# Brachiopod faunal dynamics during the Silurian Ireviken Event, Gotland, Sweden

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**Cover Picture:** The Lusklint 1 locality in August 2005. Photograph: M. Calner.

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ÅSA ERLFELDT

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**Abstract:** The brachiopod fauna from parts of the Lower and Upper Visby formations on Gotland has been investigated through a combined outcrop and literature study. The strata of these formations were formed during the Ireviken Event, one of the severest identified oceanic events on Gotland, with diversity changes and extinctions among several groups of marine taxa. Seven bulk samples were collected from stratigraphical intervals below and above datum points 1 to 5 of the Ireviken Event, yielding a total of 4261 identified brachiopod specimens. This assemblage is greatly dominated by small, millimetre-sized articulate brachiopods, mainly belonging to the genus *Orthida*, but also to the genera *Dicoelosia*, *Atrypa*, *Sphaerirhynchia*, *Katastrophomena*, *Eoplectodonta*, *Athyridida*, *Pentlandina*, *Leptaena* and *Costricklandia*. Of the twelve brachiopod species identified in the Lusklint 1 samples, six have their last occurrence in the investigated interval. Five species are interpreted as Lazarus taxa and ten species are strongly Lilliput affected. Previous literature on the brachiopods from the Lower and Upper Visby formations comprise 54 species (including many large-sized species) of which 23 species have their last occurrences within those formations. The discrepancy in brachiopod size and number of identified species, between the new samples and the literature, indicates the importance of bulk samples to uncover many small-sized species. On the basis of the combined outcrop and literature data, it is suggested that further detailed studies are needed to clarify the stratigraphic ranges of brachiopod species for the Lower and Upper Visby formations, and that substantial changes took place within the brachiopod fauna during the early Ireviken Event.

**Keywords:** Ireviken Event, brachiopods, Lilliput, Silurian, Gotland, Lower Visby Formation, Upper Visby Formation.

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# Förändringar i den gotländska brachiopodfaunan under Ireviken Event, Gotland, Sverige

ÅSA ERLFELDT

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**Sammanfattning:** Brachiopodfaunan från delar utav de Undre och Övre Visbyformationerna på Gotland har undersökts genom en kombinerad material- och litteraturstudie. Sedimentbergarterna i dessa formationer bildades under Ireviken Event, ett av de mest omfattande oceaniska event identifierat på Gotland. Eventet orsakade förändringar i artrikedom och ledde till utdöenden inom flera marina djurgrupper. Sju stora prover samlades vid lokalen Lusklint 1, från ett stratigrafiskt intervall som innefattar datumen 1 till 5 av Ireviken Event. Proverna gav totalt 4261 nu identifierade brachiopodskal. Samlingen domineras av små, millimeterstora artikulata brachiopoder, tillhörande i huvudsak släktet *Orthida* men också släktena *Dicoelosia*, *Atrypa*, *Sphaerirhynchia*, *Katastrophomena*, *Eoplectodonta*, *Athyridida*, *Pentlandina*, *Leptaena* och *Costricklandia*. Av de tolv brachiopodarterna som har identifierats i proverna, har sex sina sista förekomster i det undersökta intervallet. Fem är tolkade som Lazarus taxa och tio arter är starkt Lilliputt-påverkade. Tidigare litteratur om brachiopoder från Undre och Övre Visbyformationerna omfattar 54 arter (inklusive många släkten med stora storlekar) av vilka 23 har sin sista utbredning inom formationerna. Diskrepansen i storlekarna av brachiopoderna och antal identifierade arter, mellan de nya proverna och litteraturen, tyder på att det är viktigt att samla stora prover för att omfatta även brachiopoder med små storlekar. Utifrån den kombinerade informationen från provmaterial och litteratur, föreslås det att fortsatta detaljerade studier behövs för att klargöra arternas tidsmässiga utbredning inom Undre och Övre Visbyformationerna och att omfattande förändringar skedde i brachiopodfaunan under de tidiga delarna av Ireviken Event.

**Nyckelord:** Ireviken Event, brachiopoder, Lilliput, Silur, Gotland, Undre Visbyformationen, Övre Visbyformationen.

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## 1. Introduction

A geological section is a window to the past and a careful analysis of biological and sedimentological information can describe ecological, environmental and climatic conditions for a specific time period. With the work conducted in establishing a detailed conodont zonation based on the Silurian on Gotland (Figs. 1, 2) there appeared a pattern of recurrent change in the fauna. These patterns, found among different groups of taxa and in the composition of the strata, led to the development of a model of oceanic circulation and sequences of change termed events (e.g. Jeppsson 1990, 1998). Oceanic circulation is the main artery of nutrients for primary production, forming the base food staple for other oceanic dwellers. Changes in nutrient supply during the Silurian are reflected in the conodont, trilobite, ostracode, jawed polychaetes and phytoplankton populations, all organisms closely linked to primary production (Jeppsson 1990, 1997b; Dorning 2005; Eriksson 2005). The origination, extinction, interruption or disappearance of a species, all occurring within a short time span is described as an event (Walliser 1990; Aldridge *et al*. 1993). An event is identified by a series of datum points, which are specific steps of faunal change within events and specific datum points are in the text referred to as numbered datums (Jeppsson 1990). The identification of the Ireviken Event and the study of the spacing of datum points are based on the analysis of the conodont fauna from continuously sampled material through the Lower and Upper Visby formations (Figs. 1, 2). The datum points exhibit varying magnitudes of faunal and sedimentological change and such a pattern of datum points characterises different events (Jeppsson 1990, 1998). Distinct changes in carbon isotope values during the time interval of the Ireviken Event have also been identified (Talent *et al.* 1993; Munnecke *et al.* 2003).

This study examines brachiopod assemblages from the stratigraphical interval corresponding to the early Silurian Ireviken Event on Gotland. The conclusions are based on the combined information of new samples from the Lusklint 1 locality along with data from nine previously published works (Hede 1925, 1927, 1940, 1960; Bassett & Cocks 1974; Bassett 1979; Copper 1996, 2004; Hoel 2005). The aim is to examine the potential influence of the Ireviken Event on the brachiopod fauna.

### 1.1 Brachiopods

Brachiopods are marine, bottom-dwelling filter-feeders (Bassett 1984; Copper 2004). They are unique in that they are one of the few phyla still existing today

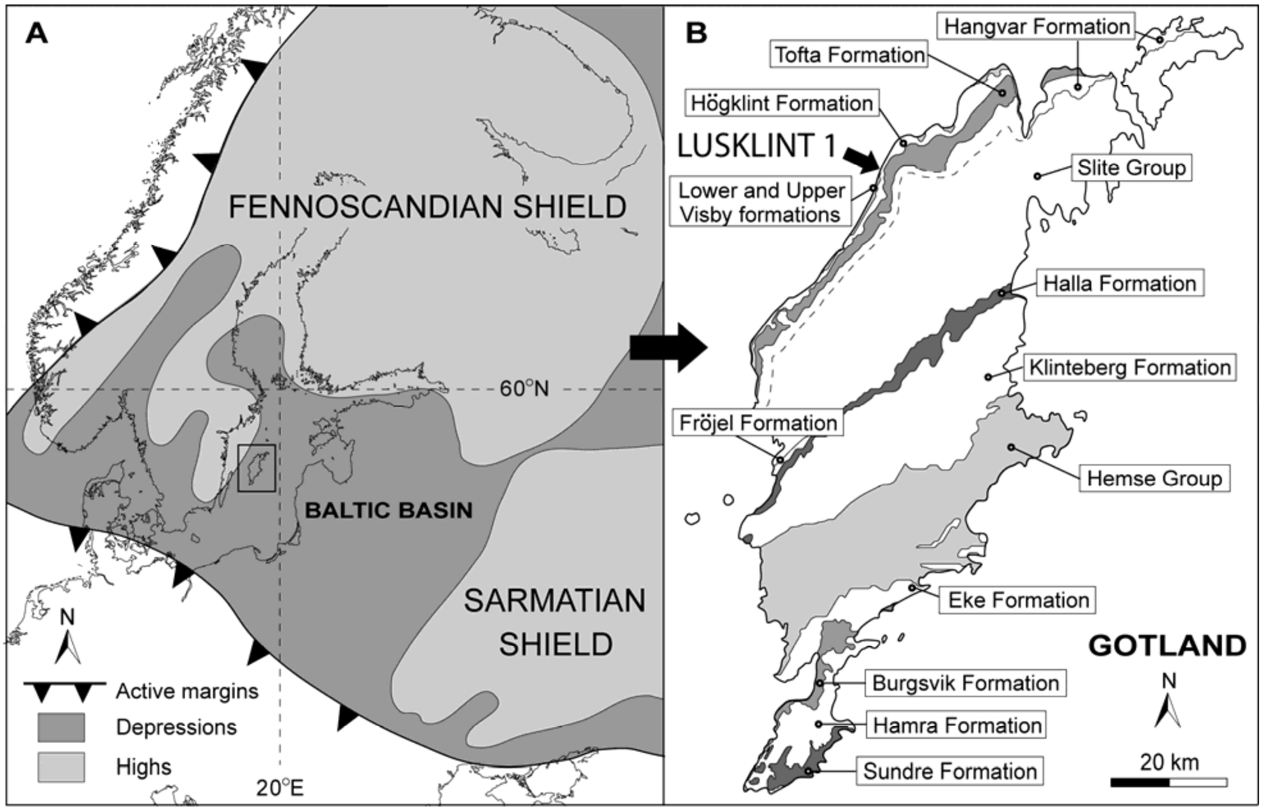


*Fig. 1.* Palaeogeography and the Silurian stratigraphy of Gotland. **A**. Palaeogeography of northern Europe and Scandinavia during the Late Silurian. The location of Gotland is within the box. **B**. The geographical distribution of the groups and formations of Gotland. The strata is successively younger towards the southeast. Note the location of the Lusklint 1 locality on north-western Gotland. Modified from Baarli et al. (2003) and Calner (2005).

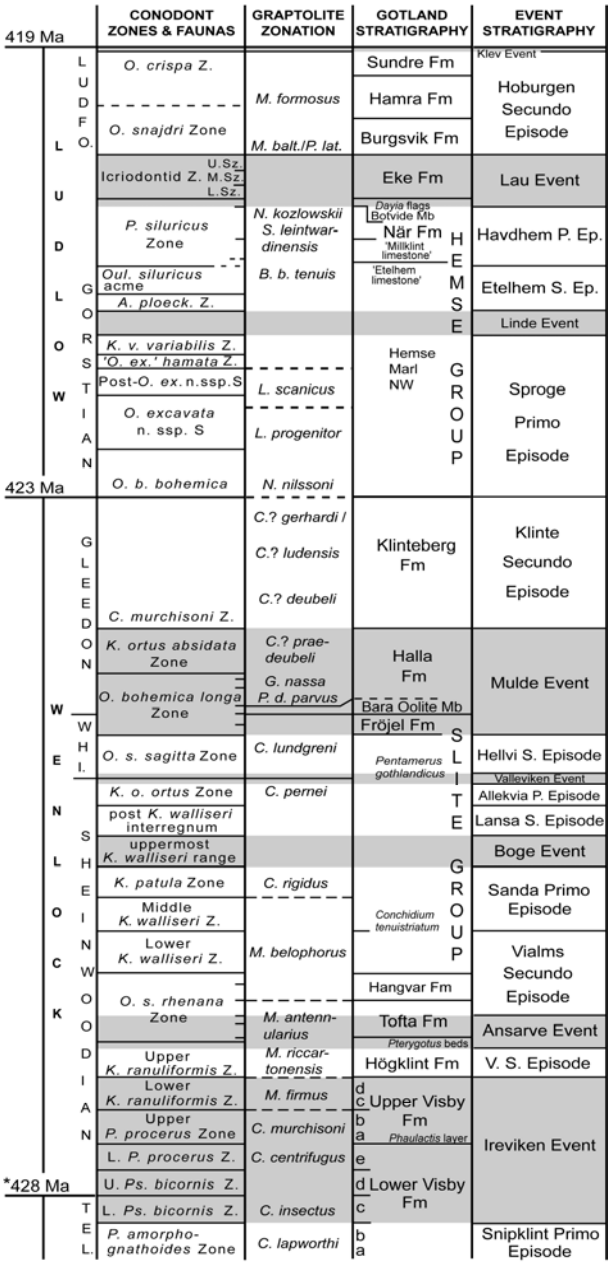


*Fig. 2.* The detailed stratigraphy of Gotland, including conodont and graptolite zonations. The eight oceanic events identified on Gotland are included here, as well as primo and secundo episodes. The Lower and Upper Visby Formations and the Ireviken Event are found at the base of the figure. Simplified and updated from Calner *et al.* (2005).

but with their period of greatest expansion and diversity behind them, found in environments of both deep and shallow waters, as well as cold and warm. The record they leave is one of great diversity and adaptability, making them excellent biostratigraphical and environmental indicators as they are highly adaptable and relatively common. A low primary production in benthic areas would invariably have an adverse affect on the brachiopod population and be reflected by a decline in population size, a decline in number of species and/or decline in size. Bassett (1984) describes a number of life habitats of Silurian brachiopods, based upon shell morphology, and changes in oceanic circulation would likely affect these habitats and be reflected in brachiopod faunal dynamics. Copper (2004) discusses the habitats of Silurian atrypids from northwestern Europe but notes the need of further studies to clarify the palaeogeographical distribution of brachiopod genera for the Silurian.

Brachiopods have been used to describe marine sedimentary environments and biotic events in other regions and for other periods, e.g. for the late Ordovician (Baarli *et al*. 2003; Brenchley *et al*. 2003), the Late Silurian in Australia (Strusz 2002, 2005), the Frasnian-Famennian event in southern Poland, Laurussia, Siberia and China (Racki 1998; Balínskí 2002), and from the Late Permian Wuchiapingian coal series of Southern China (Chen *et al*. 2005).

Brachiopod studies of contemporary Silurian strata have also been published, such as from the Oslo region in Norway (Baarli & Johnson 1988; Baarli 1995), Wales (Cocks 1967), Canada (Jin & Chatterton 1997; Jin 2002), Lithuania (Musteikis & Modzalevskaya 2002; Musteikis & Cocks 2004), and from Scotland (Clarkson *et al*. 2001).

## 2. The Ireviken Event

The Silurian events are brief periods of unstable oceanic conditions (*sensu* Jeppsson 1990) and to date eight events have been identified based on the sedimentary succession of Gotland (Fig. 2). Three of these have to date been identified globally (Jeppsson 1997a). Two distinct stable oceanic states are described in the Silurian oceanic model, viz. primo episodes and secundo episodes. The transitions from one stable episode to another are termed events (Jeppsson *et al*. 1995). There are four different types of events, primo-primo, primo-secundo, secundo-secundo and secundo-primo, each with different characteristics (Jeppsson *et al*. 1995; Jeppsson 1998, 2005). Primo episodes are characterised by a more humid climate, with an increased transport of terrigenous material to the sea and the deposition of argillaceous limestone. The secundo episodes have a more arid climate at low latitudes, favouring the expansion of reef platforms.

The Ireviken Event is a primo-secundo event, globally identified, spanning the Llandovery-Wenlock boundary. It is the most severe of hitherto studied Silurian events and lasted c. 0.2 My (Jeppsson 2005). A total of eight datum points have to date been identified for the Ireviken Event (Jeppsson 1997a, 2005; Jeppsson *et al*. 2005). The majority of extinctions took place during the first 0.1 My of the event and this study investigates strata that are associated with the five oldest datum points. Three bentonites have been identified within the alternating strata in the Lower Visby Formation (*cf.* Batchelor & Jeppsson 1994; Jeppsson *et al*. 2005). The Lusklint bentonite is the oldest of the three


*Fig. 3.* Latest Llandovery and early Wenlock sections on the north-western coast of Gotland. **A**. The Lusklint 1 locality is situated in the slope in the far right of the picture. Photograph: M. Calner. **B**. The white marker at the bottom of the figure indicates the position of the Storbrut Bentonite, followed upwards by markers for Datum 1, Datum 2, the Ireviken Bentonite, Datum 3, Datum 3.3, Datum 4, and Datum 5. Photograph: M. Calner.

and has been identified also in Estonia (Jeppsson & Männik 1993). It occurs c. 8.28 m above sea level at Lusklint 1 and is herein used as reference level for measurements. The two following bentonites are the Storbrut and the Ireviken bentonites at 1.55 m and 2.85 m respectively above the reference level (see Fig. 3B). The boundary between the Lower and Upper Visby formations lies at 5.30 m above the reference level.

Datum 1, at 1.83 ±0.03 m above the reference level (Fig. 4), affected several conodont species (Jeppsson 1997a). Datum 2 is identified at 2.71 ± 0.01 m above the reference level and this is where the greatest impact on conodont fauna during the Ireviken Event has been observed (Jeppsson 1997a). A significant change in trilobite fauna is also noted at this level (*cf.* Ramsköld 1985; Aldridge *et al*. 1993). Datum 2 also marks the level for the boundary between the Llandovery and Wenlock epochs. Datum 3 affected mainly conodont faunas and occurs at 4.25 m above the reference level. Datum 4 is identified at 5.30 ± 0.02 m above the reference level and is described as the datum point where shallow shelf region carbonate fauna was greatly influenced by the Ireviken Event (Aldridge *et al*. 1993; Munnecke *et al*. 2003). Datum 5, at 5.46 ± 0.02 m above the reference level, primarily affected the conodont fauna (Jeppsson 1997a).

The impact of the Ireviken Event on hitherto studied fauna was significant as 80% of the globally known conodont species and 50% of the trilobite species from Gotland disappeared (*cf.* Ramsköld 1985). As brachiopods are bottom-dwelling filter-feeders, reliant upon primary production, any change to or in the supply of nutrients would be reflected in the brachiopod population.

## 3. Geological setting and stratigraphy

The Silurian strata of Gotland are the remains of a stacked series of carbonate platforms and dates from the latest Llandovery through Ludlow (Hede 1960; Calner *et al*. 2005; Jeppsson *et al*. 2006). The area that is now Gotland was during the Silurian located slightly south of the paleoequator (Copper & Brunton 1991; Torsvik *et al*. 1996; Cocks & Torsvik 2005) and formed part of a warm and shallow epicontinental sea – the Baltic Basin (Bassett & Kaljo 1996; Calner *et al*. 2005). The bedrock section is c. 750 m thick (Jeppsson *et al*. 2006) and is very well preserved, protected from major tectonic disturbances due to a sheltered position with respect to active margins of the Silurian Baltic Shield (Calner *et al*. 2005). The strata generally dips 0-4º to the SE and the outcrop belts strike approximately SW-NE (Fig. 1b). Towards the NE, the outcrop belts are characterised by extensive reef complexes and shallow marine to lagoonal deposits with frequent discontinuities, whereas the SW areas are dominated by alternations of marl and argillaceous skeletal limestone (Hede 1960; Samtleben *et al*. 1996).

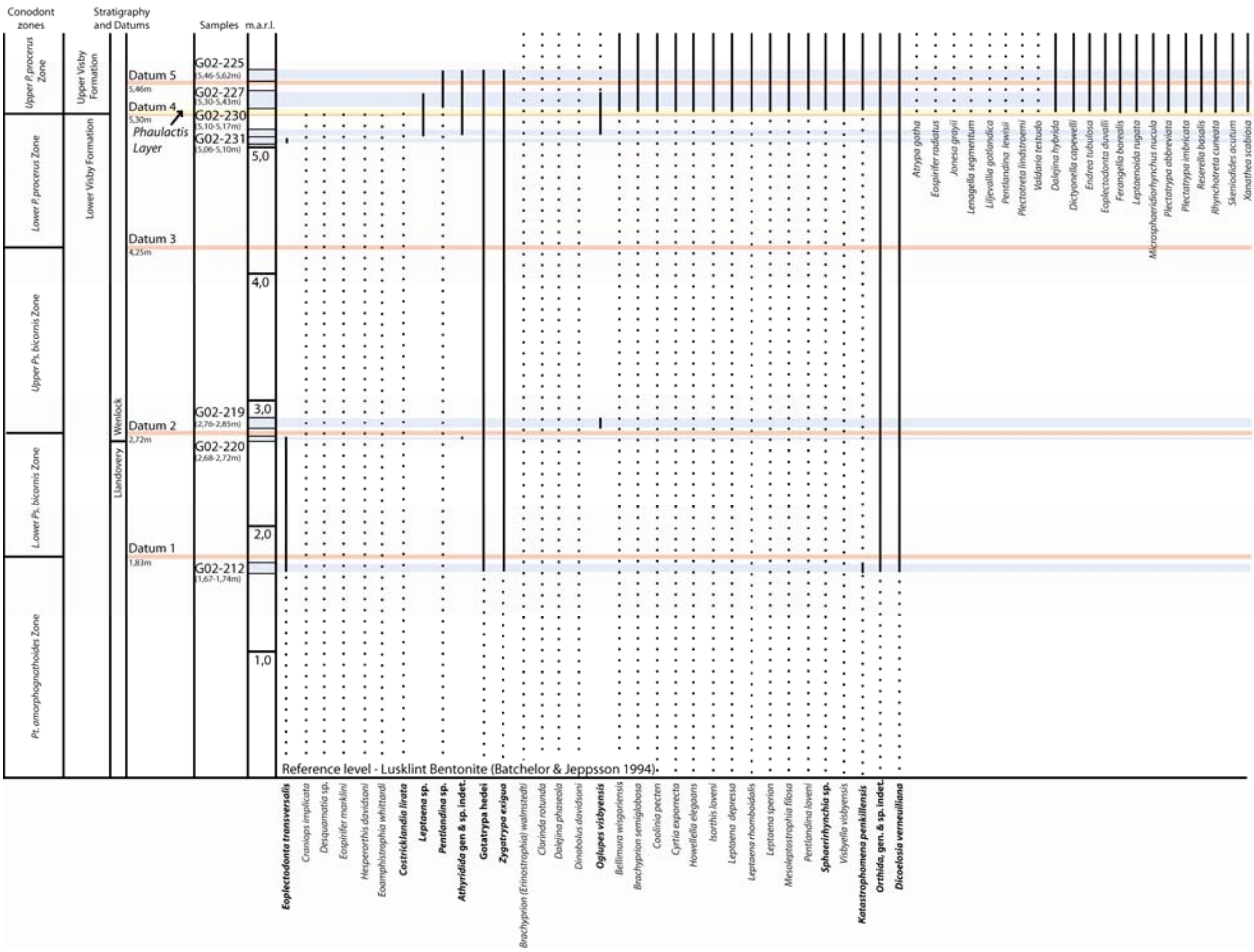


*Fig. 4.* Brachiopod ranges, based on combined data from the Lusklint 1 samples and literature studies. A dotted line indicates that the species is reported as present by literature, but with a starting and/or ending at an unspecified point in that formation. A full drawn line indicates either the presence of that species in the Lusklint 1 samples, between adjacent Lusklint 1 samples, or that the species is according to literature continues into the following formation, i.e. does not end within that formation. As there is no information on brachiopod species and species range from below the Lower Visby Formation, no indication of previous occurrences is given here. The blue zones indicate where the samples have been taken and the red lines mark the locations of datum points. The arrow and yellow line indicates the position of the *Phaulactis* layer. Species written in bold text are those identified in the Lusklint 1 samples.

## 3.1 The Lower and Upper Visby formations

The oldest strata on Gotland, those belonging to the Lower and Upper Visby formations, are exposed along the north-western coast of the island. Both the formations consist of alternating beds of limestone, argillaceous limestone and calcareous mudstones (marls), although matrix-free lithologies are more common in the Upper Visby Formation. The majority of the beds were deposited below the wave-base in a distal carbonate ramp environment. The lower boundary of the Lower Visby Formation is not exposed on Gotland. The upper boundary is defined by the disappearance of the small rugose coral and index fossil *Paleocyclus porpita*, the presence of a thin layer of pyrite and, just above the boundary, an abundance of the rugose coral *Phaulactis augusta* termed the *Phaulactis* layer (Jeppsson *et al*. 2005). It should be noted that a single example of the *Paleocyclus porpita* was found during the collection of samples from above Datum 5, well into the Upper Visby Formation, where it should have been extinct. It was embedded very loosely and on an exposed surface of the strata and although there is one other single report of a similar finding by Sheehan (1977), it is likely that this find is a result of contamination from underlying strata.

Above Datum 4, which is just below the *Phaulactis* layer and at the boundary of the Lower and Upper Visby formations, carbon isotope values begin to increase (Munnecke *et al*. 2003). Small-scale erosional surfaces and ripple marks in the Upper Visby Formation suggest a higher water energy and less depositional depth. The Upper Visby Formation has a higher limestone and carbonate content than the Lower Visby Formation (Munnecke *et al*. 2003). Facies changes from the Lower Visby Formation, through the Upper Visby Formation and into the Högklint indicate increasing water energy and progressively shallower waters (Munnecke *et al*. 2003).

Both the Lower and Upper Visby formations are accessible at the Lusklint 1 locality, situated approximately 2.08 km WNW of Lummelunda church (see Fig. 1b). The locality is a steep slope by the sea and the sampled interval is accessed by climbing down 15-20 m from a trail above the section, or climbing 10-15 m up from the shore (Fig. 3A).

# 4. Materials and methods

## 4.1 Sampled material

Seven bulk samples were investigated from the Lusklint 1 section (Fig. 4). The samples were collected from stratigraphic intervals below and above specific datum points of the Ireviken Event. Sample thickness ranges from 0.04 m to 0.30 m. The number and size of samples collected were limited according to accessibility but the aim was to collect as large a sample as possible. The degree of litification of the sedimentary rocks lead to that samples were mainly collected from the marls. The chronologically earliest sample in this work is sample G02-212, from immediately below Datum 1. The placement of datum point has after the sampling in 2002 become more precise (*cf*. Jeppsson 1997a; Jeppsson *et al*. 2005) and in some cases the Lusklint 1 samples are from what later became the error margin of the datum point placement. This may potentially affect the results. Sample G02-212 was collected below Datum 1, from between 1.67-1.74 m above reference level (Table 1) and weighed 27 kg before preparation. Sample G02-220 weighed c. 20 kg, sample G02-219 weighed c. 30 kg, sample G02-231 weighed 31.6 kg and G02-230 weighed 37.6 kg before preparation. Sample G02-227 weighed 23 kg and sample G02-225 17.5 kg before preparation.

## 4.2 Literature studies

In addition to the material collected during the fieldwork and examined in this study, data from previous works on Silurian brachiopods from Gotland was used in order to establish the dynamics of the brachiopod composition for the studied section. Hede (1925, 1927, 1940, 1960) collected and studied fauna from Gotland and although the actual thickness and specific placement of Hede's samples were not systematically recorded in his publications, the overall characters of the collections, i.e. the presence or absence of specific fossils, firmly place the separate collections in the different formations recognized today on Gotland. Such specific fossils are for example several species of ostracodes and the rugose coral *Paleocyclus porpita*, indicative of the Lower Visby Formation and not present in the Upper Visby Formation. Brachiopods identified by Bassett & Cocks (1974) in their main work on Silurian brachiopods from Gotland were identified on the basis of their own collections and on the studies of collections originally assembled in the preceding century by W. Hisinger, G. Lindström and N.P. Angelin; hence some material was not collected *in situ* by the authors. More recently, Copper (2004) has revised and described the atrypid brachiopods from Gotland and Hoel (2005) has studied the strophomenid brachiopods from Gotland.

## 4.3 Preparation

The first step in preparing the samples consisted of allowing them to dry for two to three days. To eliminate the remaining moisture, samples were then heated in an oven at 50˚ for 24 hours. Subsequently, boiling water with added sodium carbonate was poured onto the samples to dissolve the mudstone. The samples were then washed on sieves with mesh-sizes of 0.63 µm, 1 mm, 2 mm and 5.6 mm. As the 0.63 µm - 1 mm fraction yielded no material, the following fractions, starting with the largest, were sorted through, often under microscope. The brachiopod fossils were extracted, with the aim of collecting approximately 1000 specimens per sample. Two factors were considered when deciding what samples to process. First, the samples consisting of mudstone rather than limestone and of the greatest volume were considered those most likely to contain the greatest number of fossils retrievable by this extraction method, as the limestone would not disintegrate and yield material. Secondly, the samples close to but not tangent to the interval containing the datum point would most likely illustrate any significant changes across the interval. No suitable samples were collected just above Datum 1 and in the vicinity of Datum 3, due to a large amount of hard, and with this method, non-disintegrable limestone nodules in the sediment. Any attempt to disintegrate these limestone nodules would invariably damage any calcareous fossils therein.

It should be noted that this method of disintegrating samples may potentially bias the results, as the limestone-marl alternations could be interpreted as a result of a rhythmic diagenesis within an aragonite solution zone (Munnecke & Samtleben 1996). If this precipitation of calcite took place in sediments of varying porosity, this might in turn affect which fossils or fossil fractions were lithified, i.e. sediments of greater porosity would contain larger fossils and therefore become non-disintegrable limestone versus sediment of less porosity, with smaller fossils, becoming marls. The material used in this work is from the marl beds and if there is a difference in fossil composition between the limestone and marl beds, then that difference will not be reflected in this work. Although a fossil composition/size variation due to differences in primary composition is possible, Munnecke & Samtleben (1996) also assume that the very regularity of these limestone-marl alternations indicates homogenous primary sediment, therefore not relevant here.

| Sample | Fraction (mm) | *Orthida sp.* | *Dicoelosia verneuiliana* | *Zygatrypa exigua* | *Gotatrypa hedei* | *Oglupes visbyensis* | *Sphaerirhynchia sp* | *Katastrophomena penkillensis* | *Eoplectodonta transversalis* | *Athyridida gen. indet.* | *Pentlandina sp.* | *Leptaena sp.* | *Costricklandia lirata lirata* | Identified brachiopods | Unidentified fragments | Total in sample |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **G02-225** (5.46-5.62 m) | | | | | | | | | | | | | | | | |
| G02-225 | 1-2 | 259 | 8 | 0 | 51 | 0 | 0 | 0 | 0 | 5 | 7 | 0 | 0 | 330 | 276 | 606 |
| G02-225 | 2-5.6 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6 | 42 | 48 |
| G02-225 | 5.6- | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| total: | | 265 | 8 | 0 | 51 | 0 | 0 | 0 | 0 | 5 | 7 | 0 | 0 | 336 | 318 | 654 |
| **Datum 5 (5.46 ±0.02m)** | | | | | | | | | | | | | | | | |
| **G02-227** (5.30-5.43 m) | | | | | | | | | | | | | | | | |
| G02-227 | 1-2 | 319 | 4 | 21 | 62 | 0 | 0 | 0 | 0 | 63 | 7 | 1 | 0 | 477 | 152 | 629 |
| G02-227 | 2-5.6 | 52 | 0 | 0 | 72 | 0 | 0 | 0 | 0 | 51 | 0 | 1 | 0 | 176 | 19 | 195 |
| G02-227 | 5.6- | 0 | 0 | 0 | 11 | 5 | 1 | 0 | 0 | 1 | 0 | 3 | 0 | 21 | 0 | 21 |
| total: | | 371 | 4 | 21 | 145 | 5 | 1 | 0 | 0 | 115 | 7 | 5 | 0 | 674 | 171 | 845 |
| **Datum 4 (5.30 ±0.02m)** | | | | | | | | | | | | | | | | |
| **G02-230** (5.10-5.17 m) | | | | | | | | | | | | | | | | |
| G02-230 | 1-2 | 443 | 103 | 12 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 563 | 656 | 1219 |
| G02-230 | 2-5.6 | 103 | 29 | 14 | 17 | 0 | 0 | 0 | 0 | 2 | 13 | 13 | 0 | 191 | 320 | 511 |
| G02-230 | 5.6- | 3 | 0 | 5 | 1 | 5 | 0 | 0 | 0 | 0 | 5 | 5 | 0 | 25 | 5 | 30 |
| total: | | 549 | 132 | 31 | 20 | 5 | 0 | 0 | 0 | 3 | 18 | 20 | 0 | 778 | 981 | 1760 |
| **G02-231** (5.06-5.10 m) | | | | | | | | | | | | | | | | |
| G02-231 | 1-2 | 414 | 154 | 32 | 22 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 622 | 54 | 676 |
| G02-231 | 2-5.6 | 54 | 42 | 24 | 35 | 0 | 0 | 0 | 0 | 0 | 0 | 21 | 0 | 176 | 66 | 242 |
| G02-231 | 5.6- | 3 | 3 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 6 | 0 | 14 | 5 | 19 |
| total: | | 471 | 199 | 56 | 58 | 0 | 0 | 0 | 1 | 0 | 0 | 27 | 0 | 812 | 125 | 937 |
| **Datum 3 (4.25 m)** | | | | | | | | | | | | | | | | |
| **G02-219** (2.76-2.85 m) | | | | | | | | | | | | | | | | |
| G02-219 | 1-2 | 392 | 23 | 2 | 22 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 439 | 230 | 669 |
| G02-219 | 2-5.6 | 31 | 2 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 36 | 81 | 117 |
| G02-219 | 5.6- | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 4 | 7 |
| total: | | 426 | 25 | 2 | 22 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 478 | 315 | 793 |
| **Datum 2 (2.72 ±0.01m)** | | | | | | | | | | | | | | | | |
| **G02-220** (2.68-2.72 m) | | | | | | | | | | | | | | | | |
| G02-220 | 1-238719 | 497 | 28 | 12 | 14 | 0 | 0 | 0 | 59 | 3 | 0 | 0 | 0 | 613 | 504 | 1117 |
| G02-220 | 2-5.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| G02-220 | 5.6- | 15 | 0 | 1 | 0 | 0 | 0 | 0 | 30 | 0 | 0 | 0 | 0 | 46 | 0 | 46 |
| total: | | 512 | 28 | 13 | 14 | 0 | 0 | 0 | 89 | 3 | 0 | 0 | 0 | 659 | 504 | 1163 |
| **Datum 1 (1.83 ±0.03 m)** | | | | | | | | | | | | | | | | |
| **G02-212** (1,67-1,74 m) | | | | | | | | | | | | | | | | |
| G02-212 | 1-2 | 260 | 20 | 68 | 23 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 371 | 344 | 715 |
| G02-212 | 2-5.6 | 8 | 0 | 0 | 14 | 0 | 0 | 58 | 69 | 0 | 0 | 0 | 0 | 149 | 272 | 421 |
| G02-212 | 5.6- | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 4 | 42 | 46 |
| total: | | 269 | 20 | 68 | 37 | 0 | 0 | 58 | 69 | 0 | 0 | 0 | 3 | 524 | 658 | 1182 |
| | | | | | | | | Total number of identified brachiopods: | | | | | | | 4261 | |

*Table 1.* Species, fractions and quantity of brachiopods in the Lusklint 1 samples.

# 5. Results

Sample G02-212 yielded 524 identified specimens, a majority within the 1-2 mm fraction (Table 1). G02-220 yielded 659 identifiable specimens and was similar in size and distribution to sample G02-212. G02-219 yielded fewer identifiable brachiopods, only 478, all within the 1-2 mm fraction and G02-231 included several fractions and yielded 812 identifiable specimens. Samples G02-230 yielded 778 identifiable specimens and G02-227 yielded 674, both dominated by the smallest fractions but including specimens in the 2-5.6 mm fraction. The last sample, G02-225 yielded 336 identifiable specimens, all within the 1-2 mm fraction. A large number of small-sized, unidentifiable and sometimes fragmented materials were also present in the samples. The shells in this work are not differentiated in respect to dorsal or ventral shells, so the statistics do not represent the number of individual specimens present in each sample, but instead the number of identifiable shells for the investigated section.

The systematic palaeontology below lists all brachiopods from the combined outcrop and literature study (data based on samples and literature are marked with an asterisk *). The order in which the brachiopod genera are listed here follows Treatise on Invertebrate Palaeontology Part H (Williams 1965, 2000-2002).

## 5.1 Systematic palaeontology

Subphylum CRANIIFORMEA Popov *et al.* 1993

Class CRANIATA Williams *et al.* 1990

Order CRANIOPSIDA Gorjansky & Popov 1985

Superfamily CRANIOPSOIDEA Williams 1963

Family CRANIOPSIDAE Williams 1963
Genus *Craniops* Hall 1859b

*Craniops implicata* (Sowerby 1839)

This brachiopod was identified by Hede (1925, 1927, 1940, 1960) from the Lower Visby and Högklint formations and the Slite Group. Bassett (1979) reported this species as present in the Lower Visby and Upper Visby formations.

Order TRIMERELLIDA Gorjansky & Popov 1985
Superfamily TRIMERELLOIDEA Davidson & King 1872
Family TRIMERELLIDAE Davidson & King 1872
Genus *Dinobolus* Hall 1871a

*Dinobolus davidsoni* (Salter MS)

Hede (1940) reported this brachiopod as present in the Lower and Upper Visby formations.

Subphylum RHYNCHONELLIFORMEA Williams *et al.* 1996
Class CHILEATA Williams *et al.* 1996
Order DICTYONELLIDA Cooper 1956
Superfamily EICHWALDIOIDAE Schuchert 1893
Family EICHWALDIIDAE Schuchert 1893
Genus *Dictyonella* Hall 1867a

*Dictyonella capewelli* (Davidson 1848)

Hede (1940) reported this species as found in the Upper Visby and Halla formations and the Slite Group. Bassett & Cocks (1974) identified this brachiopod in the Upper Visby, Högklint, Halla and Eke formations and the Slite Group.

Class STROPHOMENATA Williams *et al.* 1996
Order STROPHOMENIDA Öpik 1934
Superfamily STROPHOMENOIDEA King 1846
Family STROPHOMENIDAE King 1846
Subfamily FURCITELLINAE Williams 1965
Genus *Bellimurina* Cocks 1968

*Bellimurina visgoriensis* (Lamont & Gilbert 1945)

This brachiopod was reported by Bassett & Cocks (1974) as *Cyphomenoidea wisgoriensis* and was reported as only found in the Lower Visby Formation. Hoel (2005) reported that most specimens previously identified as *Pentlandina loveni* in the Lower Visby Formation belong to *B. visgoriensis* which is found in the Lower Visby, Upper Visby and Högklint formations.

Genus *Katastrophomena* Cocks 1968

*Katastrophomena penkillensis* (Reed 1917) *

Hoel (2005) reported *K. penkillensis* as present in the Lower Visby, Upper Visby and Högklint formations and the Slite Group.

This brachiopod was present with 58 specimens in a single Lusklint 1 sample, below Datum 1 in sample G02-212 (Fig. 5A).

Genus *Pentlandina* Bancroft 1949

*Pentlandina* sp. *

Bassett & Cocks (1974) identified a brachiopod smaller than *P. loveni* which they referred to as *Pentlandina* sp. found in the Lower Visby Formation. The brachiopods from the Lusklint 1 samples belonging to the genus *Pentlandina* are small, not clearly identifiable as *P. loveni* and are in this work referred to as *Pentlandina* sp. (Fig. 5B).

Above the location of Datum 3 and below Datum 4, in sample G02-230 there are 18 specimens recorded. Above Datum 4 in sample G02-227 there are 7 specimens and above Datum 5 in sample G02-225 there are 7 specimens.

*Pentlandina lewisii* (Davidson 1847)

Hoel (2005) reported a single specimen of this subspecies from the Upper Visby Formation.

*Pentlandina loveni* (Verneuil 1848)

Hede (1927, 1940, 1960) identified *P. loveni* in the Lower Visby, Upper Visby and Högklint formations. Bassett & Cocks (1974) described *P. loveni* as occurring in the Upper Visby and Högklint formations. Hoel (2005) reported *P. loveni* as identified for the Högklint Formation to the middle of the Slite Group.

Subfamily LEPTAENINAE Hall & Clarke 1894
Genus *Leptaena* Dalman 1828

*Leptaena depressa* (Sowerby 1825)

*L. depressa* was reported by Basset & Cocks (1974) as present only in the Upper Visby Formation.
Hoel 2004 reported *L. depressa* from the 'lower' (sic) Visby Formation and into the upper Hemse Group.

*Leptaena rhomboidalis* (Wahlenberg 1818)

*L. rhomboidalis* was reported by Hede (1925, 1927, 1940) as present in the Lower Visby, Upper Visby and Högklint formations. Bassett & Cocks (1974) described it as restricted to the Upper Visby and Högklint formations. Hoel (2005) reported *L. rhomboidalis* from the uppermost part of the Upper Visby Formation.

*Leptaena* sp. *

Bassett & Cocks (1974) only described three species of *Leptaena*, but noted that there likely exist several more. The specimens found in the Lusklint 1 samples are small and difficult to identify, and therefore are referred to as *Leptaena* sp. (Fig. 5C).

In the Lusklint 1 samples, below the location of Datum 4 in the sample G02-230 there are 20 specimens recorded. Below Datum 5 in the sample G02-225 there are 5 specimens recorded.

*Leptaena sperion* (Bassett 1977)

Hoel (2005) reported *L. sperion* as identified in the Lower Visby, Upper Visby and Högklint formations, and the Slite Group.

Family AMPHISTROPHIIDAE Harper 1973
Subfamily AMPHISTROPHIINAE Harper 1973
Genus *Eoamphistrophia* Harper & Boucot 1978

*Eoamphistrophia whittardi* (Cocks 1967)

Bassett & Cocks (1974) reported this brachiopod as present but rare in the Lower Visby Formation.

Family LEPTAENOIDEIDAE Williams 1953
Genus *Liljevallia* Hedström 1917

*Liljevallia gotlandica* (Hedström 1917)

Hede (1927, 1940, 1960) reported this species as restricted to the Upper Visby Formation, as did Bassett & Cocks (1974) and Hoel (2005).

Family LEPTAENOIDEIDAE Williams 1953
Genus *Leptaenoidea* Hedström 1917

*Leptaenoidea rugata* (Lindström 1861)

*L. rugata* was reported by Hede (1927) from the Högklint Formations but was according to Bassett & Cocks (1974) only present in the Upper Visby Formation. Hoel (2005) reported *L. rugata* in the 'Visby' to Klinteberg formations.

Family LEPTOSTROPHIIDAE Caster 1939
Genus *Brachyprion* Shaler 1865

*Brachyprion semiglobosa* (Davidson 1871)

Hede (1940) included *B. semiglobosa* amongst the brachiopod species from the Lower Visby, Upper Visby, Högklint and Tofta formations. Hoel (2005) reported this brachiopod from the 'Visby Formations' (sic) to the Slite Group.

Subgenus: *Erinostrophia* Cocks & Worsley 1993

*Brachyprion (Erinostrophia) walmstedti* (Lindström 1861)

Hede (1927) included *B. walmstedti* amongst the brachiopods present in the Lower Visby Formation. Hoel (2005) reported this species as common in the Lower and Upper Visby formations.

Genus *Mesoleptostrophia* Harper & Boucot 1978

*Mesoleptostrophia filosa* (Sowerby 1839)

This species was reported as being present in the Upper Visby and Högklint formations and the Hemse Group (Bassett & Cocks 1974). Hoel (2005) reported it as widespread from the Lower Visby to Hamra formations.

Superfamily PLECTAMBONITIDAE Jones 1928
Family LEPTELLINIDAE Ulrich & Cooper 1936
Genus *Leangella* Öpik 1933

*Leangella segmentum* (Lindström 1861)

*L. segmentum* was reported by Bassett & Cocks (1974) as present in the Upper Visby and Mulde formations and the Slite Group.

Superfamily PLECTAMBONITOIDEA Jones 1928
Family XENAMBONITIDAE Cooper 1956
Genus *Jonesea* Cocks & Rong 1989

*Jonesea grayi* (Davidson 1848)

This brachiopod was reported by Bassett & Cocks (1974) from only the Upper Visby Formation, based upon a single specimen.

Family SOWERBYELLIDAE Öpik 1930
Genus *Eoplectodonta* Kozlowski 1929

*Eoplectodonta duvalli* (Davidson 1847)

*E. duvalli* was reported by Bassett & Cocks (1974) as found in the Upper Visby, Högklint formations and the Slite Group.

*Eoplectodonta transversalis* (Wahlenberg 1818) *

Hede (1940) documented *E. transversalis* from the Lower Visby Formation. Bassett & Cocks (1974) reported it as confined to the Lower Visby Formation of Gotland and as the most common brachiopod in the Lower Visby Formation. Bassett & Cocks (1974) and Bassett (1979) did not include *E. transversalis* in the brachiopods present in the Upper Visby Formation and the Lusklint 1 material confirms that it is confined to the Lower Visby Formation (Fig 5D).

In the Lusklint 1 samples, *E. transversalis* is present below the location of Datum 1 in sample G02-212 with 69 specimens. Below Datum 2 in sample G02-220 the species is present with 89 specimens, but it is not present in sample G02-219. Below Datum 3 in

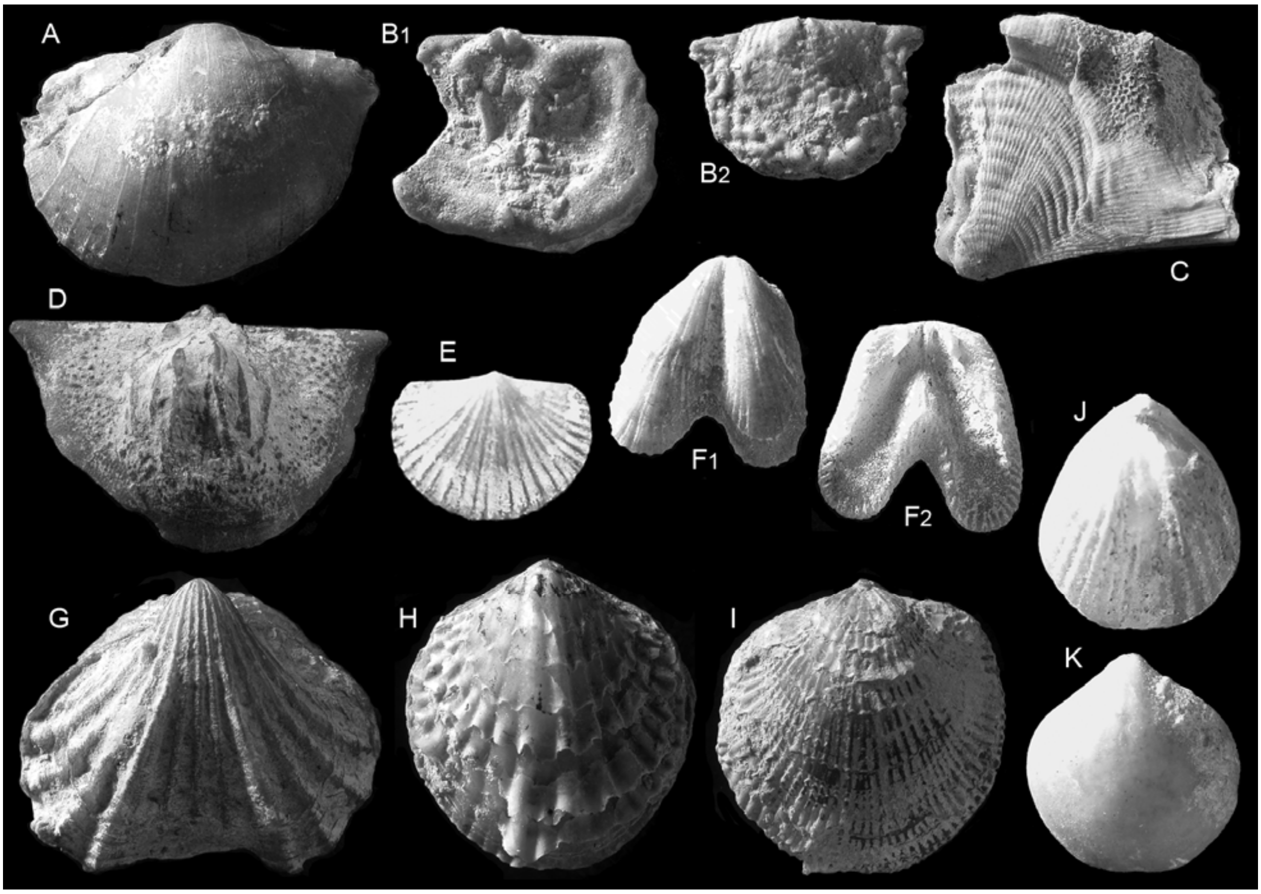


*Fig. 5.* Silurian brachiopods from the Lusklint 1 locality (Lower and Upper Visby formations) on Gotland, Sweden. **A**. The ventral valve of *Katastrophomena penkillensis*, 13 mm wide. The shell is thin and has a characteristic striped pattern. **B1**. The interior of a ventral valve of *Pentlandina* sp., 9 mm wide (across the fragmented hinge line). **B2**. Ventral valve of *Pentlandina* sp., an exterior view, 11 mm wide. Note the almost zigzag pattern of growth lines. **C**. A ventral valve of *Leptaena* sp., 16 mm across the lower hinge line. Note the characteristic shell ornamentation of finely striped lines crossing the growth lines. **D**. Dorsal valve of *Eoplectodonta transversalis*, 11 mm wide, a species both confined to the Lower Visby Formation and one of the most common species found. **E**. The dorsal valve of *Orthida* gen. & sp. indet., an exterior view, 3 mm wide. The most common brachiopod in the Lower and Upper Visby formations is a number of small orthids. **F1**. *Dicoelosia verneuiliana*, ventral valve, 5 mm wide. This brachiopod is the mostly easily identified, with a characteristic bi-lobed shell shape. **F2**. *Dicoelosia verneuiliana*, interior view of the ventral valve, 5 mm wide. **G**. The co-joined valves of the single found specimen of *Sphaerirhynchia* sp., view of the ventral valve, 12 mm wide. This species has a very characteristic, deeply indented ventral valve. **H**. Ventral valve view of co-joined valves of *Gotatrypa hedei*, 8 mm wide. This is one of the small, frilly shelled atrypids present in all Lusklint 1 samples. **I**. Ventral valve of *Oglupes visbyensis*, exterior view, 17 mm wide. This is one of the largest brachiopods found in the Lusklint 1 samples. **J**. Dorsal valve of *Zygatrypa exigua*, exterior view, 3 mm wide. This is a small atrypid confined to the Lower Visby Formation, with a characteristic indentation on the dorsal valve. **K**. Ventral valve view of co-joined valves of a specimen *Athyridida* gen. & sp. indet., 5 mm across. This brachiopod is small and smooth shelled. All photographs by F. Terfelt.

sample G02-231 there is one specimen recorded. The taxon is not present in samples above Datum 3.

Order ORTHOTETIDA
Suborder ORTHOTETIDINA
Superfamily CHILIDIOPSIDEA Boucot 1959
Family CHILIDIOPSIDAE Boucot 1959
Genus *Coolinia* Bancroft 1949

*Coolinia pecten* (Linnaeus 1758)

This species was reported by Hede (1925, 1927, 1940, 1960) from the Lower and Upper Visby and Högklint formations. Basset & Cocks (1974) identified this species from the Lower Visby, Upper Visby, Högklint, Klinteberg and Eke formations and the Slite Group.

Genus *Valdaria* Bassett & Cocks 1974

*Valdaria testudo* (Lindström MS)

This brachiopod was recorded by Bassett & Cocks (1974) as present in the Upper Visby Formation.

Suborder TRIPLESIIDINA Moore 1952
Superfamily TRIPLESIOIDEA Schuchert 1913
Family TRIPLESIIDAE Schuchert 1913
Genus *Plectotreta* Ulrich & Cooper 1936

*Plectotreta lindstroemi* (Ulrich & Cooper 1936)

This brachiopod was reported by Bassett & Cocks (1974) from the Upper Visby, Högklint and Halla formations and the Slite and Hemse groups.

Class RHYNCHONELLATA Williams *et al*. 1996
Order PROTORTHIDA Schuchert & Cooper 1931
Superfamily SKENIDIOIDEA Kozlowski 1929
Family SKENIDIIDAE Kozlowski 1929
Genus *Skenidioides* Schuchert & Cooper 1931

*Skenidioides acutum* (Lindström 1861)

Hede (1940, 1960) reported *Skenidioides acutum* as restricted to Upper Visby Formation. Bassett & Cocks (1974) collected specimens from the Upper Visby Formation and the Slite Group.

Order ORTHIDA Schuchert & Cooper 1932

Several orthids of the Lower and Upper Visby formations were described by Hede (1940), Bassett & Cocks (1974), and Bassett (1979) and are included in this work. Bassett (1979) noted a large number of orthids in the Vattenfallet section.

Small-sized orthids are found elsewhere in the world. In the Mackenzie District orthid genera such as *Dolerorthis* (Schuchert & Cooper 1931), *Hesperorthis* (Schuchert & Cooper 1931), *Skenidioides* (Schuchert & Cooper 1931), *Dicoelosia* (King 1850), *Platystrophia* (King 1850) and *Isorthis* (Kozlowski 1929), with small-sized species, have been described. The Ordovician and Silurian formations from the Oslo region also include the genera *Dolerorthis* (Schuchert & Cooper 1931), *Hesperorthis* (Schuchert & Cooper 1931), *Platystrophia* (King 1850) and *Skenidioides* (Schuchert & Cooper 1931).

*Orthida,* gen. & sp. indet. *

This term is used here in reference to a large number of unidentified orthid juveniles found in the Lusklint 1 samples (Fig. 5E).

Below the level of Datum 1, in sample G02-212, there are 269 specimens. Between datums 1 and 2, in sample G02-220, there are 512 specimens present. Above Datum 2, in sample G02-219, there are 426 specimens. In samples G02-231 and G02-230 there are 471 and 549 specimens found respectively. Between datums 4 and 5, in sample G02-227, there are 371 specimens. Above datum 5 in sample G02-225, there are 265 specimens.

Suborder ORTHIDINA
Superfamily ORTHOIDEA
Family HESPERORTHIDAE Schuchert & Cooper 1931
Genus *Hesperorthis* Schuchert & Cooper 1931

*Hesperorthis davidsoni* (Verneuil 1848)

This brachiopod was reported by both Hede (1925, 1927, 1940, 1960) and Bassett & Cocks (1974) as restricted to the Lower Visby Formation.

Suborder DALMANELLIDINA Moore 1952
Superfamily DALMANELLOIDEA Schuchert 1913
Family DALMANELLIDAE Schuchert 1913
Subfamily ISORTHINAE Schuchert & Cooper 1931
Genus *Isorthis* Kozlowski 1929

*Isorthis loveni* (Lindström 1861)

*I. loveni* was documented by Hede (1940, 1960) as restricted to the Lower Visby Formation. It was identified by Bassett & Cocks (1974) as present in the Lower Visby, Upper Visby and Högklint formations.

Subfamily RESSERELLINAE Walmsley & Boucot 1971
Genus *Resserella* Bancroft 1928

*Resserella basalis* (Dalman 1828)

Hede (1940) reported *R. basalis* from only the Högklint Formation. Bassett & Cocks (1974) identified this brachiopod as confined to the Upper Visby and Högklint formations.

Genus *Visbyella* Walmsley, Boucot, Harper & Savage 1968

*Visbyella visbyensis* (Lindström 1861)

*V. visbyensis* was confirmed by both Hede (1925, 1927, 1940, 1960) and Bassett & Cocks (1974) as present in and confined to the Lower and Upper Visby formations. Bassett (1979) extended the range of this species into the Högklint Formation.

Family DICOELOSIIDAE Cloud 1948
Genus *Dicoelosia* King 1850

*Dicoelosia verneuiliana* (Beecher 1891) *

The lectotype for this species is from the collection of brachiopods collected on Gotland by Carl von Linnaeus (Basset & Cocks 1974). It is one of the most easily identified brachiopod genera due to its characteristic shape (Fig. 5F). Hede (1925, 1927, 1940, 1960) identified the brachiopod from the Lower Visby, Upper Visby and Högklint formations. *D. verneuiliana* was collected by Bassett & Cocks (1974) from the Upper Visby and Högklint formations. Bassett & Cocks (1974) also noted that immature *Dicoelosia* found in the Lower Visby Formation may belong to a Telychian species, *D. alticavata*, due to the presence of typical Telychian fauna such as the coral *Paleocyclus porpita* and the brachiopod *Costricklandia lirata lirata*. Bassett (1979) noted the presence of *D. verneuiliana* in the upper Lower Visby Formation and all of the Upper Visby Formation. The specimens found at Lusklint 1 are small and are assigned to *D. verneuiliana*.

Below Datum 1, in Lusklint 1 sample G02-212, there are 20 specimens. Above Datum 1, in sample G02-220, there are 28 specimens and above Datum 2, in sample G02-219, 25 specimens. Below Datum 4, in samples G02-231 and G02-230 there are 199 and 132 specimens, respectively. Between datums 4 and 5, in sample G02-227 there are four specimens and above Datum 5, in sample G02-225, there are eight specimens.

Family RHIPIDOMELLIDAE Schuchert 1913
Genus *Dalejina* Havlícek 1953

*Dalejina hybrida* (Sowerby 1839)

Hede (1940) reported this brachiopod from the Upper Visby and Högklint formations, and the Slite Group.

*Dalejina phaseola* (Rubel 1963)

*D. phaseola* is a brachiopod identified as appearing exclusively in the Lower and Upper Visby formations (Bassett & Cocks 1974).

Class PENTAMERIDA
Order PENTAMERIDA Schuchert & Cooper 1931
Suborder PENTAMERIDINA Schuchert & Cooper 1931
Superfamily STRICKLANDIIDAE Schuchert & Cooper 1931
Family STRICKLANDIIDAE Schuchert & Cooper 1931
Genus *Costistricklandia* Amsden 1953

*Costistricklandia lirata lirata* (Sowerby 1839) *

Hede (1940, 1960) and Bassett & Cocks (1974) identified this species as confined to the Lower Visby Formation.

Three specimens of this brachiopod were collected *in situ* during the collection of the Lusklint 1 samples at 1.70 m above reference level, below Datum 1.

Superfamily CLORINDIDEA
Family CLORINDIDAE Rzhonsnitskaya 1956
Genus *Clorinda* Barrande 1879

*Clorinda rotunda* (Lindström 1861)

Hede (1940), Bassett & Cocks (1974), and Bassett (1979) all identified this smooth-shelled pentamerid from the Lower and Upper Visby formations.

Class RHYNCHONELLIDA
Order RHYNCHONELLIDA Kuhn 1949
Superfamily ANCISTRORHYNCHOIDEA Cooper 1956
Family OLIGORHYNCHIIDAE Cooper 1956
Genus *Rhynchotreta* Hall 1879

*Rhynchotreta cuneata* (Dalman 1928)

This brachiopod was reported by Bassett & Cocks (1974) as present in the Upper Visby, Högklint, Halla, Klinteberg and Eke formations and the Slite Group.

Superfamily RHYNCHOTREMATOIDEA
Family RHYNCHOTREMATIDAE Schuchert 1913
Genus *Ferangella* Nikiforova 1937

*Ferangella borealis* (Buch 1834)

*F. borealis* was identified by Hede (1925, 1927, 1940, 1960) and Bassett & Cocks (1974) from the Upper Visby, Högklint, Mulde and Klinteberg formations and the Slite Group.

Family TRIGONIRHYNCHIIDAE McLaren 1965
Genus *Microsphaeridiorhynchus* Sartenaer 1970

*Microsphaeridiorhynchus nucula* (Sowerby 1839)

This brachiopod was recorded by Bassett & Cocks (1974) from the Upper Visby, Högklint, Halla, Mulde, Klinteberg, Eke, Burgsvik and Hamra formations and the Slite and Hemse groups. Hede (1940) reported it from the Högklint Formation and the Slite Group.

Superfamily UNCINULOIDEA
Family UNCINULIDAE Rzhonsnitskaya 1956
Genus *Sphaerirhynchia* Cooper & Muir-Wood 1956

*Sphaerirhynchia* sp. (Sowerby 1816) *

A number of unspecified brachiopods belonging to the genera *Sphaerirhynchia* were recorded from the Lower Visby, Upper Visby, Högklint, Halla, Mulde, Klinteberg and formations and the Slite and Hemse groups (Bassett & Cocks 1974).

A single specimen was located in sample G02-227, from the interval between datums 4 and 5 (Fig. 5G).

Order SPIRIFERIDA Waagen 1883
Suborder SPIRIFERIDINA Waagen 1883
Superfamily CYRTIACEA Frederiks 1919 (1924)
Family CYRTIIDAE Frederiks 1924
Genus *Cyrtia* Dalman 1828

*Cyrtia exporrecta* (Wahlenberg 1818)

This species was reported by Hede (1927, 1940, 1960) as present in the Lower and Upper Visby formations. Bassett & Cocks (1974) documented this species as present in both the Lower and Upper Visby formations and in every consecutive formation until the Hemse Group.

Genus *Eospirifer* Schuchert 1913

*Eospirifer marklini* (Verneuil 1848)

This species was reported by Bassett & Cocks (1974) as present but rare in the Lower Visby Formation.

*Eospirifer radiatus* (Sowerby 1913)

*E. radiatus* was reported by Hede (1940) and by Bassett & Cocks (1974) as present in the Upper Visby Formation.

Superfamily SPIRIFERACEA King 1846
Family DELTHYRIDIDAE Waagen 1883
Genus *Howellella* Kozlowski 1946

*Howellella elegans* (Muir-Wood 1925)

Bassett & Cocks (1974) reported this species as present in the Lower Visby, Upper Visby, Högklint, Halla, Mulde, Eke, Hamra and Sundre formations and the Slite Group.

Class ATRYPIDA
Order ATRYPIDA

Silurian atrypid brachiopods have been revised and described by Paul Copper (2004) in a work specifically dedicated to brachiopods of this order from the British Welsh Borderland and Gotland, Sweden. Therein he concluded that many early Silurian atrypids from Gotland were previously incorrectly classified as *Atrypa reticularis* and that the diversity of this genus was actually much higher. Copper identified three atrypids species found in the Lower Visby Formation: *Zygatrypa exigua, Gotatrypa hedei* and *Oglupes visbyensis*. The species *O. visbyensis* and *Z. exigua* continue into the Upper Visby Formation and the species *Atrypa gotha, Endrea tubulosa, Xanathea scabiosa* and *Plectatrypa abbreviata* have their first occurrences in that formation.

Suborder ATRYPIDINA Moore 1952
Superfamily ATRYPOIDEA Schuchert & Levene 1929
Family ATRYPIDEA Gill 1871
Genus *Atrypa* Dalman 1828

The three species belonging to the genus *Atrypa* in the Lusklint 1 samples include a small frilly-shelled brachiopod found through all samples, i.e. from the Lower Visby Formation into the basal Upper Visby Formation. Although according to Copper (2004) both of the frilly shelled brachiopods *G. hedei* and *X. scabiosa* are present in the Upper Visby Formation, only *G. hedei* is found in the Lower Visby Formation. The frilly shelled, small-sized atrypid brachiopod of the Lusklint 1 samples is assigned to this species as it is found in both the Lower and Upper Visby formations. Copper (2004) restricts *G. hedei* to the Lower Visby Formation but the Lusklint 1 samples indicate that this species continues into the very early Upper Visby Formation. Another of the atrypid species found in the Lusklint 1 samples bears a marked indentation, matching the description of *Z. exigua*. The brachiopod *O. visbyensis* is one of the few large species present in the Lusklint 1 samples and reported by Copper (2004) from the Lower Visby Formation.

*Atrypa gotha* (Copper 2004)

This brachiopod was reported by Copper (2004) from the Upper Visby Formation.

Subgenus *Gotatrypa* Struve 1966

*Gotatrypa hedei* (Struve 1966) *

Bassett & Cocks (1974) reported *G. hedei* from the Lower Visby Formation. There are several small, frilly-shelled brachiopod species reported by Copper (2004) from the Upper Visby Formation as well, but only *G. hedei* was reported from the Lower Visby Formation. This brachiopod was described as having an average adult shell width of 13-15 mm (Copper 2004). The small, frilly-shelled brachiopods in the Lusklint 1 samples are found in both the Lower and Upper Visby formations and are therefore assigned to this species (Fig. 5H).

*G. hedei* is found in the interval below Datum 1 in sample G02-212 with 37 specimens. Below Datum 2, in sample G02-220, there are 14 specimens and between datums 2 and 3, in sample G02-219, there are 22 specimens. Below Datum 4, the sample G02-231 included 58 specimens and G02-230 included 20 specimens. In the interval between Datums 4 and 5, the sample G02-227 included 145 specimens and sample G02-225, collected above Datum 5, included 51 specimens.

Subgenus *Oglupes* Havlicek 1987

*Oglupes visbyensis* (Copper 2004) *

*O. visbyensis* ranges from the Lower Visby Formation and into the Upper Visby Formation (Copper 2004). The brachiopod reached an average size of 35 mm, i.e. larger than the majority of brachiopods found in the Lusklint 1 samples (Fig. 5I).

This species is found in the interval below Datum 3 in sample G02-219 which gave 3 specimens. Sample G02-230, collected between datums 3 and 4, gave 5 specimens. Sample G02-227, from between datums 4 and 5 included 5 specimens. This species is not found above Datum 5.

Genus *Desquamatia* Alekseeva 1960

*Desquamatia* sp.

Bassett & Cocks (1974) reported *Desquamatia sp*. from the Lower Visby, Högklint, Klinteberg, Eke and Hamra formations and the Hemse Group.

Genus *Endrea* Copper 1996b

*Endrea tubulosa* (Bassett & Cocks 1974)

Bassett & Cocks (1974) identified this species from the Upper Visby and Högklint formations. Copper (2004) reported it from the Upper Visby Formation.

Family ATRYPINIDAE McEwan 1939
Genus *Plectatrypa* Schuchert & Cooper 1930

*Plectatrypa abbreviata* (Sowerby 1839)

Bassett & Cocks (1974) reported the brachiopod *Plectatrypa imbricata* as present in the Lower Visby, Upper Visby and Högklint formations and the Slite and Hemse groups. Copper (2004) includes this species amongst the brachiopods of the Upper Visby and Högklint formations.

*Plectatrypa imbricata* (Sowerby 1839)

Hede (1925, 1927, 1940, 1960) collected *P. imbricata* from the Upper Visby and Högklint formations. Copper (2004) describes a new subspecies and includes it in the brachiopods found in the Upper Visby and Högklint formations.

Genus *Xanathea* Copper 1996b

*Xanathea scabiosa* (Copper 2004)

This brachiopod was identified from the Upper Visby and Högklint formations by Copper (2004).

Suborder ANAZYGIDINA Copper 1996
Superfamily ANAZYGOIDEA
Family ANAZYGIDAE Davidson 1882
Genus *Zygatrypa* Copper 1977

*Zygatrypa exigua* (Lindström 1861) *

Hede (1925, 1927, 1940 1960) reported *Z. exigua* as confined to the Lower Visby Formation and Bassett & Cocks (1974) reported the species as found solely in the Lower Visby Formation. Copper (1996, 2004) reported *Z. exigua* as confined to the Lower Visby Formation and described it as a small brachiopod, reaching no more than 4 mm in adult form. The specimens that are herein referred to *Z. exigua* are found only in the samples from the Lower Visby Formation, i.e. from below Datum 4. The shells are only a few millimetres wide and have a characteristic indentation on the top (Fig. 5J).

Below Datum 1 in sample G02-212, there are 68 specimens of *Z. exigua*. Below Datum 2, in sample G02-220, there are 13 specimens. Between datums 2 and 3, in sample G02-219 there are 2 specimens. Below Datum 4 in samples G02-231 and G02-230 there are 56 and 31 specimens, respectively. Above Datum 4 in sample G02-227 there are 21 specimens. The species is not found above Datum 5.

Class ATHYRIDIDA
Order ATHYRIDIDA

The small, smooth shelled brachiopods found in the Lusklint 1 samples are not easily identified. Although the smooth shelled pentamerid *Clorinda rotunda* was reported by Hede (1925, 1927, 1940 1960) and Bassett & Cocks (1974), it is also described as being uncommon and of an adult size larger than the smooth shelled specimens from the Lusklint 1 samples. These earlier works also included reports of the atrypid genera *Glassia* and *Lissatrypa*, both of which later were subject to revision by Copper (1996), whereby they were excluded from the Lower and Upper Visby formations fauna.

*Athyridida* gen. & sp. indet. *

Bassett (1979) reports a brachiopod with smooth shells belonging to this order, as present in the Vattenfallet section, encompassing part of the Lower Visby, the Upper Visby and Högklint formations. Copper (1996) stated that smooth-shelled atrypids are absent from Lower Visby strata and that any such reported belong instead to the order *Athyridida*, therefore the brachiopods matching this description are assigned to *Athyridida* gen. & sp. indet (Fig. 5K).

This small and smooth brachiopod in the Lusklint 1 samples is first below Datum 2, in sample G02-220 with 3 specimens. It is present below Datum 4 in sample G02-230 with 3 specimens. It increases infrequency above Datum 4, in sample G02-227, i.e. the Upper Visby Formation, to 115 specimens. Above Datum 5 in sample G02-225 there are 5 specimens identified.

## 6. Discussion

This work aims to study brachiopod faunal dynamics across the stratigraphical range of the Ireviken Event on Gotland. This has been done by analysing the combined information from large samples collected at the Lusklint 1 locality and literature studies. Despite systematic and comprehensive sampling, the composition of the brachiopod fauna as described in the literature is not reflected in the sampled material from Lusklint 1.

## 6.1 Comparison of sampled material and data from literature

Two aspects of the Lusklint 1 material must be addressed. The first is the absence of 41 out of 54 previously reported species from the Lower and Upper Visby formations in the literature. The second is the strong dominance of small-sized brachiopods.

### 6.1.1 The number of brachiopod species in the Lower and Upper Visby formations

About 75% of the species previously reported in the literature as present in the Lower and Upper Visby formations were not found in the samples from Lusklint 1, despite large sample sizes and high sampling precision (Fig. 4). Some of these missing brachiopod species may have been misidentified in this study, or by earlier authors, but many have distinct characteristics and are not easily missed. None of the brachiopod species reported in the literature as present in the Upper Visby Formation were found in the Lusklint 1 samples. This is not surprising since only two of the samples for the present study is from that formation, taken from its lowermost three decimetres (*cf.* Table 1). Hence, the missing species may have their first occurrence higher up. Despite this explanation for the discrepancy in number of species found in the Upper Visby Formation, it is notable that 21 brachiopod species previously reported from the Lower Visby Formation were not found in the Lusklint 1 samples. Some of these missing species could have disappeared before the deposition of the strata from which the oldest of the Lusklint 1 sample was collected. But 16 of these 21 missing brachiopod species, e.g. 76%, are reported from above the Lower Visby Formation and therefore do not have their last occurrences in that formation. In contrast, in the Lusklint 1 samples, only five of the twelve confirmed brachiopod species, e.g. 41% are found in following formations. If the brachiopod species missing in the Lower Visby Formation samples are present in strata from before the first, oldest Lusklint 1 samples and above the last of the samples, they could indicate an occurrence of Lazarus taxa. But the percentage of missing species ranging into later formations reported in the literature studies is greater than that of the Lusklint 1 samples, indicating a greater likelihood of contamination in the material upon which the literature is based, (e.g. a brachiopod taxon assigned in the literature to the Lower Visby and/or Upper Visby formations may actually come from other formations). This in turn raises questions about the stratigraphical precision and the sampling methods in previous works.

### 6.1. Brachiopod size and sampling methods

Also the discrepancy in the size of the brachiopod shell assemblage from Lusklint 1 could reflect earlier inadequate sampling methods. The absolute majority of brachiopods recovered from the Lusklint 1 samples are articulate brachiopods with a shell width of only a few millimetres (Table 1). The larger-sized brachiopods belong primarily to the species *O. visbyensis* and *C. lirata lirata* and they comprise only a small number of the identified brachiopod shells. Bassett & Cocks (1974) and Bassett (1979) reported the presence of many small orthids, but these did not dominate the brachiopod fauna. Copper (2004) wrote that most of the atrypid species from the Lower and Upper Visby formations never reached an adult size of more than a few millimetres and that small brachiopods are easily missed if samples are not collected in bulk and sieved. Field work in association with many earlier works concerning brachiopods from the Lower and Upper Visby formations may not have been thorough enough to result in samples of a magnitude enough to uncover the mass of small-sized brachiopods present in the Lusklint 1 samples.

## 6.2 Changes within the Lusklint 1 brachiopod assemblage

The stratigraphic precision and size of the Lusklint 1 samples, together with previously published data, makes it possible to study changes to a brachiopod species and to the whole of the brachiopod assemblage, across the datums points of the Ireviken Event. The documented changes indicate that the brachiopod faunal composition was affected at least during the early parts of the event.

### 6.2.1 The occurence of brachiopod species below and above datum points

Of the 33 species reported from combined literature studies and the samples from the Lower Visby Formation, eight are not found above Datum 4 , i.e. 24 % of the species disappear at or below the boundary between the Lower and Upper Visby formations (Fig. 4). An additional four of these 33 species are not present above Datum 5 in the lower Upper Visby Formation. Of the remaining 21 that continue above Datum 5, five disappear at some point during the deposition of the Upper Visby Formation (Fig. 4). Hence, all together 17 of the total 33 brachiopod species in the Lower Visby Formation disappear at some point during the deposition of the Lower and Upper Visby formations. 21 species are reported as having their first occurrence in the Upper Visby Formation and of these, seven also have their last occurrence in that same formation (Fig. 4). In total, of the 54 species found in the Lower and Upper Visby formations, 23 also have their last occurrence during the event, comprising 42%.

Six of the twelve species found in the Lusklint 1 samples have their last occurrence in the investigated section (Fig. 4), e.g. 50%. The brachiopod species *C. lirata lirata* is not found above Datum 1, *E. transversalis* is not found above Datum 4 and *Leptaena* sp. is not found above Datum 5. The species *Pentlandina* sp., *G. hedei,* and *Z. exigua* are not reported as present in the Upper Visby Formation in previous works and therefore herein assumed to disappear closely above sample G02-225, in the lower Upper Visby Formation. Here again the Lusklint 1 samples show the need for detailed sampling to enable the precise identification of first and last occurrences.

There are a few general changes in the Lusklint 1 brachiopod assemblage worth noting. *D. verneuiliana* drops from 132 specimens in sample G02-230 to 4 specimens in sample G02-227 from below and above Datum 4, indicating a decrease in population size. Five species (*E. transversalis*, *O. visbyensis*, *K. penkillensis, Sphaerirhynchia* sp. and *Athyridida* sp. & gen. indet.) found in the Lusklint 1 samples show 'gaps' in their ranges, characteristic of Lazarus taxa, a response linked to low primary production (Twitchett 2001). Lazarus taxa have been documented among conodonts during the Ireviken Event (Jeppsson 1998). The orthids appear to remain relatively unaffected throughout the Lower Visby Formation and continue into the Upper Visby Formation.

### 6.2.2 The presence of small-sized brachiopod species

There are several explanations for the mass occurrence of small-sized brachiopod species, none of which necessarily exclude the others. The presence of small-sized brachiopods in the Lusklint 1 samples could be due to a Lilliput effect, with dwarfed or stunted forms, all indicating a stressed environment (Price-Lloyd & Twitchett 2002). Clarkson *et al*. (2001) describe a section from the early Silurian in Scotland as having an increasing number of and a decrease in size of the strophomenid brachiopod *Eoplectodonta penkillensis*, a synonym of *Katastrophomena penkillensis* (also present on Gotland; Fig. 6A). This decrease in size is interpreted as being a result not of dwarfing or size stunting, but of high juvenile mortality leading to an overrepresentation of juvenile brachiopods in the section. Bassett (1979, p. 188) interprets the small orthids in the Vattenfallet section as "…probably representing immature growth stages." i.e. juveniles.). He also writes that small and/or thin shelled species indicate a low energy deep water environment, as expected from areas of low nutrient and oxygen supply and of areas of fine grained sediment, the second explanation. Small-sized atrypids were favoured in deep water habitats, specifically those belonging to the genera *Zygatrypa, Lissatrypa* and *Glassia*, common to abundant in deep water, offshore, rarer in shallow waters (Copper 1996, 2004). Small-sized brachiopods are also found in the Mackenzie District in Canada (Jin & Chatterton 1997) and the Oslo region in Norway (Baarli 1995), although together with larger species and without any specific comment on size. In conclusion, small-sized, potential Lilliput affected taxa are present in many Silurian brachiopod assemblages globally and clearly manifested in the Lusklint 1 samples. Further detailed research including small-sized taxa is necessary to clarify the dynamics of the Ireviken Event.

## 7. Conclusions

This study has resulted in the following conclusions (see above for details):

• The end ranges for several brachiopods have been specified for the early Ireviken Event on Gotland. *Eoplectodonta transversalis* ends in the interval between datums 3 and 4 and *Leptaena* sp. has a last occurrence in samples below Datum 5. The ranges of *Pentlandina* sp, *Gotatrypa hedei* and *Zygatrypa exigua* are extended into the very basal Upper Visby Formation and assumed to end shortly thereafter as they are not reported from that formation by previous literature. *Costricklandia lirata lirata*, only found in the Lower Visby Formation, is not found above Datum 1, indicating a disappearance at that datum point.
• Brachiopods in the Lusklint 1 samples show distinct Lilliput effects. The majority of specimens in ten out of twelve brachiopod species have shell widths of only a few millimetres.
• Five of twelve species found in the Lusklint 1 samples show Lazarus gaps. *Eoplectodonta transversalis* and *Athyridida* gen. & sp. indet. are missing in the sample from between datums 2 and 3. *Oglupes visbyensis* disappears in the interval between datums 3 and 4. *Katastrophomena penkillensis* and *Sphaerirhynchia* sp. are absent in the samples from the upper Lower Visby Formation but reported as present in the Upper Visby Formation, indicating potential Lazarus taxa.
• The shell sizes and assemblage dynamics of the Lusklint 1 samples indicate a stressed, deep-water environment, consistent with the model of change in oceanic circulation and of decrease in primary production.
• With respect to the combined Lusklint 1 samples and literature, 23 out of 54, i.e. 42% of the brachiopod species have their last occurrence during the early Ireviken Event. With respect to only the Lusklint 1 samples, 50% of the brachiopod species during the early Ireviken Event have their last occurrence in the Lower and Upper Visby formations. The Lusklint 1 samples illustrate the need for fossil assemblages to be based on samples which are large and collected with great stratigraphic detail to avoid contamination and incorrect stratigraphical assignment of specific species. Small-sized brachiopods are likely underrepresented in earlier studies of the Lower and Upper Visby formations and the ranges of brachiopod species can be improved. Accordingly, further studies based on suitable samples are necessary to clarify the brachiopod dynamics during the early Ireviken Event.

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