideans *Coolinia* and *Fardenia*.

1. Laurentia

Most of Laurentia has substantial Ordovician–Silurian unconformities, but there are some key areas where the Rhuddanian occurs. In addition to the localities noted below, there are others of possible Rhuddanian age but whose dating is uncertain through lack of diagnostic graptolites or conodonts. In particular, all the widespread assemblages dominated by the pentamerid *Virgiana* were previously thought to be of Mid Llandovery (Aeronian) age, but some are now known to be Upper Rhuddanian, for example, those documented by Jin *et al.* (1993) listed below. Other possible Upper Rhuddanian candidates include the lower parts of the Manitoulin Formation of Manitoulin Island, Ontario, the Mayville Dolostone of Wisconsin, the Fisher Branch Formation of Manitoba, and the lower part of the Lake Town Dolomite of Nevada; however, the genera illustrated from those horizons by various authors are all included in the Laurentian Rhuddanian localities listed

below. Many *Virgiana* localities still seem correctly dated as Aeronian in age, e.g. the Michigan Basin localities of Watkins & Kuglitsch (1997), but uncertainty remains in many cases; for example, the Mayville Dolostone in Eastern Wisconsin is stated to be of Rhuddanian age by Harris *et al.* (1998) but there seems to be no evidence for that apart from the presence of *Virgiana mayvillensis*.

1.1. Locality 1: Anticosti Island, Quebec, Canada

The Hirnantian–Rhuddanian boundary is very near the top of the Ellis Bay Formation (Cocks & Copper 1981; Copper 1999), and the Rhuddanian extends certainly to the top of the overlying Becscie Formation and probably just into the lower part of the overlying Merrimack Formation, but because of doubts about the precise position of the Rhuddanian–Aeronian boundary within the Merrimack Formation, records from the latter are not included here. Lower Rhuddanian (Fox Point Member) brachiopods are *Saukrodictya*, *Platystrophia*, *Mendacella*, *Isorthis*, *Diceromyonia*, *Biparetis*, *Leptaena*, *Eopholidostrophia*, **Palaeoleptostrophia*, *Viridita*, *Beccscia*, *Cryptothyrella*, **Atrypina* and *Platytrocalos*. Upper Rhuddanian (Chabot Member): *Diceromyonia*, *Isorthis*, *Mendacella*, *Brachyprion*, *Eomegastrophia*, *Virgiana*, *Stricklandia*, *Fenestrirostra*, *Rhynchotrema*, *Rhynchotretra*, *Stegerhynchus* and *Cerasina* (distilled from Cocks & Copper 1981; Copper 1995, 1999; Dewing 1999; Jin 1989; Jin & Copper 2000; Li & Copper 2006).

1.2. Locality 2: Avalanche Lake area, District of Mackenzie, Canada

The Ordovician–Silurian boundary lies within the Whitaker Formation (Jin & Chatterton 1997, p. 7). Brachiopods from near the base of the formation are *Skenidioides*, *Epitomyonia*, *Dalmanella*, **Jonesea*, *Katastrophenomena*, *Leptaena*, *Pentlandina*, *Brevilammulella*, *Eospirigerina* and *Cyclospira*. Of these, *Brevilammulella* is known from the Hirnantian to the Aeronian; however, the first previously-recorded occurrences of the strophomenoid *Pentlandina* and the plectambonitoid *Jonesea* are Aeronian (Cocks & Rong 2000). There may be two successive faunas involved, the lower one Hirnantian and the upper one basal Rhuddanian, and thus, in view of the dating uncertainty, these have not been included in the overall summary but they are shown on Figure 2. The *Pentlandina* and

the *Jonesea* records appear to be the earliest occurrences of the two genera globally.

1.3. Locality 3: Hudson Bay Lowlands, Canada

Only late Rhuddanian brachiopods are known, in the *Virgiana decussata* Zone in the Severn River Formation (Jin *et al.* 1993), including *Virgiana*, *Stegerhynchus* and *Alispira*.

1.4. Locality 4: Oklahoma, Illinois and Missouri, USA

Amsden (1974) has monographed the brachiopods of this extensive area, where the Ordovician–Silurian boundary occurs above the Nora Limestone with a distinctive Hirnantian brachiopod fauna, and below the succeeding Bryant Knob and Bowling Green Formations, all within the Edgewood Group. The Bryant Knob has yielded *Platystrophia?*, *Dolerorthis*, *Dalmanella*, *Diceromyonia?*, *Mendacella?*, *Leptaena*, *Coolinia*, *Brevilamulella*, *Stegerhynchus*, *Thebesia*, *Cryptothyrella*, *Eospirigerina* and ‘*Homoeospira?*’. The Bowling Green includes *Dolerorthis*, *Dalmanella*, *Diceromyonia?*, *Dicoelosia* and *Eospirigerina*. Firm correlation is difficult: there are no associated graptolites, but there are some conodonts noted by Bergström & Boucot (1988), and the Bryant Knob Formation is assessed by the present authors as Hirnantian and the Bowling Green as Lower Rhuddanian.

1.5. Locality 5: Girvan, Scotland

There is an Ordovician–Silurian unconformity; however, the Lady Burn Conglomerate is of *acuminatus* Biozone age, and the succeeding Mulloch Hill Formation and its age-equivalent Woodland Formation are well dated as *cyphus* Biozone (Cocks & Toghil 1973). The Lower Rhuddanian Lady Burn conglomerate has yielded *Lingula*, *Coolinia*, *Cryptothyrella* and **Rhynchotretra?*, and the Upper Rhuddanian Mulloch Hill and Woodland Point formations *Lingula*, **Petrocrania*, *Dolerorthis*, *Skenidioides*, *Schizonema*, *Dalmanella*, *Protocortezorthis*, *Mendacella*, *Triplesia*, *Streptis*, *Katastrophenomena*, *Leptaena*, *Palaeoleptostrophia*, *Leangella*, *Eoplectodonta*, *Fardenia*, *Saughina*, *Stricklandia*, **Clorinda?*, *Rostricellula*, *Eospirigerina*, *Cryptothyrella*, *Meifodia*, *Zygospiraella* and **Alispira*.

2. Kolyma Terrane

2.1. Locality 6: Mirny Creek, NE Siberia

From the Chalmak Horizon, Oradovskaya (in Koren *et al.* 1983) recorded *Leptaena*, *Protatrypa*, *Eospirigerina*, **Skenidioides?*, *Zygospiraella* from the *acuminatus* Zone (Lower Rhuddanian), and from the Upper Rhuddanian *cyphus* Zone *Eospirigerina*, **Skenidioides?*, *Protozeuga?* and *Zygospiraella*. She also recorded *Draborthis?* and *Hyattidina*, but the present authors cannot confirm those identifications and have omitted them from this survey.

2.2. Omulev Region, NE Siberia

Although not included in Figures 1 and 2, Kovalevskii *et al.* (1991) recorded *Skenidioides* and *Protatrypa* from beds of

probable Rhuddanian age in the Omulev area, and *Virgiana* from possible Rhuddanian beds in the Sette-Daban area.

3. Avalonia-Baltica

Avalonia and Baltica collided obliquely with each other at almost exactly Ordovician–Silurian boundary time, and thus they are grouped here. Avalonia includes the Llandovery district, Wales, where the type sections for the Llandovery Series are located, including the Rhuddanian Stage (Cocks *et al.* 1984). Despite the title of the paper, the brachiopods described by Boucot & Johnson (1964) from the Ede Quartzite of Sweden are now thought to be of Aeronian rather than Rhuddanian age.

3.1. Locality 7: Llandovery area, Wales

Cocks *et al.* (1984) recorded *Dolerorthis*, *Schizonema*, *Skenidioides*, *Dicoelosia*, *Ravozetina*, *Resserella*, *Triplesia*, *Anisopleurella*, *Eoplectodonta*, *Leangella*, *Eopholidostrophia*, *Katastrophenomena*, *Leptaena*, **Crassitestella*, **Palaeoleptostrophia*, *Fardenia*, **Clorinda?*, *Rhynchotrema*, *Plectatrypa*, ‘*Protozyga?*’, *Meifodia* and *Cryptothyrella* from the Bronydd Formation in the northern Llandovery area, which is of Early Rhuddanian age. The recorded ‘*Protozyga?*’ is not that Caradoc genus and is omitted from the present summaries. From the overlying Crychan Formation in the northern part of the area and the lateral equivalent lower parts of the Goleugoed Formation in the southern part of the area, which are Upper Rhuddanian, were found *Dolerorthis*, *Schizonema*, *Giraldiella*, *Skenidioides*, *Resserella?*, *Ravozetina*, **Templeella*, *Visbyella*, *Dicoelosia*, *Saukrodictya*, *Triplesia*, *Leangella*, *Anisopleurella*, *Eoplectodonta*, *Katastrophenomena*, *Leptaena*, **Crassitestella*, **Mesoleptostrophia*, *Eopholidostrophia*, *Eostrophonella*, *Fardenia*, *Stricklandia*, **Clorinda?*, *Rhynchotrema*, *Eospirigerina*, *Plectatrypa*, *Meifodia*, *Hindella* and *Cryptothyrella*. From the adjacent Garth area, 10 km N of Llandovery, Williams & Wright (1981) listed faunas which they stated to be of Rhuddanian age; however, since *Eocoelia* and *Pentamerus* are included, some at least are Aeronian. The other genera are the same as those recorded above from Llandovery, apart from *Dictyonella* and *Reuschella* (reidentified here as *Dysprosorthis*), both of which would be the only Lower Rhuddanian records of those genera if that were their age, and thus they have been included in the Upper Rhuddanian lists in this paper. The former is now termed *Eodictyonella*.

3.2. Locality 8: Meifod, Wales

Temple (1970) monographed the following Upper Rhuddanian brachiopods: *Paracraniops*, *Toxorthis*, *Dolerorthis*, *Schizonema*, *Giraldiella*, *Skenidioides*, **Templeella*, *Resserella*, *Dicoelosia*, *Epitomyonia*, **Visbyella*, *Saukrodictya*, *Triplesia*, *Streptis*, *Leangella*, *Anisopleurella*, *Eoplectodonta*, *Katastrophenomena*, *Leptaena*, *Eopholidostrophia*, **Mesoleptostrophia*, *Fardenia*, *Stricklandia*, **Clorinda?*, *Rhynchotrema*, *Plectatrypa* and *Meifodia*. His *Protozyga* is not that Caradoc genus, and remains unidentified here.

3.3. Locality 9: Pembrokeshire, Wales

The Ordovician–Silurian boundary lies within the Haverfordwest Mudstone Formation, from which Cocks & Price (1975)

Figure 2 Rhuddanian brachiopod occurrences. Early Rhuddanian shown by black circles in upper left corner of boxes. Late Rhuddanian by open circles in lower right corner. Less specifically dated occurrences are shown as pentagons. Question marks denote unclear occurrences or questionable identifications. Not included are the records of orthides from Locality 1, Anticosti Island (Li & Copper 2006) and the Saelabonn Fm of Locality 11 (Thomsen *et al.* 2006).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	Total	
<i>Aegiria</i>											○						●	●													1	
<i>Alispira</i>			○		○							○					●	●					?		●						4	
<i>Aneillotoecchia</i>																													?		1	
<i>Anisopleurella</i>							●	○	○																						2	
<i>Athyrisinoides</i>																								○	○						2	
" <i>Atrypina</i> "	●																							○	○						1	
<i>Atrypinopsis</i>																									○						1	
<i>Beescea</i>	●																														1	
<i>Beitania</i>																							○		○						2	
<i>Biparetis</i>	●																														1	
<i>Borealis</i>																									○						1	
<i>Brachyprion</i>		○																													1	
<i>Brevilamnella</i>		◻															●	○					○		●						2	
<i>Cerasina</i>		○																													1	
<i>Chrystenopora</i>												○																			1	
<i>Cliftonia</i>																		●													1	
<i>Clintonella</i>												○																			1	
" <i>Clorinda</i> "							●	○	○	○	○	○	○				○	●					○		○						3	
<i>Coolinia</i>					●																				○	○					2	
<i>Cordatomyonia</i>																														?	1	
<i>Crassitestella</i>							●	○				○																			1	
<i>Cryptothyrella</i>	●				●		●	○				○						●												◻	4	
<i>Cyclospira</i>		◻																													1	
<i>Dalmanella</i>		◻		●	○						●																			◻	3	
<i>Deliella</i>																										●					1	
<i>Dedzetina</i>																														?	1	
<i>Diceromyonia</i>				?																											1	
<i>Dicoelosia</i>				●			●	○	○		●	○																			3	
<i>Dolerorthis</i>				●		○	●	○	○	○	○	○				○		●												◻	5	
<i>Drabovia</i>												○																			1	
<i>Dysprosorthis</i>								○																							1	
<i>Eodictyonella</i>								○																							1	
<i>Eomegastrophia</i>		○																													1	
<i>Eopholidostrophia</i>	●						●	○	○	○	○	○				○															2	
<i>Eoplectodonta</i>					○		●	○	○	○	○	○					●	●							●					◻	6	
<i>Eospirifer</i>																									○	○	○	○				2
<i>Eospirigerina</i>		◻		●	○	○	○	○	○	○	○	○												○	○	○	○	○				5
<i>Eostropheodonta</i>												○													○	○				◻	1	
<i>Eostrophonella</i>								○		○																						2
<i>Epitomyonia</i>		◻							○		○															●						3
<i>Eridorthis</i>																	●	○														1
<i>Fardenia</i>					○		●	○	○			○	○																	◻	◻	1
<i>Fenestriostria</i>		○																														1
<i>Giraldiella</i>								○	○	○						○																5
<i>Glyptorthis</i>																										●						1
<i>Hemitoecchia</i>																																1
<i>Hesperorthis</i>																															?	1
<i>Heterorthisella</i>																														◻		1
<i>Hindella</i>								○			●		○												●		?			◻		3
<i>Hirnantia</i>											●																					1
<i>Holorhynchus</i>																																1
<i>Idiospira</i>											○	○																				1
<i>Isorthis</i>	●																●	○														2
<i>Jerzercia</i>																															?	1

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	Total						
<i>Jonesca</i>		◻																													1						
<i>Katastrophomena</i>		◻				○	●	○	○	○	○							●								●						3					
<i>Kinnella</i>											●																					1					
<i>Leangella</i>						○	●	○	○	○	○	●				○				○												2					
<i>Leptaena</i>	●	◻			○	●	●	○	○	○	○	○	○					●						●		●			◻	◻	8						
<i>Levenea</i>												○												○		●						1					
<i>Lingula?</i>					●	○			●															○		●						3					
<i>Mendacella</i>	●				○	○					?	○												●				◻		◻		2					
<i>Meifodia</i>					○	○	●	○	○			○				○		●				○	○				○				◻	2					
<i>Merciella</i>																								○									1				
<i>Mesoleptostrophia</i>								○	○																								2				
<i>Mirorthis</i>											●																						1				
<i>Nalivkina</i>														○										●	○			○					1				
<i>Onniella</i>														○																			1				
<i>Orbiculoidea</i>											●																						1				
<i>Orthokopis</i>												○																					1				
<i>Palaeoleptostrophia</i>	●					○	●				○																						2				
<i>Paracranioops</i>																								●		●							2				
<i>Parastrophinella</i>									○			○																						2			
<i>Paromalomena</i>											●													○		●								2			
<i>Pentlandella</i>												○																						1			
<i>Pentlandina</i>		◻																																1			
<i>Petrocrania</i>						○																												1			
<i>Platyrocalos</i>	●																																	1			
<i>Plectatrypa</i>							●	○	○																										1		
<i>Plectorthis?</i>																																			1		
<i>Plectothyrella</i>											●														●					◻					1		
<i>Protatrypa</i>						●						○		○																					1		
<i>Protocortezorthis</i>					○						●	○							●													?			3		
<i>Protozeuga</i>							?																												1		
<i>Ravozetina</i>							●	○	○																											1	
<i>Resserella</i>							●	?	○	○	○																									2	
<i>Rhynchotrema</i>							●	○	○																											1	
<i>Rhynchotreta</i>	○				?			○	○																										1		
<i>Rostricellula</i>						○																			●		●				◻				2		
<i>Saughina</i>						○											○																			3	
<i>Saukrodictya</i>								○	○	○	○																									2	
<i>Schizonema</i>						○	○	○	○	○	○	○																								3	
<i>Skenidioides</i>		◻				○	?	?	○	○	○	○																				◻			3		
<i>Stegerhynchus</i>	○		○																●																1		
<i>Streptis</i>						○			○			○																								3	
<i>Stricklandia</i>	○				○	○	○	○	○	○	○	○	○						●																1		
<i>Stricklandistrophia?</i>																																				1	
<i>Strispirifer</i>																																				1	
<i>Strophomena</i>																		○																		1	
<i>Templeella</i>																									○	○										3	
<i>Thebesia</i>											○																									1	
<i>Toxorthis</i>																																				1	
<i>Triplesia</i>						○	●	○	○			●																								3	
<i>Virgiana</i>		○		○											○																					1	
<i>Virgianella</i>																																					2
<i>Viridita</i>	●																																			1	
<i>Visbyella</i>											○	○																									2
<i>Whitfieldella</i>																																					3
<i>Zygospiraella</i>						○	●	?				○	○	○	○	○		○	○																	2	
																																					9

(revised herein) identified **Lingula?*, *Orbiculoidea*, *Skenidioides*, *Dolerorthis*, *Schizonema*, *Resserella*, *Leptaena*, *Eoplectodonta*, *Anisopleurella* and *Eospirigerina* in the Lower Rhuddanian, and *Skenidioides*, *Dolerorthis*, *Schizonema*, *Giraldiella*, *Resserella*, *Katastrophomena*, *Leptaena*, *Palaeoleptostrophia*, *Eopholidostrophia*, *Eostrophonella*, *Leangella*, *Eoplectodonta*, *Saughina*, *Stricklandia*, **Clorinda?*, *Pentlandella* and *Eospirigerina* from the Upper Rhuddanian.

3.4. Locality 10: Lake District, England

Harper & Williams (2002) recorded *Dolerorthis?*, *Dalmanella*, *Kinnella*, *Mirorthis*, *Hirnantia*, *Jerzercia?*, *Paromalomena*, *Hindella*, *Plectothyrella* and *Cyclospira?* from the *acuminatus* Zone at Yewdale Beck in the English Lake District. This is one of the few known Silurian occurrences of the *Hirnantia* Fauna, which is usually found in the underlying Ashgill Series.

3.5. Locality 11: Oslo region, Norway

Baarli (1987, 1988, 1995) and Baarli & Harper (1986) identified Rhuddanian brachiopods from the lower part of the Solvik Formation (Myren Member): her various lists have been interpreted as follows. Lower Rhuddanian: *Dolerorthis*, *Schizonema*, *Skenidioides*, *Protocortezorthis*, *Dicoelosia*, *Epitomyonia*, *Leptaena*, *Leangella*, *Eoplectodonta*, **Clorinda?*, *Eospirigerina* and *Idiospira*. In addition, the present authors have collected *Skenidioides*, *Dolerorthis*, *Leptaena*, *Eoplectodonta*, *Triplesia*, **Clorinda* and *Eospirigerina* from very near the base of the Myren Member at Konglungen. Upper Rhuddanian: *Paracraniops*, *Orthokopis*, *Dolerorthis*, *Schizonema*, *Hesperorthis?*, *Plectorthis?*, *Skenidioides*, *Ravozetina*, *Protocortezorthis*, *Levenea*, **Mendacella?*, *Dicoelosia*, *Epitomyonia*, *Drabovia*, *Chrustenopora*, *Jezerca*, *Katastrophomena*, *Leptaena*, *Crassitestella*, *Eopholidostrophia*, *Leangella*, *Aegiria*, *Eoplectodonta*, *Stricklandia*, **Clorinda?*, *Eospirigerina*, *Protatrypa*, *Idiospira*, *Cryptothyrella* and *Meifodia*. In addition, they have collected *Eostropheodonta*, *Fardenia* and *Streptis* from the same Upper Rhuddanian beds. From the Hadeland and Ringerike Districts to the north of Oslo they have also collected *Zygospiraella* and *Eostropheodonta*. At Ringerike, the Saelabonn Formation has yielded *Mendacella*, *Rostricellula*, *Platyrochalos* and *Zygospiraella* to Thomsen *et al.* (2006) and is of definite Rhuddanian age, but whether Lower or Upper Rhuddanian or both is less certain.

3.6. Locality 12: Estonia

Rubel (1970) analysed the brachiopods from the lowermost parts of the Silurian sequence, and from the Varbola Formation, which the present authors assess as Upper Rhuddanian, listed *Hesperorthis*, **Mendacella*, *Onniella*, *Leptaena*, *Fardenia*, **Clorinda?*, *Stricklandia*, *Alispira*, **Clintonella*, **Eospirigerina*, *Zygospiraella* and *'Hindella'*.

3.7. Locality 13, Northern Urals

Beznošova (1994, 1996) described brachiopods which the present authors assess as Upper Rhuddanian from the Yarenei Formation at the Kozhym River, to the NW of the northern Urals: *Virgiana*, **Hemitoechia?*, [= *Pseudocamarotoechia?*], *Zygospiraella*, *Protatrypa*, *Idiospira* and *Nalivkinia*.

4. Kazakh Terranes

A great many Lower Palaeozoic terranes exist in Kazakhstan and its neighbouring areas, and they lay between Baltica, Siberia and Gondwana. During the Palaeozoic, these united progressively to form the Kazakhstania Terrane; however,

during the Silurian many were independent and thus each terrane is listed separately here. The palaeogeography of these terranes is far from clearly understood, and is outside the scope of this paper, although there are preliminary surveys in Cocks & Torsvik (2002) and Fortey & Cocks (2003). However, Lower Silurian brachiopods have so far only been documented from the Chingiz, Chu-Ili and Karaganda terranes (Koren *et al.* 2003).

4.1. Locality 14: Chingiz Terrane

Borisiak (1964) described the following from the basal Alpeis Horizon: *Holorhynchus*, *Conchidium*, *Virgiana* and *Eospirifer?* However, Sapelnikov & Rukavishnikova (1975) emended these records to identify the *Conchidium* as *Proconchidium* and the *Virgiana* as *Eoconchidium*, with both originating from Ashgill age rocks. Nevertheless the present authors assess the other two genera as probably Rhuddanian in age, although there are no associated graptolites.

4.2. Locality 15: Chu-Ili Terrane

Modzalevskaya & Popov (1995) recorded the following from the Akkerme Peninsula, whose rocks accreted to the Chu-Ili Terrane in the Caradoc: *Dolerorthis*, *Giraldiella*, *Protocortezorthis*, *Eopholidostrophia*, *Eostropheodonta*, *Leangella*, *Saughina*, *Stricklandia*, *Eospirigerina*, *Zygospiraella* and *Meifodia*. In addition, Popov (in Koren *et al.* 2003, p. 337) listed *Eospirifer* from the same assemblage. They regarded this fauna as Lower Rhuddanian, but in the absence of supporting graptolites, and because of the presence of *Stricklandia*, it is reassessed here as Upper Rhuddanian.

4.3. Locality 16: Karaganda Terrane

Koren *et al.* (2003, p. 332) reported *Holorhynchus* from the Algabaz River area in beds of Upper Rhuddanian age.

5. Siberia

Cocks and Torsvik (2007) have reviewed the Palaeozoic geology of the Siberian craton and adjacent terranes and also analysed which of the latter moved and rotated with the craton: those which did are termed Peri-Siberia here.

5.1. Locality 17: West-Central Siberia

Tesakov *et al.* (2003) did not subdivide the Rhuddanian of what they termed 'east' Siberia, but what appears from their maps to be in fact the west and centre of the old Siberian Terrane. They show 11 successive time horizons within the Rhuddanian, labelled 1 to 11; however, on the same charts they show undoubted Aeronian graptolites from their Horizon 5 upwards, and the characteristic late Rhuddanian *Coronograptus cyphus* in their Horizon 4. Thus the present authors have taken Horizons 1 and 2 as Lower Rhuddanian and 3 and 4 as Upper Rhuddanian. From the revised Lower Rhuddanian (1 and 2) they record *Eridorthis*, *Isorthis*, *Eoplectodonta*, *Brevilammulella*, *Alispira* and *Zygospiraella*; and from the Upper Rhuddanian (3 and 4) *Eridorthis*, *Isorthis*, *Strophomena*, *Eoplectodonta*, *Brevilammulella*, **Clorinda?*, *Stegerhynchus*, *Alispira*, *Idiospira* and *Zygospiraella*.

6. Peri-Siberia

6.1. Locality 18: Gorny Altai

Kulkov & Severgina (1987) recorded from the Stugen Formation the following brachiopods which they correlated with the

acuminatus Zone: *Cliftonia*, *Epitomyonia*, *Alispira*, *Dolerorthis*, *Protocortezorthis*, *Eoplectodonta*, *Katastrophomena*, *Leptaena*, *Stricklandistrophia?*, *Stricklandia*, *‘*Clorinda*’, *Stegerhynchus*, *Meifodia*, *Cryptothyrella*, and from correlatives of the *cyphus* Biozone only *Leangella* and *Protocortezorthis*. However, as the correlations with the graptolite zones are indirect, we reassess the age of both faunas as more likely to be Upper Rhuddanian.

6.2. Locality 19: Tuva

Kulkov *et al.* (1985) described the following brachiopods from the lower part of the Alash Formation which the present authors consider to be of Rhuddanian age, probably Late Rhuddanian, but the age control is weak: *Hesperorthis*, *Stegerhynchus*, *Alispira*, *Protatrypa*, *Whitfieldella* and *Eospirigerina*. Since the upper part of the same formation contains *Pentamerus*, we assess that as being Aeronian.

7. Tien-Shan

7.1. Locality 20L Tien-Shan Mountains

From the Archalyk and Minkutchar formations of the Zeravshano-Gissar section, SE Tien-Shan, Nikiforova (1978) recorded *Giraldiella*, *Isorthis*, *Parastrophinella*, *‘*Clorinda*’, *Stricklandia*, *Virgiana*, *Virgianella*, *Eospirigerina*, *Meifodia*, *Plectatrypa*, *Protatrypa*, *Zygospiraella*. The probable age is assessed here as Late Rhuddanian.

7.2. Locality 21: Tadzhikistan

Menakova (in Babaeva *et al.* 1991) listed *Isorthis*, *Stricklandia*, *Virgianella*, *Brevilammulella*, *Thebesia*, *Eospirigerina*, *Meifodia* and *Whitfieldella* from the upper Archalyk Formation and Minkuchar Formation. The probable age is also assessed here as Late Rhuddanian.

8. Tarim

8.1. Locality 22: Western Tarim

An Upper Rhuddanian to lowest Aeronian assemblage occurs in the lower Kalpingtag Formation in the Kalping area, western Tarim (Rong *et al.* 2003). The Upper Rhuddanian brachiopods include *Isorthis*, *Beitaia* and dominant *Eospirifer*.

9. South China

9.1. Locality 23: Upper Yangtze Region, Northern Guizhou Province

Rong *et al.* (2003b) have recorded the following Lower Rhuddanian brachiopods in the upper Kuanyinqiao Beds and the Wulipo Beds: *Paracranioops*, *Dalmanella*, *Eostropheodonta*, *Leptaena*, *Paromalomena*, *Plectothyrella*, *Hindella*, *Eospirifer*, *Nalivkinia*, *Mendacella*, *Rostricellula* and *Alispira?* From the Upper Rhuddanian, in the lower part of the Niuchang Formation, came: *Levenea*, *Strophomena*, *Eostropheodonta*, *Merciella*, *Nalivkinia*, *Eospirifer*, *Athyrisinoides*, *Whitfieldella* and *Zygospiraella*.

9.2. Locality 24: North-eastern Guizhou Province

Rong & Yang (1981) recorded the following from the basal part of the Xiangshuyuan Formation, which is Late Rhuddanian to earliest Aeronian in age. The Upper Rhuddanian brachiopods are *Borealis*, *Isorthis*, *Strophomena*, *Beitaia*,

Eospirifer, *Atrypinopsis*, *Athyrisinoides*, *Coolinia* and *Eostropheodonta*.

9.3. Locality 25: Jiangnan Region, south-west Zhejiang Province

Rong & Zhan (2006) have recorded the following which are lateral equivalents and securely dated by graptolites as *ascensus* Biozone and therefore of Early Rhuddanian age from the basal parts of the Shiyang and Anji formations: *Paracranioops*, *Deliella*, *Lingula?*, *Levenea*, *Glyptorthis*, *Epitomyonia*, *Eoplectodonta*, *Katastrophomena*, *Leptaena*, *Coolinia*, *Triplesia*, *Brevilammulella*, *Rostricellula*, *Alispira*, *Eospirigerina*, *Hindella?* and *Eospirifer*.

10. North China

10.1. Locality 26: Central Ningxia

Rong & Chen (2003) and Rong *et al.* (2004) recorded the following probable Upper Rhuddanian brachiopods from the Zhaohuajing Formation, at Tongxin County, Ningxia Province: *Dolerorthis*, *Holorhynchus*, *Eospirifer*, *Strispirifer*, *Nalivkinia* and *Meifodia*. This locality lay within the marginal area of the North China Terrane.

11. Gondwana

Despite its enormous size in the Early Palaeozoic, and also despite it covering every palaeolatitude from the South Pole to 35°N (Cocks 2001, fig. 2), there are surprisingly few records of Rhuddanian brachiopods on and around it, although deeper-water graptolite-bearing Rhuddanian facies are known from many higher-latitude Gondwanan areas, particularly in North Africa.

11.1. Locality 27: Morocco

Havlíček (1971) recorded *Salopina* (probably *Protocortezorthis*) and *Ornothyrella* from the Flysch de Goulbet, south of Jbel Kraro in the Anti-Atlas Mountains of probable basal Rhuddanian age: they occur above typical Hirnantian faunas in the area. *Ornothyrella* requires reinvestigation and it has not been included in Appendix 1 and Figure 2.

11.2. Locality 28: Argentina

Isaacson *et al.* (1976) described brachiopods from Cerro Rincon, Salta Province: **Mendacella*, **Eostropheodonta*, *Fardenia* and **Hindella*. The age is certainly Early Llandovery, but whether Lower or Upper Rhuddanian is uncertain. The locality is within Gondwana, rather than peri-Gondwanan as in Locality 29.

11.3. Locality 29: Argentina (Precordillera)

Benedetto (1995) listed brachiopods from the La Chilca Formation of the Precordillera of Argentina. During the Cambrian and early to mid Ordovician, the Precordillera formed a separate terrane close to Laurentia, but by the end of the Silurian it had accreted to Gondwana. By interpolation, Cocks & Torsvik (2002) showed the Precordillera as still separate from Gondwana in the earliest Silurian (Fig. 1), but analysis of the various Silurian faunas can attribute the terrane as peri-Gondwanan, although the precise date of the docking remains uncertain. The brachiopods are *Dalmanella*, *Dedzetina?*, *Cordatomyonia*, *Heterorthella*, *Leptaena*, **Eostropheodonta*, *Rostricellula* and **Plectothyrella*.

11.4. Locality 30: Venezuela

Boucot *et al.* (1972) described the brachiopods from the Merida Andes, and their lowest two faunas are the *Meifodia*

Fauna: *Hesperorthis?*, *Dolerorthis*, *Skenidioides*, *Resserella?*, *Leptaena*, *Eoplectodonta?*, *Meifodia* and *Cryptothyrella?*: the *Eostropheodonta* Fauna: *Resserella?*, *Mendacella*, *Leptaena*, *Fardenia*, *Eostropheodonta*, *Eoplectodonta*, *Ancillotoechia?*, *Eospirigerina* and *Cryptothyrella*. They assessed the lower fauna as 'Early Llandovery', and the second 'Lower to Middle Llandovery': there are no recorded graptolites. Above both there is a probable Aeronian fauna with *Eocoelia*. All the genera from the lower two faunas are known from the Rhuddanian elsewhere, and the present authors assess the lower one as probable Rhuddanian, and the second one as possible Rhuddanian.

11.5. Locality 31: Tasmania, Australia

Laurie (1991) listed *Isorthis*, *Onniella?*, *Hirnantia* and *Eospirifer?* from the upper part of the Westfield Sandstone, and they co-occur with graptolites assessed as being *persculptus* or *ascensus* Biozone. His *Hirnantia* is not that genus, but may represent a new one. The present authors are not sure whether this fauna is late Hirnantian or early Rhuddanian: the locality is shown on Figure 1, but the generic records are not included in the analysis (Fig. 2 and Appendix).

12. Discussion

At the time when the Ordovician–Silurian boundary was internationally agreed in 1985, it was thought that the well-known *Hirnantia* brachiopod fauna was entirely confined to the Ordovician. However, some characteristic elements of that fauna are now known from the basal Silurian, well dated by co-occurring graptolites of the lower *acuminatus* Biozone, from the English Lake District (Harper & Williams 2002), and also from the *ascensus* Biozone of northern Guizhou Province, South China (Rong *et al.* 2003a).

Following the present survey, it is striking that the numbers of the genera at the different localities vary greatly. The most diverse Lower Rhuddanian fauna recorded above is 22 genera (from the type Llandovery area) and the most diverse Upper Rhuddanian fauna is 30 genera (from the Oslo Region), but, in contrast, several of the assemblages have as few as only two genera. Those figures are substantially below maximum generic numbers recorded from carbonates in the Ashgill (for example, there are more than 40 genera known from the Boda Limestone of Sweden and the Middle Ashgill of eastern China) or Telychian (over 40 brachiopod genera documented from Anticosti Island), but are very comparable to the 24 genera found in the lower Telychian in the clastic rocks of the type Llandovery area (Cocks *et al.* 1984). Therefore it is concluded, somewhat surprisingly, that, although the number of Rhuddanian brachiopod global occurrences is somewhat few and far between by comparison with those in older and younger rocks, and reef flank deposits are not known, brachiopods obviously flourished on the early Silurian shelves. It is also very noticeable that the faunas are distributed very widely, not only around the globe but at a large variety of palaeolatitudes (Fig. 1), which helps to explain why so many of the Ordovician superfamilies survived and flourished in the Silurian.

The sizes of the earliest Silurian brachiopods are variable. Unlike the basal Triassic brachiopod survivors from the end-Permian extinctions, which were almost invariably small, the basal Rhuddanian species varied from 'small' to 'normal'. However, what is very noticeable is that the Lower Rhuddanian abundances are in general lower, both within individual rock assemblages and in the number of fossiliferous bands within the many sections, than both the underlying Hirnantian faunas and the overlying Upper Rhuddanian faunas. The

speed of the post-Hirnantian recovery is also noteworthy, and appears to have been much more rapid than at the end of the Permo-Triassic extinction event. It is also very important to note that the sediments enclosing the brachiopods are almost entirely clastic with a few carbonate interbeds: substantial bioherms and other carbonate build-ups are characteristic by their absence. This is in great contrast to both the preceding Ashgill, which has widespread carbonate bioherms, particularly in the Mid Ashgill, but a few also in the Hirnantian, for example in Anticosti Island, Canada; and also the parts of the Silurian later than the Rhuddanian, in which bioherms are also widespread from the mid-Aeronian upwards. Thus the very diverse brachiopod faunas found in reef flank deposits, such as in the middle Ashgill Boda Limestone of Sweden (Cocks 2005) simply do not occur in the Rhuddanian; however, many of their relatives in the same family or superfamily appear to have adapted well to the changes.

It should be borne in mind that, although the Hirnantian glaciation appeared relatively quickly (the mid-Ashgill was in fact a period of global warming – Boucot *et al.* 2003; Fortey & Cocks 2005), the global ice-cap was much slower to clear, and certainly persisted well into Llandovery and perhaps even into the early Wenlock in high palaeolatitudes, for example in South America (Caputo 1998).

As noted by Cocks (1988), and still true, is that the superfamilies Trimerelloidea, Acrotretoidea, Siphonotretoidea and Chonetoidea have good records from both the upper Ordovician and from Silurian rocks later than the Rhuddanian, and thus they must have survived in as yet unrecorded (or destroyed by subsequent tectonics) localities during the Rhuddanian: that topic is further developed in Rong *et al.* (2006). In addition, with analysis of the relatively new volumes of the *Treatise* (Kaesler 2000–2002), the present survey has revealed representatives of 27 superfamilies within the Rhuddanian, with only the Acrotretoidea (Cambrian to Devonian), Trimerelloidea (Llandeilo to Upper Silurian), Chonetoidea (Ashgill to Permian), Porambonitoidea (Cambrian to Wenlock), Ancistrohynchoidea (Llanvirn to Devonian) and Athyrdoidea (Caradoc to Jurassic?) not represented, although representatives of all those superfamilies must have existed in the Rhuddanian. Some superfamilies are represented by only a single genus, for example only *Archeochonetes* is known from the Ordovician within the Chonetoidea, and only *Hyattidina* is known from the Ordovician within the Athyrdoidea. It is from the latter genus that the whole post-Rhuddanian athyrdoid clade evolved (Alvarez & Rong *in* Kaesler 2002). The total number of Lower Rhuddanian brachiopod genera recorded here is 60 and Upper Rhuddanian 87, a significant increase on the 54 noted by Cocks (1988) from the whole Rhuddanian.

It is also interesting to survey the benthic assemblages present in the Lower Rhuddanian. No representatives of the shallowest-water benthic assemblage (BA 1) have been found, but, by comparison with the well-defined later Llandovery assemblages, which range from BA 1 to BA 5, it is only possible to subjectively assess the various Lower Rhuddanian assemblages as probably 'shallow-shelf' or 'deeper-shelf'. However, in eastern China, Rong & Zhan (2006) have identified BA 2 and BA 3–4 assemblages, although many of the taxa in those assemblages are the same but occur in differing proportions and palaeogeographical locations. In contrast, more pentameroids appeared in the Upper Rhuddanian, and depth-related assemblages more easily separable. For example, it seems unlikely that the *Stricklandia*-dominated assemblages of the Upper Rhuddanian were shallower than BA 3 and were more probably BA 4. The assemblages became even more distinctive in the succeeding Aeronian. In other words, as the Llandovery epoch progressed, the ecological partition of

the benthic assemblage niches developed so that the various assemblages became more truly distinctive.

13. Conclusions

During the earliest part of the Silurian, the Rhuddanian, brachiopods were much less abundant on a global scale than in the preceding latest Ordovician, the Hirnantian. This reduction can be directly attributed to the Hirnantian glaciation. However, where Rhuddanian brachiopods do occur, the generic numbers vary from a sparse two to as many as 30: the latter a figure which does not depart greatly from the Middle Palaeozoic average.

In the Lower Rhuddanian, although 'shallower-water' and 'deeper-water' benthic assemblages can be assessed subjectively and loosely differentiated, the BA 1 to BA 5 sequence of depth-related brachiopod assemblages well-known from the later Llandovery cannot be clearly recognised. However, in the Late Rhuddanian, especially with the advent of pentameroids such as *Virgiana* and *Stricklandia*, which occur in abundance at many localities, BA 3 and BA 4 communities can be recognised clearly for the first time in the Silurian, as the assemblages became progressively more differentiated as time went by.

Despite the Hirnantian extinction events (documented elsewhere), few brachiopod superfamilies actually became extinct at the end of the Ordovician, and through the global analysis of Rhuddanian brachiopods presented here, it is found that a surprising 60 genera in 20 superfamilies occur in the Lower Rhuddanian and 87 genera in 25 superfamilies in the Upper Rhuddanian. Despite the relative paucity of localities (chiefly due to the widespread unconformities present over the Ordovician–Silurian transition), only six superfamilies which undoubtedly existed during those times are not represented in the present survey. Thus the global scenario presented here for the Rhuddanian includes far more brachiopod genera in more localities scattered round the globe than was previously appreciated, certainly by the present authors. This is in contrast to the trilobites, which in the Llandovery appear to have been less abundant and widespread than in the latest Ordovician; for example, those well-described from the Rhuddanian of Anticosti Island (Chatterton & Ludvigsen 2004).

14. Acknowledgements

We dedicate this paper to the memory of Alwyn Williams, who was a leader not only in the understanding of brachiopod zoology and systematics but also in their distributions in the Ordovician. Thanks to Jin Jisuo and David Harper for helpful comments on the manuscript, and to the Major Project of MST of China (2006CBB06400), the Chinese Academy of Sciences (KZCX3–SW-149), and the grant of NSF of China (40472002), which supported Rong's research work and paid for Cocks' visit to China in October 2005. The Natural History Museum is thanked for facilities and Abigail Brown for drafting Figure 1. This is a contribution to IGCP Project 503.

15. Appendix 1. Summary of genera, allocated to superfamilies and families

From the Lower Rhuddanian, records of the following genera have been located or revised. These are allocated to the following families and superfamilies in accordance with the *Treatise on Invertebrate Paleontology* (Kaesler 2000–2002): **Linguloidea**; Lingulidae, *Lingula*: **Discinoidea**; Discinididae,

Orbiculoidea: **Craniopsoidea**; Craniopsidae, *Paracraniops*: **Cranioidea**; Craniidae, *Deliella*: **Strophomenoidea**; Strophomenidae. *Katastrophomena*; Rafinesquinidae, *Biparetis*, *Crassitestella*, *Leptaena*; Glyptomenidae, *Paromalomena*; Leptostrophiidae, *Eostropheodonta*, *Palaeoleptostrophia*; Eopholidostrophiidae, *Eopholidostrophia*: **Plectambonitoidea**; Leptestiidae, *Leangella*; Sowerbyellidae, *Anisopleurella*, *Eoplectodonta*; **Chilidiopsoidea**; Chilidiopsidae, *Coolinia*, *Fardenia*; **Triplesioidea**; Triplesiidae, *Cliftonia*, *Triplesia*; **Skenidioidea**; Skenidiidae, *Skenidioides*: **Orthoidea**; Glyptorthidae, *Eridorthis*, *Glyptorthis*; Hesperorthidae, *Dolerorthis*, *Schizonema*; **Dalmanelloidea**; Dalmanellidae, *Dalmanella*, *Isorthis*, *Levenea*, *Mirorthis*, *Protocortezorthis*, *Ravozetina*, *Resserella*; Platyorthidae, *Diceromyonia*; Dicoelosiidae, *Dicoelosia*, *Epitomyonia*: Rhipidomellidae, *Mendacella*; **Enteletoidea**; Draboviidae, *Hirnantia*, *Kinnella*, Chrustenoporidae, *Jezercia*: **Pentameroidea**; Virgianidae, *Brevilammulella*, *Viridita*; **Clorindoidea**; Clorindidae, '*Clorinda*'; **Rhynchotrematoidea**; Rhynchotrematidae, *Rhynchotrema*, *Stegerhynchus*; Leptocoeliidae, *Platyrochalis*; Trigonirhynchiidae, *Plectothyrella*, *Rhynchotreta*, *Rostricellula*: **Atrypoidea**; Atrypidae, *Protatrypa*, *Zygospiraella*; Atrypinidae, *Alispira*, *Atrypina*, *Eospirigerina*, *Nalivkinia*, *Plectatrypa*; Septatrypidae, *Bescia*: **Lissatrypoidea**; Lissatrypidae, *Meifodia*; Septatrypidae; *Idiospira*: **Protozygoidea**; Cyclospiridae, *Cyclospira*: **Meristelloidea**; Meristellidae, *Cryptothyrella*, *Hindella*: **Cyrtioidea**; Eospiriferidae, *Eospirifer*.

From the Upper Rhuddanian, the present authors have recorded:- **Linguloidea**; Lingulidae, *Lingula*: **Cranioidea**; Craniidae, *Petrocrania*; **Craniopsoidea**; Craniopsidae, *Paracraniops*: **Eichwaldioidea**; Eichwaldiidae, *Eodictyonella*: **Strophomenoidea**; Strophomenidae, *Katastrophomena*, *Strophomena*; Rafinesquinidae, *Crassitestella*, *Leptaena*; Eopholidostrophiidae, *Eopholidostrophia*; Leptostrophiidae, *Brachyprion*, *Eomegastrophia*, *Eostropheodonta*, *Mesoleptostrophia*, *Palaeoleptostrophia*; Strophonellidae, *Eostrophonella*: **Plectambonitoidea**; Leptellinidae, *Merciella*; Leptestiidae, *Leangella*; Sowerbyellidae, *Anisopleurella*, *Eoplectodonta*; Xenambonitidae, *Aegiria*: **Chilidiopsoidea**; Chilidiopsidae, *Coolinia*, *Fardenia*, *Saughina*: **Triplesioidea**; Triplesiidae, *Streptis*, *Triplesia*: **Skenidioidea**; Skenidiidae, *Skenidioides*: **Orthoidea**; Orthidae, *Orthokopis*; Glyptorthidae, *Eridorthis*; Hesperorthidae, *Hesperorthis*, *Dolerorthis*, *Schizonema*: **Plectorthoidea**; Plectorthidae, *Plectorthis*; Giraldiellidae, *Giraldiella*; Wangyuiidae, *Toxorthis*: **Dalmanelloidea**; Dalmanellidae, *Dalmanella*, *Dedzetina*, *Isorthis*, *Levenea*, *Onniella*, *Protocortezorthis*, *Ravozetina*, *Resserella*, *Templeella*, *Visbyella*; Chrustenoporidae, *Chrustenopora*, *Dysprosorthis*, *Jezercia*; Dicoelosiidae, *Dicoelosia*, *Epitomyonia*; Heterorthidae, *Heterorthella*; Proschizophoriidae, *Cordatomyonia*; Rhipidomellidae, *Mendacella*; **Enteletoidea**; Saukrodictyidae, *Saukrodictya*; Draboviidae, *Drabovia*: **Pentameroidea**, Virgianidae, *Borealis*, *Brevilammulella*, *Holorhynchus*, *Virgiana*, *Virgianella*: **Camerelloidea**; Parastrophinidae, *Parastrophinella*: **Stricklandioidea**; Stricklandiidae, *Stricklandia*, *Stricklandistophia*?; **Clorindoidea**; Clorindidae, '*Clorinda*'; **Rhynchotrematoidea**; Rhynchotrematidae, *Rhynchotrema*, *Stegerhynchus*; Trigonirhynchiidae, *Ancillotoechia*, *Hemitoechia*, *Plectothyrella*, *Rhynchotreta*, *Rostricellula*, *Thebesia*: **Camarotoechioidea**; Camarotoechiidae, *Fenestrirostra*; **Anazygoidea**; Anazygidae, *Pentlandella*: **Atrypoidea**; Atrypidae, *Protatrypa*, *Zygospiraella*, Atrypinidae, *Alispira*, *Athyrisinoides*, *Atrypinopsis*, *Beitaia*, *Clintonella*, *Eospirigerina*, *Nalivkinia*, *Plectatrypa*: **Lissatrypoidea**; Lissatrypidae, *Cerasina*, *Meifodia*; Septatrypidae, *Idiospira*: **Meristelloidea**; Meristellidae, *Cryptothyrella*, *Hindella*, *Whitfieldella*: **Dayioidea**; Dayiidae, *Protozeuga*?; **Cyrtioidea**; Eospiriferidae, *Eospirifer*, *Striispirifer*.

16. References

- Amsden, T. W. 1974. Late Ordovician and Early Silurian articulate brachiopods from Oklahoma, southwestern Illinois, and eastern Mississippi. *Oklahoma Geological Survey Bulletin* **119**, 1–54.
- Babayeva, V. S., Dzhililov, N. R., Melnikova, G. K., Sabirov, A. A., Salibayev, G. K. & Khakimov, F. K. (eds) 1991. *Atlas of fossil faunas and floras of Tadzhikistan. Ordovician, Silurian, Devonian*, 272 pp. Donish, Dushanbe. [In Russian.]
- Baarli, G. B. 1987. Benthic faunal associations in the Lower Silurian Solvik Formation of the Oslo-Asker Districts, Norway. *Lethaia* **20**, 75–90.
- Baarli, G. B. 1988. The Llandovery eleteacean brachiopods of the central Oslo region, Norway. *Palaeontology* **31**, 1101–29.
- Baarli, G. B. 1995. Orthacean and strophomenid brachiopods from the Lower Silurian of the central Oslo Region. *Fossils and Strata* **39**, 1–93.
- Baarli, G. B. & Harper, D. A. T. 1986. Relict Ordovician brachiopod faunas in the Lower Silurian of Asker, Oslo Region, Norway. *Norsk Geologisk Tidsskrift* **66**, 87–98.
- Benedetto, J. L. 1995. Braquiopodos del Silurico temprano malvinocáfrico (Formación La Chilca), Precordillera Argentina. *Geobios* **28**, 425–57.
- Bergstrom, S. M. & Boucot, A. J. 1988. The Ordovician–Silurian boundary in the United States. *Bulletin of the British Museum (Natural History) Geology* **43**, 273–84.
- Beznosova, T. M. 1994. *Stratigraphy and brachiopods of the Silurian of northeast European Russia*, 127 pp. St Petersburg, Nauka. [In Russian.]
- Beznosova, T. M. 1996. Silurian brachiopod biostratigraphy, NE Timan – N Urals, Russia. In Copper, P. & Jin, J. (eds) *Brachiopods*, 35–40. Rotterdam: Balkema.
- Borisiak, M. A. 1964. Lower Llandovery brachiopods from northeast Kazakhstan. *Trudy Paleontologia i Stratigrafia VSEGEI* **93**, 71–80. [In Russian.]
- Boucot, A. J., Johnson, J. G. & Shagam, R. 1972. Braquipodos siluricos de los Andes meridenos de Venezuela. *Boletín de Geología Publicación Especial* **5**, 585–727.
- Boucot, A. J., Rong J.-y., Chen, X. & Scotese, C. R. 2003. Pre-Hirnantian Ashgill climatically warm event in the Mediterranean region. *Lethaia* **36**, 119–32.
- Boucot, A. J. & Johnson, J. G. 1964. Brachiopods of the Ede Quartzite (Lower Llandovery) of Norderon, Jamtland. *Bulletin of Geological Institutions University of Uppsala* **42** (9), 1–11.
- Brenchley, P. J., Marshall, J. D., Carden, G. A. C., Robertson, D. B. R., Long, D. G. F., Meidla, T., Hints, L. & Anderson, T. F. 1994. Bathymetric and isotopic evidence for a short-lived late Ordovician glaciation in a greenhouse period. *Geology* **22**, 295–8.
- Caputo, M. V. 1998. Ordovician–Silurian glaciations and global sea-level changes. *New York State Museum Bulletin* **491**, 15–25.
- Chatterton, B. D. E. & Ludvigsen, R. 2004. Early Silurian trilobites of Anticosti Island, Québec, Canada. *Palaeontographica Canadiana* **22**, 1–264.
- Cocks, L. R. M. 1988. Brachiopods across the Ordovician–Silurian boundary. *Bulletin of the British Museum (Natural History) Geology* **43**, 311–15.
- Cocks, L. R. M. 2001. Ordovician and Silurian global geography. *Journal of the Geological Society, London* **158**, 197–210.
- Cocks, L. R. M. 2005. Strophomenate brachiopods from the Late Ordovician Boda Limestone of Sweden: their systematics and implications for palaeogeography. *Journal of Systematic Palaeontology* **3**, 243–82.
- Cocks, L. R. M., Woodcock, N. H., Rickards, R. B., Temple, J. T. & Lane, P. D. 1984. The Llandovery Series of the type area. *Bulletin of the British Museum (Natural History) Geology* **38**, 131–82.
- Cocks, L. R. M. & Copper, P. 1981. The Ordovician–Silurian boundary at the eastern end of Anticosti Island, Canada. *Canadian Journal of Earth Sciences* **18**, 1029–34.
- Cocks, L. R. M. & Price, D. 1975. The biostratigraphy of the upper Ordovician and lower Silurian of south-west Dyfed, with comments on the *Hirnantia* Fauna. *Palaeontology* **18**, 703–24.
- Cocks, L. R. M. & Rong Jia-yu 2000. Order Strophomenidina. In Kaesler, R. L. (ed) *Treatise on Invertebrate Paleontology. H. Brachiopoda (revised)*, Vol. 2, 216–348. Boulder, Colorado and Lawrence, Kansas: Geological Society of America and Kansas University Press.
- Cocks, L. R. M. & Toghil, P. 1973. The biostratigraphy of the Silurian rocks of the Girvan District, Scotland. *Journal of the Geological Society, London* **129**, 209–43.
- 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, London* **159**, 631–44.
- Cocks, L. R. M. & Torsvik, T. H. 2007. Siberia, the wandering northern terrane, and its changing geography through the Palaeozoic. *Earth-Science Reviews* **82**, 29–74.
- Copper, P. 1995. Five new genera of Late Ordovician – early Silurian brachiopods from Anticosti Island, eastern Canada. *Journal of Paleontology* **69**, 846–62.
- Copper, P. 1999. Brachiopods during and after the late Ordovician extinctions on Anticosti Island, E. Canada. *Acta Universitatis Carolinae – Geologica* **43**, 207–9.
- Dewing, K. 1999. Late Ordovician and Early Silurian strophomenoid brachiopods of Anticosti Island, Québec, Canada. *Palaeontographica Canadiana* **17**, 1–143.
- 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. & Cocks, L. R. M. 2005. Late Ordovician global warming – the Boda Event. *Geology* **33**, 405–8.
- Harper, D. A. T. & Williams, S. H. 2002. A relict Ordovician brachiopod fauna from the *Parakidograptus acuminatus* Biozone (lower Silurian) of the English Lake District. *Lethaia* **35**, 71–8.
- Harris, M. T., Kuglitsch, J. J., Watkins, R., Hegrenes, D. P. & Waldhuetter, K. R. 1998. Early Silurian stratigraphic sequences of eastern Wisconsin. *New York State Museum Bulletin*, **491**, 39–49.
- Havlíček, V. 1971. Brachiopodes de l'Ordovicien du Maroc. *Notes et Mémoires du Service Géologique du Maroc* **230**, 1–135.
- Isaacson, P. E., Antelo, B. & Boucot, A. J. 1976. Implications of a Llandovery (Early Silurian) brachiopod fauna from Salta Province, Argentina. *Journal of Paleontology* **50**, 1103–12.
- Jin, J. 1989. Late Ordovician – Early Silurian rhynchonellid brachiopods from Anticosti Island, Québec. *Biostratigraphie de Paléozoïque* **10**, 1–217.
- Jin, J., Caldwell, W. G. E. & Norford, B. S. 1993. Early Silurian brachiopods and biostratigraphy of the Hudson Bay Lowlands, Manitoba, Ontario and Québec. *Geological Survey of Canada Bulletin* **457**, 1–221.
- Jin, J. & Chatterton, B. D. E. 1997. Latest Ordovician–Silurian articulate brachiopods and biostratigraphy of the Avalanche Lake area, southwestern District of Mackenzie, Canada. *Palaeontographica Canadiana* **13**, 1–167.
- Jin, J. & Copper, P. 2000. Late Ordovician and Early Silurian pentamerid brachiopods from Anticosti Island, Quebec, Canada. *Palaeontographica Canadiana* **18**, 1–140.
- Kaesler, R. L. (ed.) 2000–2002. *Treatise on Invertebrate Paleontology, Part H Brachiopoda (revised)*, **2**, 1–424; **3**, 425–920; **4**, 921–1688. Boulder, Colorado and Lawrence, Kansas: Geological Society of America and University of Kansas Press.
- Koren, T. N., Oradovskaya, M. M., Polma, L. J., Sobolevskaya, R. F. & Chugaeva, M. N. 1983. The Ordovician and Silurian boundary in the northeast of the U.S.S.R. *Ministry of Geology of USSR Interdepartmental Stratigraphic Committee Transactions* **11**, 1–205. [In Russian.]
- Koren, T. N., Popov, L. E., Degtjarev, K. E., Kovalevsky, O. P. & Modzalevskaya, T. L. 2003. Kazakhstan in the Silurian. *New York State Museum Bulletin* **493**, 323–43.
- Kovalevskii, O. P., Kolobova, I. M., Koren, T. N., Modzalevskaya, T. L., Popov, L. E., Sobolevskaya, R. F. & Stukalina, G. A. 1991. *Biozonal distribution of the Ashgill and Lower Llandovery in the USSR*, 44 pp. VSEGEI, Leningrad. [In Russian.]
- Kulkov, N. P. & Severgina, L. G. 1987. Ordovician and Silurian boundary in Gornoi Altai. *Seriya Geologicheskaya* **9**, 69–74. [In Russian.]
- Kulkov, N. P., Vladimirskaia, E. V. & Rybkina, N. L. 1985. The brachiopods and biostratigraphy of the Upper Ordovician and Silurian of Tuva. *Transactions of the Institute of Geology and Geophysics, Siberian Branch Academy of Sciences of USSR* **635**, 1–208. [In Russian.]
- Laurie, J. R. 1991. Articulate brachiopods from the Ordovician and Lower Silurian of Tasmania. *Association of Australasian Palaeontologists Memoir* **11**, 1–106.
- Li, R. & Copper, P. 2006. Early Silurian (Llandovery) orthide brachiopods from Anticosti Island, eastern Canada: the O/S extinction event recovery fauna. *Special Papers in Palaeontology* **76**, 1–71, pls 1–19.
- Modzalevskaya, T. L. & Popov, L. E. 1995. Earliest Silurian articulate brachiopods from central Kazakhstan. *Acta Palaeontologica Polonica* **40**, 399–426.

- Nikiforova, O. I. 1978. Brachiopods of the Tchasmanalon, Artchalyk and Minkutcher Beds, *Trudy Institute Geologi i Geofiziki Sibirskoe Otdelenii Akademii Nauk SSSR* **397**, 102–25. [In Russian.]
- Rong, J.-y., Chen, X. Su, Y.-z., Ni, Y.-n., Zhan, R.-b., Chen, T.-e., Fu, L.-p., Li, R.-y. & Fan, J.-x. 2003a. Silurian paleogeography of China. In Landing, E. & Johnson, M. E. (eds) *Silurian Lands and Seas, Paleogeography Outside of Laurentia*. *New York State Museum Bulletin* **493**, 243–98.
- Rong, J.-y., Zhan, R.-b. & Harper, D. A. T. 2003b. Rhuddanian (Llandovery, Silurian) brachiopod assemblages from the Yangtze Region, South China. *INSUGEO Serie Correlacion Geologica* **18**, 173–8.
- Rong, J.-y., Zhan, R.-b. & Jin, J. 2004. The Late Ordovician and Early Silurian pentameride brachiopod *Holorhynchus* Kiaer, 1902 from North China. *Journal of Paleontology* **78**, 287–99.
- Rong, J.-y., Boucot, A. J., Harper, D. A. T., Zhan, R.-b. & Neuman, R. B. 2006. Global analyses of brachiopod faunas through the Ordovician and Silurian transition: reducing the role of the Lazarus effect. *Canadian Journal of Earth Sciences* **43**, 23–39.
- Rong, J.-y. & Chen, X. 2003. Silurian biostratigraphy of China. In Zhang, W.-t., Chen, P.-j. & Palmer, A. R. (eds) *Biostratigraphy of China*, 173–236. Beijing: Science Press.
- Rong, J.-y. & Harper, D. A. T. 1999. Brachiopod survival and recovery from the latest Ordovician mass extinctions in South China. *Geological Journal* **34**, 321–48.
- Rong, J.-y. & Yang, X.-c. 1981. Brachiopod faunas of middle and late Early Silurian from southwestern China. *Nanjing Institute of Geology and Palaeontology, Academia Sinica Memoir* **13**, 164–270. [In Chinese with English summary.]
- Rong, J.-y. & Zhan, R.-b. 2006. Surviving the end-Ordovician extinctions: evidence from the earliest Silurian brachiopods of north-eastern Jiangxi and western Zhejiang provinces. East China. *Lethaia* **39**, 39–48.
- Rubel, M. 1970. On the distribution of brachiopods in the lowermost Llandovery of Estonia. *Eesti NSV Tead Akademii Toimestee* **19**, 69–79. [In Russian.]
- Sapelnikov, V. P. & Rukavishnikova, T. B. 1975. *Upper Ordovician, Siberian and Lower Devonian pentamerids of Kazakhstan*, 227 pp. Moscow: Nauka. [In Russian.]
- Sheehan, P. M. 2001. The late Ordovician mass extinction. *Annual Reviews of Earth and Planetary Sciences* **29**, 331–64.
- Sheehan, P. M. & Coorough, P. J. 1990. Brachiopod zoogeography across the Ordovician–Silurian extinction event. *Geological Society, London, Memoir* **12**, 181–7.
- Temple, J. T. 1970. The Lower Llandovery brachiopods from Fridd Mathrafal, near Meifod, Montgomeryshire. *Monograph of the Palaeontographical Society* **124**, 1–76.
- Tesakov, Y. I., Predtetchensky, N. N., Khromych, V. G., Berger, A. Y. & Kovalevskaya, E. O. 2003. Stratigraphy and paleogeography of the Silurian of East Siberia. *New York State Museum Bulletin* **493**, 345–400.
- Thomsen, E., Jin, J. & Harper, D. A. T. 2006. Early Silurian brachiopods (Rhynchonellata) from the Saelabonn Formation of the Ringerike district, Norway. *Bulletin of the Geological Society of Denmark* **53**, 111–26.
- Watkins, R. & Kuglitsch, J. J. 1997. Lower Silurian (Aeronian) megafaunal and conodont biofacies of the northwestern Michigan Basin. *Canadian Journal of Earth Sciences* **34**, 753–64.
- Williams, A. & Wright, A. D. 1981. The Ordovician–Silurian boundary in the Garth area of southwest Powys, Wales. *Geological Journal* **16**, 1–39.

MS received 31 March 2006. Accepted for publication 24 July 2007.

