

The Late Silurian Lau Event and brachiopods from Gotland, Sweden

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The impact of the Ludfordian Lau Primo-Secundo Event on brachiopods from Gotland has been investigated. About 12 000 individuals were identified from five samples. The results are supplemented by an extensive literature study. On Gotland, the Lau Event spans the Botvide Mbr (uppermost När Fm, upper Hemse Group) and the Eke Fm. It caused extinctions, faunal, sedimentary and isotopic changes. Conodonts responded heavily; more than 50% of the taxa became extinct or disappeared and during the later part of the event the conodont fauna became dominated by a single taxon. Brachiopod diversity was not as dramatically affected, but there was a considerable faunal re-organisation. Based on mainly brachiopod frequencies and ranges, the investigated interval have been subdivided into five parts: before and after the event, and early, intermediate and late during the event.

Out of the 63 listed taxa in this study, 42 existed already before the investigated interval. However, only 27 taxa are reported from the När Fm and only 18 from localities containing strata deposited before the onset of the event. Ten of those are for the first time proven to occur in the upper När Fm. During the early part of the event at least five taxa became extinct (e.g. *Jonesea grayi*, *Atrypa* (A.) *sowerbyi*, cf. *Kirkidium knighti*) and five other first appeared (*Ptychopleurella bouchardi*, *Atrypa* (A.) *alata*, *Endrea ekenia*, *Navispira pusilla*, *Boucotinskia sulcata*). More than nine Lazarus taxa are also reported from the early part, the majority known from a wide range of facies. The intermediate part of the Lau Event seems to have allowed for the greatest diversity among brachiopods at Gotland. Out of the 42 pre-event taxa, 31 occur at the upper Lower Eke locality Lau Backar 1, together with six taxa first appearing during the event. By the end of the intermediate part at least seven taxa became extinct (e.g. "*Dinorthis rigida*", *Endrea ekenia*, *Mesopholidostrophia laevigata*, *Janius barrandi*). During the later part of the event no taxa are proven extinct, except for at the Eke-Burgsvik boundary, where lithology as well changed considerably. The majority of the eight disappearing species seems to have been more or less facies dependent and whether they responded to direct event conditions or facies changes is not clear. Only *Atrypa* (A.) *alata*, and possibly *Nucleospira pisum*, are considered extinct due to the changing oceanic conditions. At least 25 of the 42 pre-event taxa survived the event. Among taxa that first appeared during the event, at least two (*Navispira pusilla* and *Boucotinskia sulcata*) also occur in the Burgsvik and Hamra formations. After the event especially the atrypids radiated quickly. Only nine or ten taxa have more or less continuous ranges through the whole event. Nevertheless, several of these probably suffered from adverse conditions. *Isorthis canaliculata*, *Protochonetes striatellus* and *Microsphaeridiorhynchus? nucula* show distinct Lilliput effects, and the pentamerids may also have been affected.

The herein established re-organisation pattern among brachiopods from Gotland is also found in other brachiopod faunas, on Baltica and outside. It is clearly visible in published faunas from Lithuania, Ukraine, Russia, Australia, and to some extent also from Bohemia.

Lastly, the extended ranges of *Ptychopleurella bouchardi*, *Mesopholidostrophia laevigata*, *Strophonella euglypha*, *Endrea ekenia* and *Nucleospira pisum*, as well as the identification of cf. *Kirkidium knighti* at Botvide 1, reflects the importance of large collections.

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Gotlands brachiopoder och det sensiluriska Lau Event

Event är korta tidsintervall som skiljer längre episoder med stabila oceaniska förhållanden från varandra. När cirkulationen i världshaven tillfälligt stängs av under ett event förändras fauna- och bergartssammansättningen, och även isotopförhållandena. Målet med detta arbete har varit att utröna hur de sensiluriska brachiopoderna reagerade på det globalt kända Lau Event. På Gotland omfattar det lagerföljden från Närformationen (övre Hemse-gruppen) till och med Ekeformationen. Eventet är där framför allt känt via studier av en numera utdöd djurgrupp, conodonterna. Dessa reagerade kraftigt på förändringarna och bl. a. zonfossiliet *Polygnathoides siluricus* dog ut tidigt under eventet. Mer än 50% av conodontarterna försvann och under den senare delen av eventet blev en enda art den helt dominerande.

Brachiopoderna påverkades inte på samma dramatiska sätt, även om en omfattande omorganisation skedde även inom den djurgruppen. Av de 63 arter som ingår i studien existerade visserligen 42 redan före det undersökta intervallet, men bara 18 arter har påträffats i avlagringar från tiden precis före början av eventet. Under den tidiga delen av eventet dog minst fem arter ut eller försvann åtminstone från Gotland. Samtidigt tillkom fem nya arter och ett tiotal s.k. Lazarusarter återkom efter att under en period ha varit frånvarande i avlagringarna. Under den mellersta delen av eventet var artmångfalden bland Gotlands brachiopoder som störst. Av de 42 arterna från tiden före eventet har 31 stycken hittats på lokalen Lau Backar 1, överst i undre delen av Ekeformationen. Där finns dessutom sex andra arter som tillkommit under eventet. I slutet av eventets mellersta del försvann minst sju arter. Under eventets senare del har inga utdöenden säkert kunnat fastställas, förutom vid gränsen mellan Eke- och Burgsvikformationerna, där också bergarten förändras radikalt. Huvuddelen av de åtta arter som försvann då ställde förmodligen ganska specifika krav på sin närmaste levnadsmiljö. Därför är det svårt att säga om dessa försvann på grund direkta förändringar beroende på eventet eller pga att bottenförhållandena förändrades. Minst 25 av de 42 tidigare nämnda arterna överlevde Lau Event, liksom minst två av de som tillkom under tiden. Dock förekommer endast nio eller tio arter kontinuerligt under hela tiden, och flera av dessa påverkades förmodligen också av de besvärliga förhållandena. Lilliputeffekter, när medelstorleken hos individerna i en population tillfälligt minskar under en tidsperiod, har säkert kunnat fastställas inom tre arter, och möjligen också inom ytterligare en artgrupp.

Det beskrivna omorganisationsmönstret, som är en reaktion på Lau Event, har också konstaterats hos publicerade brachiopodfaunor från Baltikum, norra Ryssland, Australien och delvis också från Böhmen. Slutligen, sex arter har genom denna studie konstaterats ha betydligt längre utbredning i tiden än vad man tidigare känt till, även om de endast förekommer i litet antal. Detta belyser tydligt betydelsen av att arbeta med stora kollektioner. Slutsatserna i detta arbete bygger på ca 12 000 identifierade individer från fem prover, samt en omfattande litteraturstudie.

Handledare: **Lennart Jeppsson** och **Mikael Calner**

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Front cover photo: *Liothyrella neozelanica* Thomson 1918
It exists today outside the coast of New Zealand, e.g. at c. 20 m of depth in Doubtful Sound.
For information on reproduction, see Chuang 1994. For molecular information, see Cohen *et al.* 1997.
Photo from <http://www.ryanphotographic.com/Brachiopoda.htm>

Detailed knowledge on the Ludfordian Lau Event at Gotland is restricted to extinctions and fauna changes related to conodonts. The objective of this work is to investigate brachiopods for any reactions to the event. About 12 000 individual brachiopods were identified from five samples. The conclusions are supplemented with a literature study.

Potential bias is addressed by reflecting the result of different methods. The new identifications reported herein are based on collections from only few localities. On the other hand, the literature study comprises a high number of localities and the new identifications a high number of specimens. Therefore, both the stratigraphical and the taxonomic resolution are high in this study.

The Lau Event spans part of the upper Hemse Group (När Fm) and the Eke Fm (Fig. 1). The siliciclastic input that forms the succeeding Burgsvik Fm meant substantial changes in the living environment, outside of the oceanic constraints. Consequently the Lower Hamra Fm is also a part of this investigation.

Silurian oceanic cycles and events

Over the past 15 years several Silurian global events affecting sediments, marine water chemistry and organisms have been identified (cf. e.g. Jeppsson 1990, 1998; Munnecke *et al.* 2003). The old assumption of the stable Silurian period, with only few plate tectonic movements, i.e. the Caledonian Orogeny (Bassett 1985) and no substantial faunal overturns (Boucot 1991) is no longer relevant.

Jeppsson (1990, 1998) and Jeppsson & Aldridge (2000) proposed and refined a model for oceanic states and cycles (Fig. 2). In this model there are two stable oceanic conditions. They are called **primo** and **secundo** *episodes* and are separated by short-lived *events*. These are recognisable by faunal changes and extinctions, together with sedimentary and isotopic effects. The faunal changes are stepped and occur at successive *datum points*.

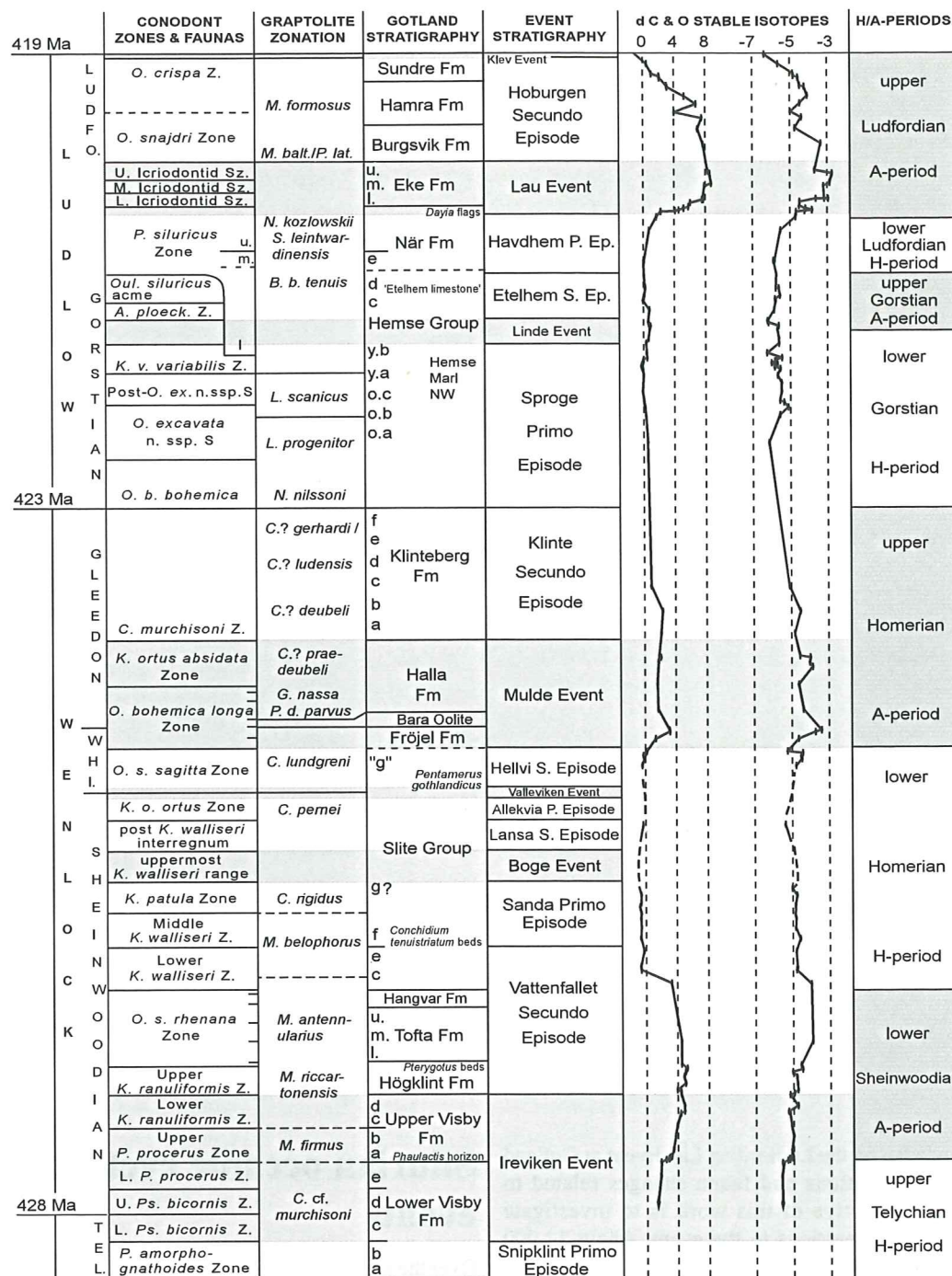


Fig. 1. Summary of bio-, litho- and eventstratigraphy at Gotland, with respect to relative sea-level change and stable isotope evolution. After Calner *et al.* 2004a.

The driving mechanism in this model is the intensity of deep-water formation in the high latitudes. Primo episodes can be characterised by cold, dense water sinking at the high latitudes and upwelling of oxygen-rich deep water at the low latitudes. The climate is generally humid around the equator and cool towards the poles. In Silurian Gotland, primo episodes are linked to marly limestone successions. During secundo episodes the tropics are drier and the source of oceanic deep water is salinity dense surface water at the intermediate to low latitudes.

The high latitudes are then also slightly warmer, reducing the ventilation of the ocean. Upwelling deep water during secundo episodes is less substantial and also less oxygen-rich. This leads to euxinic conditions in the deep sea. In the Silurian Baltic Basin reef belts formed and the platform expanded seawards.

A modified model was put forward by Bickert *et al.* (1997), based on stable carbon and oxygen isotope data (Fig. 2). Primo episodes roughly coincide with the H (Humid) periods and

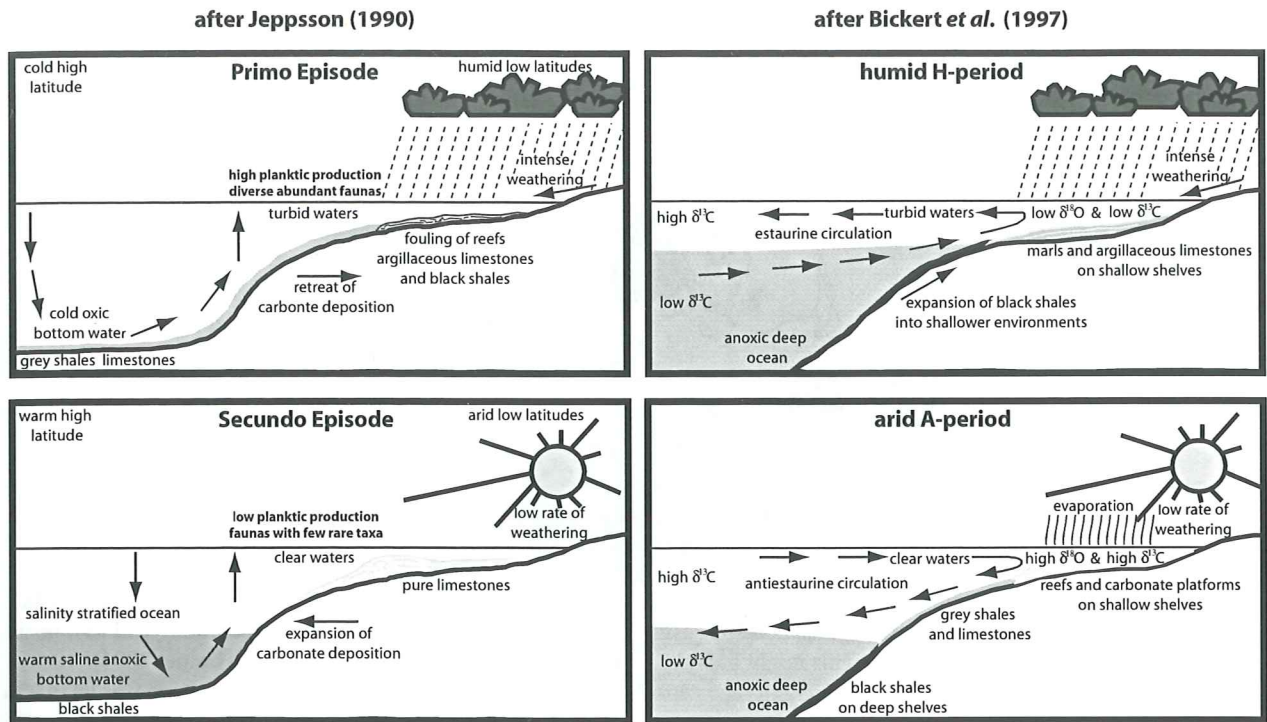


Fig. 2. Oceanic models.

The Jeppsson model to the left, and the Bickert *et al.* model to the right. The latter do not incorporate the low latitudes. After Calner *et al.* 2004.

secundo episodes with the A (Arid) periods of that model. Even so, there is not a complete correspondence and the model does not take into account the high latitudes.

The driving mechanism is precipitation changes, causing shifts between estuarine and anti-estuarine circulation in shallow seas. The basis is the assumption of Silurian permanent anoxic conditions below *c.* 100 m in the tropical ocean (Wilde *et al.* 1999). Photosynthesis preferentially uses the ^{12}C , causing an enrichment of ^{13}C in the surface water, while in the Silurian deep ocean organic carbon was buried in black shales (Samtleben *et al.* 1996; Bickert *et al.* 1997). H-periods are represented by low $\delta^{13}C$ and $\delta^{18}O$ values in the sedimentological record, due to the influx of fresh water and upwelling of ^{12}C -rich deep water. A-periods produces high stable isotope values, connected to the anti-estuarine circulation, i.e. downwelling of saline, oxygen rich, but ^{12}C depleted, surface waters to the deeper shelves (Bickert *et al.* 1997; Samtleben *et al.* 2000).

This stable isotope behaviour is however also in accordance with the Jeppsson model. The evaporation during arid periods would lead to a salinity increase, and hence a stronger ^{18}O fractionation, while in humid times the fresh water input would give a salinity reduction and lower $\delta^{18}O$ values (Calner *et al.* 2004a).

So, generally a primo episode or a Humid period is characterised by high rates of precipitation, weathering, erosion and clay input to the basins, where the waters are agitated and the benthic productivity relatively low, while the planktic and nektonic faunas are diverse and plentiful (Jeppsson 1990, 1998; Jeppsson & Aldridge 2000; Samtleben *et al.* 1996; Bickert *et al.* 1997). During secundo episodes or Arid periods the lower precipitation rates lead to decreased weathering and

clay input, favouring benthic production and reef building, while the planktic and nektonic faunas are impoverished.

There are four potential types of events: primo-primo, primo-secundo, secundo-secundo and secundo-primo. Only the primo-primo type has not yet been found in the geological record (Jeppsson 1998; Calner *et al.* 2004a). During the end of an episode, instability slowly increases as the climate changes due to changing CO_2 -concentrations in the atmosphere. The waters from the two possible deep water sources are then approaching the same density value. Events occur when the vertical circulation ceases as a result of that. The final trigger could be minor disturbances from the Milankovitch cyclicity (Jeppsson 1998).

Faunal extinctions during the Silurian events were stepped, and are interpreted as due to short-term severe drops in primary planktic productivity, causing starvation among planktic larvae (Jeppsson 1990; Jeppsson & Aldridge 2000). The latter comprised geologically brief intervals, probably less than the oceanic mixing time, *c.* 1000 years (Kaljo & Martma 2000), or less (Jeppsson 1998). The whole event perhaps encompassed *c.* 100 000 years (Jeppsson 1998). At Gotland, and elsewhere in the world, three major events has been recognised; the Ireviken Primo-Secundo Event, the Mulde Secundo-Secundo Event and the Lau Primo-Secundo Event (Fig. 1; Jeppsson 1998; Calner *et al.* 2004a).

Comparing the severity of Silurian events is hard, since the conditions before the individual event can be widely differing. If the fauna has already been heavily impoverished, the subsequent event will not be as severe if based on the extinction percentage. Nevertheless, it will still show up as sedimentological changes and often also as isotopical

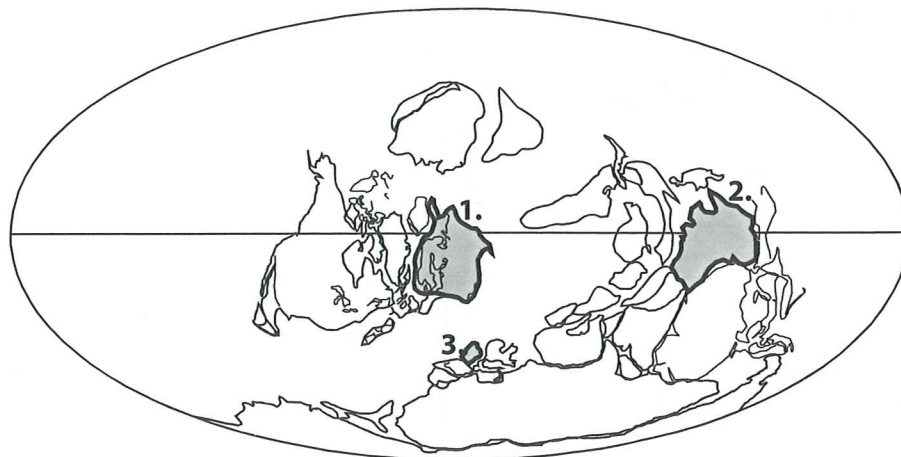


Fig. 3. The Late Silurian World.

Mentioned herein: 1. Baltica, 2. Australia, 3. Bohemia. Modified after McKerrow & Scotese 1990 and Golonka 2002.

excursions (Urbanek 1993; Jeppsson & Calner 2003). In general, transitions from primo to secundo episodes are often the most dramatic (Kaljo & Martma 2000). This might be linked to release of methane (hydrates) when the CO_2 -storage capacity of the oceans are lowered due to the higher temperature of the deep water of secundo episodes (Jeppsson 1998).

Most authors now reject the single parameter explanations for the lithological and isotopical evidence related to events, and argues for co-operative factors (Wenzel & Joachimski 1996; Samtleben *et al.* 2000). To accommodate for the greatest amplitudes of the stable isotope excursions most single factors would give unrealistic effects, e.g. water temperatures exceeding the thermal limits for invertebrates (Wenzel & Joachimski 1996; Samtleben *et al.* 2000). In fact, Kaljo & Martma (2000) argue that there is no unambiguous relationship between the type of episode or event and the $\delta^{13}\text{C}$ record changes; the main reason for each event might be different from the next.

Another well-known explanation is sea-level fluctuations. This scenery is rejected as well. In general, with shifts from primo episodes in the Silurian, the first faunal change occurred before the first increase in the stable isotope ratios and facies change. After this followed a rapid increase in isotope values and a strong facies change, together with a short-term drop in sea level (Jeppsson 1990; Jeppsson & Aldridge 2000; Samtleben *et al.* 2000; Jeppsson & Calner 2003).

The Lau Event

At Gotland, the Lau Primo-Secundo Event starts at the base of the Botvide Mbr (När Fm) and ends at the top of the Eke Fm (Fig. 1; Jeppsson & Aldridge 2000; Calner *et al.* 2004ab). During the event new types of sediments developed and the fauna changed considerably. The zone fossil *Polygnathoides siluricus* became extinct during the early part of the event. No platform-equipped conodont taxa survived, and during the latter part of the event the conodont fauna became strongly dominated by a single taxon (Jeppsson & Aldridge 2000). This was a situation similar to the worst parts of the Ireviken and Mulde events. Several other groups were also affected (see

data in e.g. Martinsson 1962, 1967; Laufeld 1974a). Bioturbation rates were lowered substantially and as a result microbially mediated facies increased (Calner 2005).

The amplitude of the positive $\delta^{13}\text{C}$ excursion was up to 9‰ at Gotland, in the W increasing continuously, but in the E with a jump, created by erosion (Samtleben *et al.* 2000). This excursion, one of the greatest during the entire Phanerozoic, has also been identified in other parts of Europe, in Australia and in America (Calner *et al.* 2004a). The datum points have not yet been pinpointed, but according to Samtleben *et al.* (2000), the first "event" coincides with the initial increase in $\delta^{13}\text{C}$ values, and the second is hidden in the hiatus in the E and associated with the *P. siluricus* extinction. At least three other are located within the Eke Fm (Samtleben *et al.* 2000). It is obvious that they here refer to datum points within the event, even if their source for the statements is obscure.

Geological setting and background

During the Silurian Baltica was located somewhat south of the paleoequator (Fig. 3; Copper & Brunton 1991; Torsvik *et al.* 1996) and Gotland was part of a warm epicontinental sea in the intracratonic Baltic Basin (Bassett & Kaljo 1996). Drillcore data reveals the existence of the late Silurian carbonate sediments between the outcrops in Skåne, Estonia and Podolia (W Ukraine) (Manten 1971; Bassett *et al.* 1989 and references therein). To the SE was a large bay with graptolite-rich shales, continuing beyond to Poland and Denmark (McKerrow & Scotese 1990). The Prague Basin (Bohemia) was part of another, more or less distal micro-plate, located to the S, probably close to cooler water Gondwana (Torsvik *et al.* 1996; McKerrow & Scotese 1990; Golonka 2002; Kriz *et al.* 2003). The water depth at Gotland rarely exceeded 50 m during the entire Silurian (Hede 1960; Samtleben *et al.* 2000).

The strata today dip 0–4° towards the SE and narrow outcrop belts strike SW-NE (Fig. 4; Hede 1960). While uniform sequences of micritic limestones and marls with sparse graptolites are developed in the SW, there are extensive reef

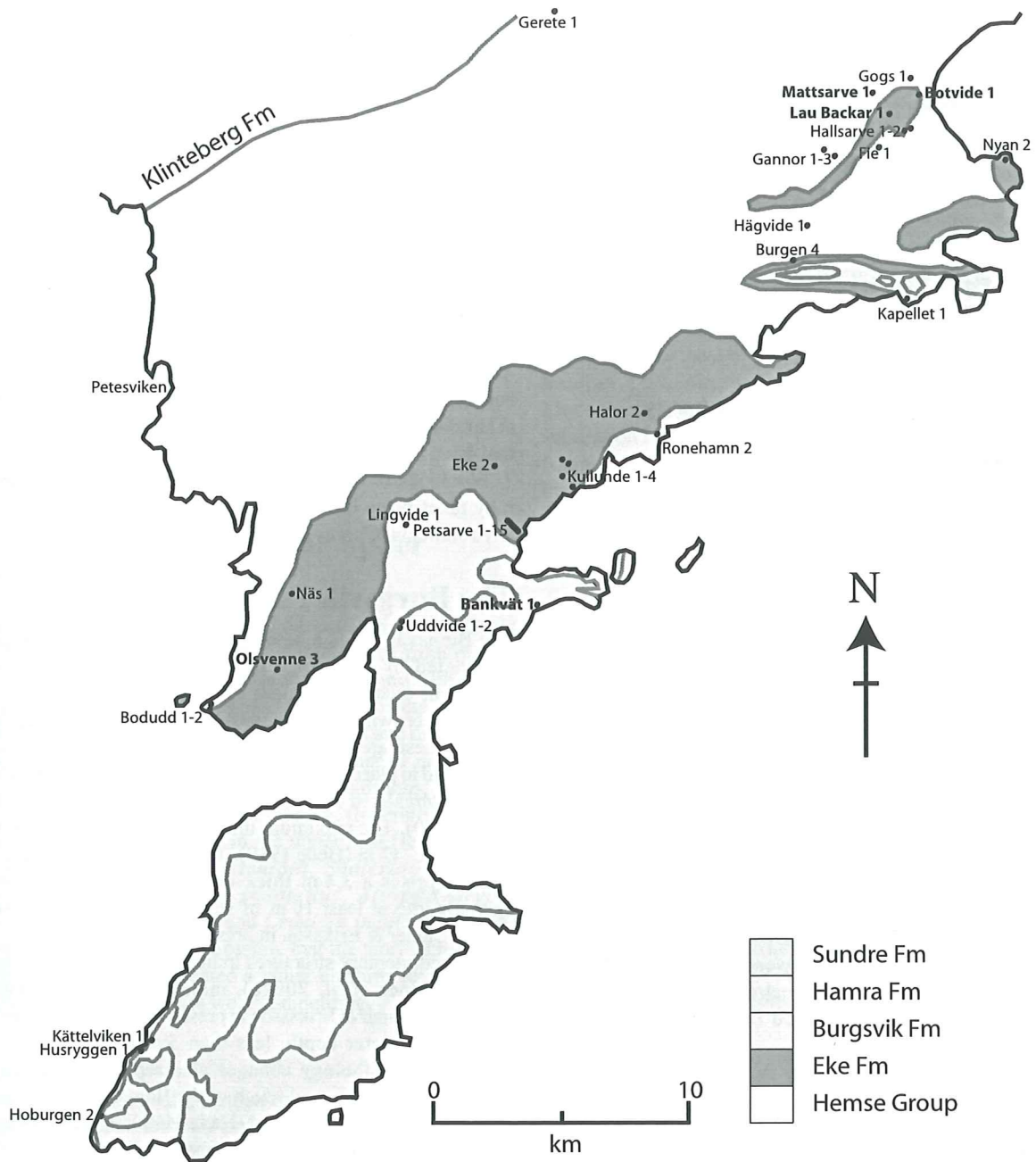


Fig. 4. The topostratigraphical units of southern Gotland and localities mentioned herein. Localities sampled in this study in bold. Modified after Hede 1921, 1925, 1927; Munthe 1921 and Calner *et al.* 2004.

complexes and shallow marine to lagoonal deposits with frequent discontinuities in NE (Hede 1960; Cherns 1982; Samtleben *et al.* 1996). Minor sand- and siltstone occurrences also exist in the succession, e.g. the Burgsvik sandstone discussed herein (Hede 1960; Long 1993). No tectonic or thermal alteration has significantly affected the carbonate platform (Laufeld & Bassett 1981).

The exposed sequence at Gotland has long been estimated to be about 500 m thick (however, see below) and comprises the period from the latest Llandovery to latest Ludlow (Hede 1960; Martinsson 1962, 1967).

The extensive scientific research on Gotland and its brachiopods stems from the days of Linnaeus and continues

forward. Much confusion about the stratigraphy was settled by the 13 topostratigraphic units defined by Hede (1921-1942, 1960). They were based on lithological and palaeontological observations and are still in use. Among others, Laufeld (1974a) furthered this work and Jeppsson (submitted) refines and adds considerable precision to the units and thickness data. He now calculates the Ludlow alone to be 337-425 m instead of the usually given 215 m. Isotopic analyses also generally confirm Hede's results (Samtleben *et al.* 1996).

The more important taxonomic work on brachiopods from Gotland includes Dalman (1828), de Verneuil (1848), Lindström (1860), Bassett and Cocks (1974), Copper (2004) and Hoel (in press, submitted).

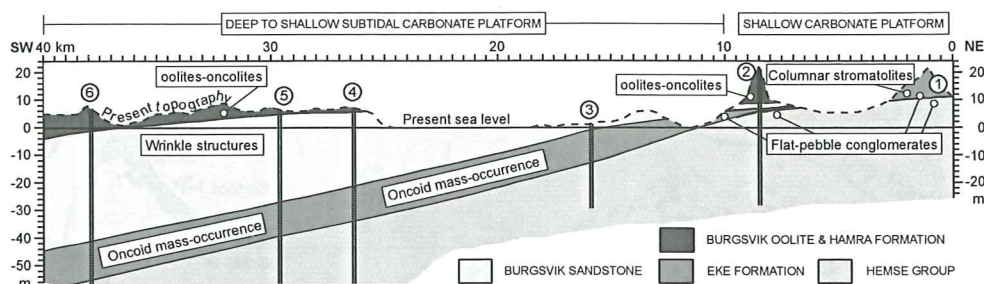


Fig. 5. Transect showing relationships between lithological units discussed herein. Numbers refer to drillcores and a locality: 1 - Botvide 1, 2 - Burgen-1 core, 3 - Ronehamn-1 core, 4 - Grötlingbo-1 core, 5 - Uddvide-1 core, 6 - Burgsvik-1 core. After Calner 2005.

The Late Ludlow strata of Gotland

For stratal relationships, see Fig. 4 and Fig. 5.

The Hemse Group

The Hemse Group is a complex of varying sediment types, in the NE developed as stratified limestones with bioherms and in the S and SW as marlstone and argillaceous limestone (Hede 1960). The Hemse Marl can be divided into an older and a younger part (Hede 1960). The latter (När Fm) is at least 65 m thick (Jeppsson submitted).

The När Fm can be subdivided into three biostratigraphical subunits, the Lower, Main and Upper *Polygnathoides siluricus* Subzones. The latter has the same boundaries as the Botvide Mbr (Jeppsson submitted).

The Botvide Mbr is c. 2.15 m thick at Botvide 1, the reference locality (Jeppsson submitted). The upper part of the Botvide Mbr has been called the "Dayia flags" (Munthe 1902, 1910). It stands out as a more weathering resistant strata, estimated to be only some decimetres thick, dolomitic, and rich in coquinas of the brachiopod *Dayia navicula* (Munthe 1902, 1910; Hede 1925b).

The Eke Fm

The Eke Fm generally consists of bluish grey, almost unstratified, somewhat sandy and micaceous marlstone, alternating with more calcareous and harder strata, the latter increasing towards the NE (Munthe 1910; Hede 1921, 1960). The Eke Fm is estimated to be 10-15 m thick (Hede 1921, 1925b), thinning toward the NE (Laufeld 1974a).

In the E the Hemse-Eke boundary is a submarine discontinuity surface (Munthe 1902; Spjeldnes 1950; Cherns 1982, 1983). Together with the conglomeratic basal Eke it marks a break in deposition (Cherns 1982) and an abrupt change in lithology, into the basal Eke crinoidal oncoloidal limestone (Munthe 1902; Hede 1921). The conglomeratic clasts have an origin in the Hemse Marl. The submarine discontinuity surface and the conglomerate is also present in the Burgen outlier (Calner & Eriksson in press), but distally in the SW, the conglomerate is missing and the change in lithology is more gradual (Jeppsson *et al.* submitted), as is the macroscopic faunal change according to Cherns (1982, 1983). Jeppsson (submitted) has divided the Botvide Mbr into faunal intervals based on

conodonts. According to him it is only a few decimetres missing at Botvide 1, when compared to the probably continuous Bodudd 1.

Formation of oncolites requires agitated waters, and generally takes place in the photic zone of very shallow subtidal environments (Cherns 1983).

The Burgsvik Fm

The Burgsvik Fm is a heterogeneous sedimentary complex, dominated by more or less calcareous, argillaceous and micaceous quartz sandstones of blue grey (unweathered), or yellow to brownish (weathered) colour (Munthe 1921; Hede 1921). These are intercalated with thin marl- and claystone layers, and in places overlain by a thin sheet of oolitic limestone, or has intercalated oolitic limestone near the top (Hede 1919, 1921, 1960). The maximum thickness of the Burgsvik Fm in the SW is c. 47 m (Hede 1919). The Burgen-1 drillcore in the NE comprises a 3.4 m thick clastic-rich interval, passing upwards into at least 10 m of shoal and reef complex sediments (Calner & Eriksson in press).

The sedimentary structures indicate periods of rapid deposition (Calner *et al.* 2004a), mainly below fair-weather wavebase (Calner & Eriksson in press). The oolite could reflect a minimum water depth, less than 5 m (Long 1993). The Burgsvik Fm lithology changes also represent a changing environment for life, and much of the flora and fauna known from the Eke Fm disappeared (Hede 1921); some to reappear in younger beds and others to be lost forever.

The Hamra Fm

The Hamra Fm is another complex of lithologically relatively heterogeneous units. However, they do not adequately reflect age relationships, but rather different environments (Munthe 1921; Jeppsson submitted). Recent investigations point to a maximum thickness for the Hamra, together with the succeeding Sundre Fm, of somewhere between 88 and 124 m (Jeppsson submitted).

The lowermost Hamra strata often consists of more or less oncolitic, argillaceous limestone, rich in "*Sphaerocodium* algae" or of argillaceous, very fossil rich, biohermal limestone (Munthe 1921; Hede 1921). Distally it is followed by the "typical" Hamra limestone, which is dense, somewhat argillaceous, blue grey to dark grey (unweathered) to brownish (weathered) and occasionally somewhat bituminous (Munthe 1921; Hede 1921).

Living environment and facies

Generally at Gotland, the rich shelly faunas in the reefs are coral-stromatoporoid assemblages, but in interreef limestone and in marl facies most of the preserved level-bottom shelly assemblages are dominated by brachiopods (Cherns & Wright 2000; Brennan & Lowenstein 2002).

A few brachiopod species are reported only from specific environments. *Endrea ekenia* locally thrived in the crinoidal NE facies around Lau, while *Atrypa (Atrypa) alata* mainly lived in the SW, often almost fully overgrown with algae, nevertheless still functioning (Copper 2004). Others seem to have been less facies dependent and occur more or less abundantly through the whole Lau Event, e.g. *Isorthis canaliculata*.

Samtleben *et al.* (2000) investigated facies complexes at Gotland as part of their isotopic studies. Their results are applied to the identified localities used in this study (Table 1).

The environments of the upper Hemse Group

Samtleben *et al.* (2000) describes the distal shelf with *Dayia* in the W upper Hemse Group as virtually free from preserved macroscopic life, with few fossils and almost no reworking observed. The opposite is said for the proximal shelf in the E, where the faunas are very rich and diverse, and the sediments intensely bioturbated. Calner *et al.* (2004a) discusses unfavourable bottom water conditions, based on the generally sparse fauna in the När Fm. Generally, the most common brachiopod fauna in the uppermost Hemse Group consists of *Isorthis canaliculata*, *Shaleria (Shaleria) ornatella*, *Protochonetes striatellus*, *Atrypa (Atrypa) sowerbyi*, *Dayia navicula*, and *Craniops implicata* (Cherns 1983; Copper 2004). It is possible that the marl facies of the upper Hemse Group created a rather uniform environment, where only a few species were competitive.

There are complementary explanations. Taxa that had disappeared from Gotland earlier are found in beds of equal age or younger in the E Baltic, e.g. *Atrypoidea prunum* (Männil & Rubel 1999; Copper 2004). That is, if the stratigraphical correlations are right (see "Lithuania", p. 25, "Podolia", p. 26). The pattern at Gotland might however also be a case of gaps in the scientific record, since the När Fm mainly crops out as inconspicuous ditch sections. So, even if the total number of species reported from the entire Hemse Group exceed the number from the Eke Fm, the greater part has been found at localities in the lower parts of the group (Hede 1921, 1925b, 1927, 1960).

Besides the brachiopod taxa described in this study, seven additional taxa have been reported from upper Hemse Group localities containing strata deposited after the late Gorstian Linde Event (Fig. 1), but still before the younger parts of the succession investigated in this study. Several of the localities comprising older strata represent environments with a relatively high amount of carbonate. Hence, it is possible that some of these species in reality have extended ranges outside Gotland and that their final demise is connected to the Lau Event. *Morinorhynchus crispus* has a similar range and will be further discussed below, as will *Kirkidium knighti* (Sowerby 1839).

Coquinas of *Dayia navicula* are common throughout the När Fm, and are often interbedded with coquinas of *Shaleria (Shaleria) ornatella* (Munthe 1921; Hede 1925b; Cherns 1983). In general, at least *D. navicula* could probably sustain rather low-level oxygen rates, as well as higher turbulence and clastic input (Musteikis & Paškevičius 1999; Pushkin & Modzalevskaya 1999). *S. (S.) ornatella* is widespread in all facies in Lithuanian strata from the Ludfordian and Pridoli (Musteikis & Cocks 2004) and occurs in the Ludfordian Wales and the Welsh Borderland area, as well as in Polish strata from Pridoli (Cherns 1999b; Lawson 1999bc; Teller & Boucot 1999). It is considered to be adapted to increased sedimentation and rather high turbulence (Cherns 1999b; Lawson 1999bc; Teller & Boucot 1999). Cherns (1983) argues that these species were opportunistic and flourished intermittently.

Table 1. Environmental development according to Samtleben *et al.* (2000), applied to identified localities used herein and in their order of appearance in App. 1. "Locality correlation". *Tentative correlation from fig. 2 in Samtleben *et al.* (2000). # Observation by the present author. Localities sampled herein in bold.

	Locality	Environment		Locality	Environment
A	Gogs 1	*Proximal shelf	M	Kullunde 3-4	Proximal shelf w. oncolites
	Mattsarve 1	*Proximal shelf		Lingvide 1	*Proximal shelf w. oncolites
B	Hallsarve 2	*Proximal shelf		Eke 2	*Proximal shelf w. oncolites
	Fie 1	*Proximal shelf	N	Bodudd 2	Proximal shelf w. oncolites
C	Gannor 3	Proximal shelf		Kullunde 2	Proximal shelf w. oncolites
D	Botvide 1	Prox. shelf w. <i>Dayia</i>		Petsarve 1-15	Proximal shelf w. oncolites
	Nyan 2	Prox. shelf w. <i>Dayia</i>		Olsvenne 3	*Proximal shelf #w. oncolites
	Hägvide 1	*Proximal shelf	O	Ronehamn 2	Proximal shelf w. oncolites
E	Gannor 1	*Proximal shelf	P	Kapellet 1	*Shoals
	Hallsarve 1	*Proximal shelf	Q	Uddvide 1	*Back reef area
J	Bodudd 1	Distal shelf w. <i>Dayia</i>		Uddvide 2	Back reef area
	Burgen 4	*Proximal shelf		Hoburgen 2	*Fore shore sandstones./reef
	Näs 1	Proximal shelf w. oncolites		Kätteviken 1	*Fore shore sandstones/reef
K	Lau Backar 1	Reef complex	R	Husryggen 1	*Fore shore sandstones/reef
L	Halor 2	*Proximal shelf w. oncolites		Bankvät 1	*Back reef area

Table 2. Quantitative study sample details.

Sample id.	Locality	Bulk weight (g)	Residue weight (g)	Brachiopod weight (g)	Brachiopods (st)
G03-007LG	Mattsarve 1	47 140	410	30	284
G03-019LG	Botvide 1	34 190	11 630	40	1166
G03-004LG	Lau Backar 1	34 080	11 020	455	4375
G03-017LG	Olsvenne 3	42 530	21 980	100	3670
G03-374LJ	Bankvät 1	5020	1020	70	2876

Part I – Quantitative data

Material and methods

During the fieldwork, five samples were collected from marly beds at the localities Mattsarve 1, Botvide 1, Lau Backar 1, Olsvenne 3 and Bankvät 1; for details see Table 2 and App. 2 "Locality data". When sampling, only the washable material was collected, if possible. All field measurements were conducted using a ruler, and a levelling instrument. The samples were treated with sodium carbonate and washed through a 1 mm sieve under flowing water. For possible bias, see App. 2 "Locality data, Washed sample description".

The obtained fossils were identified under a light microscope. Selected specimens were photographed with a

digital camera and the pictures were adapted in Adobe PhotoShop Elements and CombineZ4. The data is presented in Table 3, Fig. 6 and Fig. 7.

Every still articulated specimen was counted as one individual. The number of either the ventral or dorsal non-articulated valves, depending on which was in majority for each taxa, was added. In the case of broken strophic shells, only left halves (when seen from the ventral side), were counted. The number of *Craniops* was received by dividing all the identified shells by 2. The reported Spiriferid indet. sp. C from Mattsarve 1 comprises only ventral valves. At Lau Backar 1, about 150 fragments of smooth brachiopods, probably either *Nucleospira pisum* or *Dayia navicula* or both, were not possible to identify to species or even as parts of dorsal/ventral valves. For further possible bias, see App. 3 "Selected taxonomic remarks".

Table 3. Frequencies and ranges of brachiopods identified in the quantitative study.

% - amount of that taxon in sample. For Lau Backar 1 & Olsvenne 3 only 1/6 of 1-2 mm fraction was picked, and number of counted specimens is given first, calculated number for whole 1-2 mm fraction second, e.g. 77/462.

Taxon	Size	Mattsarve 1		Botvide 1		Lau Backar 1		Olsvenne 3		Bankvät 1		Sum of taxon	
		(st)	(%)	(st)	(%)	(st)	(%)	(st)	(%)	(st)	(%)		
<i>Jonesea grayi</i>	1-2 mm	188	67									188	
	2-4 mm	2										2	190
<i>Atrypa (A.) sowerbyi</i>	4-8 mm	4	4									4	
	>8 mm	7										7	11
Atrypid indet. sp. F	1-2 mm	4										4	
	2-4 mm	7	4									7	
	4-8 mm	1										1	12
Spiriferid indet. sp. C	4-8 mm	5	2									5	5
<i>Morinorhynchus?</i> sp. A	2-4 mm			1	-							1	1
cf. <i>Kirkidium knighti</i>	2-4 mm			8	1							8	
	4-8 mm			1								1	9
Strophomenid indet. sp. G	4-8 mm			1	-							1	1
<i>Dayia navicula</i>	1-2 mm	19		96		77/462						192	
	2-4 mm	28	18	704	73	399	15					1131	
	4-8 mm	5		55		168						228	1551
<i>Ptychopleurella bouchardi</i>	1-2 mm					1/6						1	
	2-4 mm			3	-		-					3	
	4-8 mm					3						3	7
<i>M. laevigata</i>	1-2 mm			5	-	15/90	-					20	
	2-4 mm			1								1	21
<i>Lepidoleptaena poulsoni</i>	4-8 mm				-	6	-					6	
	>8 mm			3		3						6	12
<i>Strophonella euglyphia</i>	1-2 mm					176/1056						176	
	2-4 mm			1	-	162	8					163	
	4-8 mm					4						4	
	>8 mm					2						2	345

Taxon	Size	Mattsarve 1		Botvide 1		Lau Backar 1		Olsvenne 3		Bankvät 1		Sum of taxon	
		(st)	(%)	(st)	(%)	(st)	(%)	(st)	(%)	(st)	(%)		
<i>Endrea ekenia</i>	1-2 mm			4		9/54						13	
	2-4 mm			9	1	33	3					42	
	4-8 mm			3		64						67	
	>8 mm					43						43	165
<i>Hesperorthis gotlandica</i>	1-2 mm					1/6	-					1	
	2-4 mm					2						2	3
"Dinorthis rigida"	1-2 mm					1/6	-					1	
	2-4 mm					1						1	2
Orthid indet. sp. K	2-4 mm					1	-					1	1
<i>Leptostrophia filosa</i>	1-2 mm					141/846						141	
	2-4 mm					183	8					183	
	4-8 mm					5						5	329
<i>Sphaerirhynchia wilsoni</i>	2-4 mm					7	-					7	
	4-8 mm					35						35	42
cf. <i>Glassina laeviscula</i>	1-2 mm					1/6						1	
	2-4 mm					21	-					21	
	4-8 mm					1						1	23
<i>Janius barrandi</i>	1-2 mm					2/12						2	
	2-4 mm					5	-					5	
	4-8 mm					4						4	
	>8 mm					5						5	16
<i>Striispirifer</i> sp. L	1-2 mm					6/36	-					6	
	2-4 mm					5						5	11
<i>Delthyris elevata</i>	2-4 mm					3	-					3	
	4-8 mm					5						5	8
Atrypid indet. sp. D	2-4 mm							21	-			21	21
Atrypid indet. sp. E	1-2 mm							14/84				14	
	2-4 mm							168	6			168	
	4-8 mm							33				33	215
<i>S. (S.) hoburgensis</i>	2-4 mm									5	-	5	5
<i>Craniops implicata</i>	1-2 mm	3	1	7	1	4/24	-	163/978	8	93	3	270	
	2-4 mm	1				10		122				133	403
<i>Microsphaeridio-rhynchia? nucula</i>	1-2 mm			2		54/324		189/1134		1461		1706	
	2-4 mm	2	1		-	83	7	247	12	1117	93	1449	
	4-8 mm					154		11		101		266	3421
<i>Protochonetes striatellus</i>	1-2 mm			5				1/6				6	
	2-4 mm	1	-	13	2	6	-	1	-			21	
	4-8 mm			1		5						6	33
<i>Isorthis canaliculata</i>	1-2 mm	3		78		35/210		376/2256				492	
	2-4 mm	1	1	122	19	69	3	642	29			834	
	4-8 mm			21		18		40				79	1405
<i>Shaleria (S.) ornatella</i>	1-2 mm			6		21/126		140/840				167	
	2-4 mm	1	-	7	1	35	1	327	13			370	
	4-8 mm					5		18				23	
	>8 mm					2						2	562
<i>Howellella elegans</i>	1-2 mm			2		106/636		124/744				232	
	2-4 mm	2	1	5	1	400	16	37	5			444	
	4-8 mm			1		174		22				197	873
<i>Nucleospira pisum</i>	1-2 mm			1		177/1062		95/570		1?		274	
	2-4 mm				-	390	15	344	12		-	734	
	4-8 mm					110		8				118	1126
<i>Morinorhynchus? sp. B</i>	1-2 mm					3/18	-	8/48	-			11	
	2-4 mm					2		8				10	21
<i>Homeospira baylei</i>	1-2 mm					36/216		11/66				47	
	2-4 mm					263	13	62	2			325	
	4-8 mm					259		3				262	634
<i>Gypidula galeata</i>	1-2 mm					166/996	8	393/2358	12	87	3	646	
	2-4 mm					188		42		11		241	887
Sum of individuals at locality:		284		1166		4375		3670		2876		Total sum:	12 371

Results of the quantitative study

The observed ranges are presented in Table 3 and compared to literature data in Fig. 7. Selected photographed taxa in Fig. 6.

Before the event and the earliest part of the event – the upper Hemse Group

Jonesea grayi, *Atrypa (Atrypa) sowerbyi*, Atrypid indet. sp. F and Spiriferid indet. sp. C were restricted to Mattsarve 1 and do not occur further up in the succession. One shell of *J. grayi* was found in the Botvide 1 material, most probably due to contamination. This is indicated by the fact that the species is tiny, with delicate low-weight shells. Moreover, both colour of the specimen and texture of the adhering matrix closely resemble the Mattsarve 1 material. The Botvide 1 material on the other hand has a very typical patina due to the dolomitisation of strata.

Botvide 1 exhibits the only occurrence of Strophomenid indet. sp. G and cf. *Kirkidium knighti*. Other taxa encountered for the first time at Botvide 1 are *Ptychopleurella bouchardi*, *Mesopholidostrophia laevigata*, *Strophonella euglypha*, *Lepidoleptaena poulsenii* and *Andrea ekenia*. Further, one small specimen of *Nucleospira pisum* was found, as well as one specimen of *Morinorhynchus?* sp. A. Neither of these taxa constitutes more than 1% of the brachiopod fauna at the locality. The same is true for Strophomenid indet. sp. G, that was only found at Botvide 1.

J. grayi comprises c. 67% of the brachiopod individuals at Mattsarve 1, and *Dayia navicula* c. 18%. At Botvide 1 *D. navicula* dominates (c. 73%), together with *Isorthis canaliculata* (c. 19%).

The intermediate and later part of the event – the Eke Fm

In this study, *Hesperorthis gotlandica*, "*Dinorthis rigida*", Orthid indet. sp. K, *Leptostrophia filosa*, *Sphaerirhynchia wilsoni*, cf. *Glassina laeviscula*, *Janius barrandi*, Striispirifer sp. L, *Delthyris elevata*, *Morinorhynchus?* sp. B, *Homeospira baylei* and *Gypidula galeata* have their first appearances at the lower Eke locality Lau Backar 1. *Nucleospira pisum* occurs for the first time in greater numbers. The first eight mentioned taxa are only identified at Lau Backar 1. Last occurrences at Lau Backar 1 is otherwise connected to *P. bouchardi*, *M. laevigata*, *L. poulsenii*, *S. euglypha*, *E. ekenia*, *D. navicula* and *J. barrandi*.

Contrary to the situation at the other localities investigated in the quantitative study, no individual species dominates the Lau Backar 1 brachiopod fauna. Nevertheless, *H. baylei*, *D. navicula*, *Howellella elegans* and *N. pisum* between them comprise c. 60% (c. 13-16% each) of the present individuals at Lau Backar 1. For a comparison with the only other quantitative investigation found in the literature, see below: "Discussion, Lau Backar 1 – a quantitative studies comparison", p. 21 and Table 4.

Atrypid indet. sp. E and Atrypid indet. sp. D are only found at the middle/upper Eke locality Olsvenne 3, where probably also *N. pisum* have its last appearance. Other taxa with seemingly last appearances there are *I. canaliculata*, *S. (S.) ornatella*, *Morinorhynchus?* sp. B, *P. striatellus*,

H. baylei and *H. elegans*. At Olsvenne 3 *I. canaliculata* dominates (c. 29% of the brachiopod fauna).

After the event – the Hamra Fm

After the completion of this study, it was clear that the Bankvät 1 sample is probably not representative for the lower Hamra Fm known from the literature. From Bankvät 1, supposedly representing post-event strata, only five species were recovered (Table 3). Two of them, *Microsphaeridiorhynchus? nucula* and *Craniops implicata* are present at all the studied localities and *Gypidula galeata* at two other localities. *Strophodonta (Strophodonta) hoburgensis* (Hoel submitted) is only present at Bankvät 1. The fifth species is smooth and globose and is only represented by one tiny individual, slightly resembling a juvenile *N. pisum*. Over 90% of the individual brachiopod shells recovered at Bankvät 1 are referable to *M.? nucula*.

Relative frequency

Most taxa occurring early during the event at Botvide 1, as well as later at Lau Backar 1, are present with a higher relative amount of shells at Lau Backar 1. Only *D. navicula*, *I. canaliculata* (and *P. striatellus*) have a higher relative frequency at Botvide 1. The number of species is also higher at Lau Backar 1 than at Botvide 1. When comparing Lau Backar 1 with Olsvenne 3, the latter representing the later part of the event, the number of species in common are lower and the result is more varied. *I. canaliculata* and *S. (S.) ornatella* clearly have a higher relative frequency at Olsvenne 3, while *H. baylei* and *H. elegans* is clearly relatively more common in the Lau Backar 1 brachiopod fauna. The frequency of *M.? nucula* is somewhat higher at Olsvenne 3 than at Lau Backar 1, and it totally dominates the fauna at the post-event locality Bankvät 1.

Some taxa occur only in small numbers, even though they are present at more than one locality. *P. bouchardi*, *M. laevigata*, *L. poulsenii* and *Morinorhynchus?* sp. B each constitutes less than 1% of the brachiopod fauna at any locality.

Size distribution and articulation

The size distribution within certain species at different localities is interesting. At Botvide 1 c. 36% of all *I. canaliculata* identified belong to the smallest fraction, 1-2 mm, while at Lau Backar 1, that fraction incorporates c. 70% and at Olsvenne 3 c. 77% of the *I. canaliculata* individuals, respectively. At Lau Backar 1 c. 58% of the identified *M.? nucula* belongs to the size fraction 1-2 mm, and c. 27% to the 4-8 mm fraction. At Olsvenne 3 c. 81% belongs to the smallest fraction and less than 1% to the coarser.

The amount of still articulated specimens is much higher at both Lau Backar 1 and Olsvenne 3, than at the Hemse Group localities. This former notion is true also for Bankvät 1.

Long-ranging species

M.? nucula and *C. implicata* are present in all samples. *I. canaliculata*, *S. (S.) ornatella*, *P. striatellus* and *H. elegans* are other long-ranging species, however not occurring at Bankvät 1.

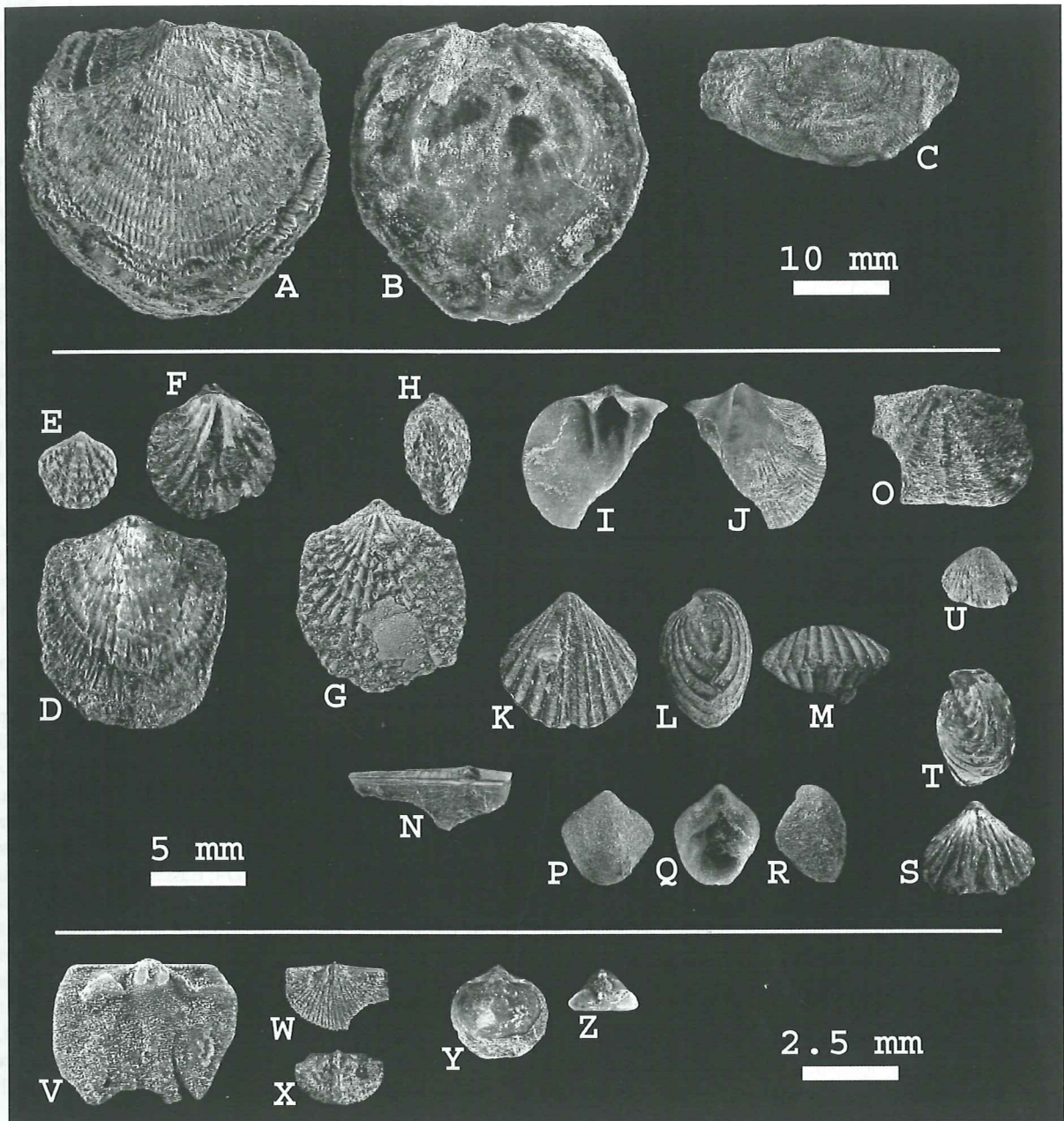


Fig. 6. Selected photographed taxa.

A-B. *Atrypa* (A.) *sowerbyi*, Mattsarve 1, dorsal valve. C. *Lepidoleptaena poulsenii*, Lau Backar 1, ventral v. D-F. *Endrea ekenia*, D-E Lau Backar 1, ventral v., F Botvide 1, dorsal v. G-H. Atrypid sp. E, Olsvenne 3, G dorsal v., H side view. I-J. *Isorthis canaliculata*, Botvide 1, ventral v. K-M. *Homeospira baylei*, Lau Backar 1, K ventral v., L side view, M - commissure. N. *Strophodonta* (S.) *hoburgensis*, Bankvät 1, hinge line. O. *Ptychopleurella bouchardi*, Lau Backar 1, ventral v. P-R. *Dayia navicula*, ventral v. P, R Lau Backar 1, Q Botvide 1. S-T. *Microsphaeridiorhynchus? nucula*, Bankvät 1, S dorsal v., T side view. U. *Kirkidium knighti*, Botvide 1, ventral v. V. *Mesopholidostrophia laevigata*, Botvide 1, dorsal v. W-X. *Jonesea grayi*, Mattsarve 1, W ventral v., X dorsal v. Y-Z. *Gypidula galeata*, Bankvät 1, Y dorsal v., Z hinge line.

Part II – Literature data

Nomenclature and taxonomy

Taxonomy and nomenclature have changed one or more times since the first paper included herein (Lindström 1860). A synonym table (App. 4 "A selection of...") was therefore constructed to bring the disparate observations together within a modern nomenclature. The main frame is according to Bassett & Cocks (1974) and Cocks (1978), while Copper (2004) and Hoel (in press, submitted) is followed concerning the atrypids and the leptaenids, respectively. Davidson (1866-1871, 1882-1883) still has the best drawings and was probably used as a standard on Silurian brachiopods for a long time. A few taxa could not be determined to belong to any of the taxa described in the modern monographs, and remain in this work under their original names. They are given as e.g. "*Lingula Lewisi*". The locality information recovered from the literature was reinterpreted to meet the requirements of the modern understandings of relations within and between rock units, as well as their ages. The stratigraphic placement (App. 1 "Locality correlation") mainly follows Jeppsson (submitted), Jeppsson & Jerre (ms) and Laufeld (1974a), in that order. That means that most of the datings are conodont based.

Copper (2004) revised the story on atrypids completely and earlier observations must now be considered obsolete, especially if only the literature is consulted. Misidentifications and recent taxonomic splitting make it impossible for the reader to know what taxa are really intended. For example, *Atrypina barrandei*, previously frequently reported from the Burgsvik and the Hamra Fm, are by Copper considered to only reach the lower Klinteberg Fm. The species intended by earlier writers is probably *Atrypina cf. gallina*. The catch-all taxon *Atrypa reticularis* was earlier considered to be very long-lived, but *Atrypa reticularis sensu stricto* is actually restricted to a short interval well before the Lau Event. All the old atrypid designations are included in App. 5 "Original literature data", while only Coppers data are used for conclusions. An exception is the older records of *Spirigerina quinquecostata*, since that species has a very special appearance (Copper 2004), distinct from other atrypids.

Bassett & Cocks (1974) pointed out that there are several forms of *Leptaena* on Gotland, and although describing three species, none of them were reported from the here studied interval. Hoel (in press), working mostly with museum collections, recently concluded that only one leptaenid species exists in the upper part of the Gotlandic succession, *Lepidoleptaena poulsoni*. All observations of leptaenids made by other writers are therefore in Fig. 7 treated as that single species *L. poulsoni*. According to Hoel (in press) it ranges from the upper Hemse Group to the Sunde Fm, except for the Burgsvik Fm. Other writers report leptaenids also from the Burgsvik Fm.

The number of cited localities are lower for the atrypids and the leptaenid, hence their ranges are less well constrained than those of the other taxa; especially so that of *L. poulsoni*. Another taxon reported only from a few localities is *Shaleria* (*Shaleriella*) *ezerensis* (Rybnikova 1966) (cf. Musteikis & Cocks 2004). Harper and Boucot (1978b) gives it (as "*Shaleriella delicata*") the range Wenlock to late Ludlow, including the upper Hemse and the Eke Marls. Hoel (submitted) reports its existence in the upper Burgsvik Fm as well.

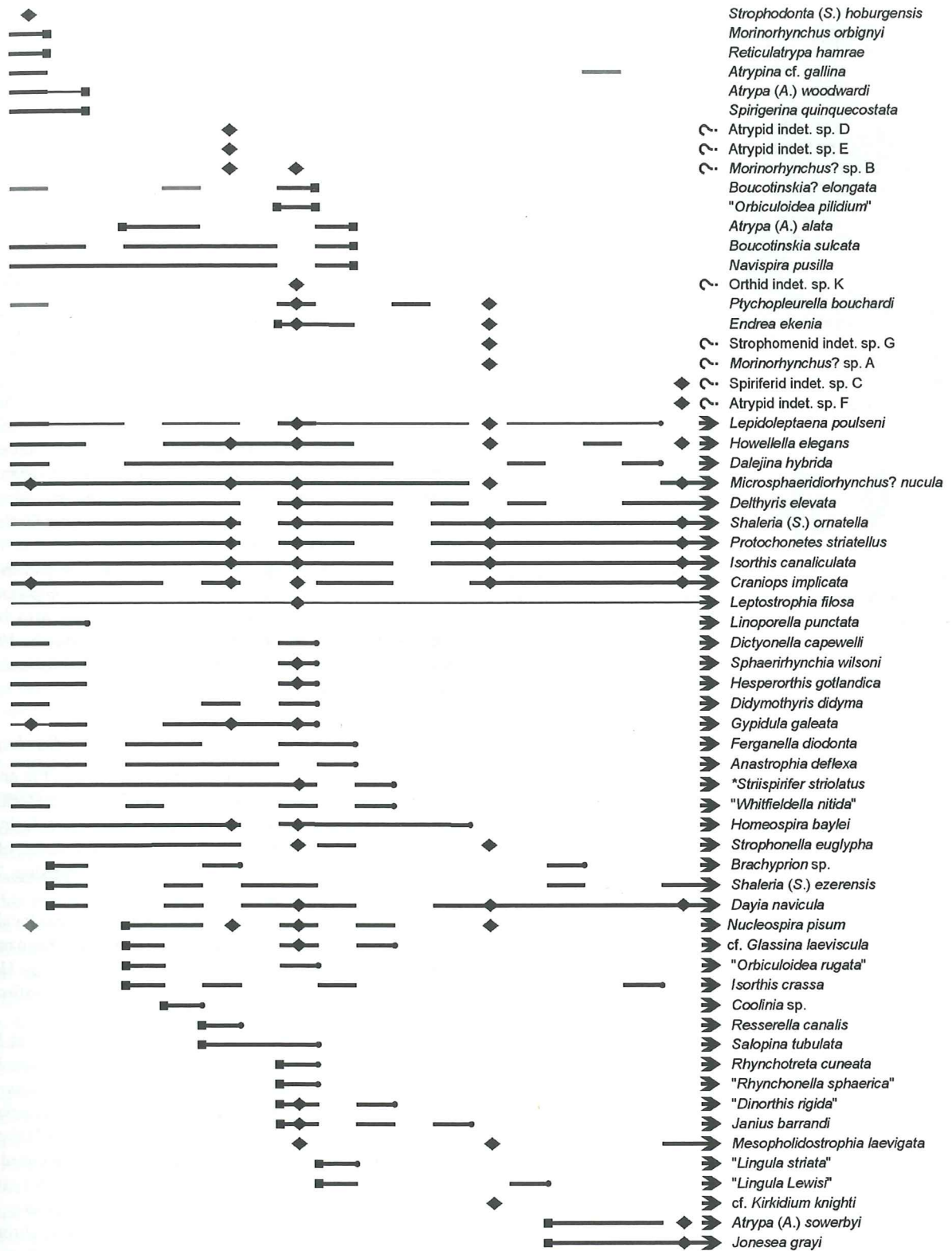
Microsphaeridiorhynchus? nucula and *Rhynchotrete cuneata* might in reality be species groups and are like *Brachyprion* sp., *Whitfieldella* sp. and *Howellella elegans* in need of a revision, according to Bassett & Cocks (1974). The same authors also notes that the pentamerid *Gypidula galeata* has a slightly different appearance in the Eke Fm, when compared to the Hemse Group specimens. Talent *et al.* (1993) described the probable Lau Event as affecting the pentamerids especially. It can not be excluded that the *G. galeata*-record from Gotland does not comprise an evolutionary succession between morphologically only slightly differing populations. The genus *Striispirifer* needs further research since neither nomenclature nor ranges are in concert between writers. Generally, when it comes to identifying every synonym, the lists for *Jonesea grayi*, *Didymothyris didyma*, "*Whitfieldella nitida*" and *Boucotinskia? elongata* are less secure. Especially the connection between *Boucotinskia? elongata* and the synonyms "*Spirifera Schmidtii* var. *elongata*" and "*Spirifera sulcata* var. *elongata*", used by Munthe (1902, 1910) are weak.

Some examples of probable misidentifications are also present in the material, and a few taxa are omitted from Fig. 7. Even so, these reports are still possible to extract from App. 5 "Original literature data" in combination with App. 1 "Locality correlation". *Protochonetes minimus* (as "*Chonetes* cfr. *minima*") was reported by Munthe (1910) from the uppermost Hemse Group (*Dayia* flags) and from unspecified Eke strata. By others it is not considered to have even reached the lower Hemse beds (Bassett & Cocks 1974; Bassett 1977), even though Hurst (1975) claims its existence at the locality Gerete 1, high up in the Hemse Marl NW. Munthe could possibly have confused the observations in the *Dayia* flags with *Jonesea grayi* (cf. Bassett & Cocks 1974; Cocks 1978). Moreover, the same author also claims the existence of *P. minimus* in the "*Sphaerocodium* Marl", i.e. in the Eke Fm (Munthe 1910, p. 1420) and that is harder to explain. The report of *J. grayi* from Late Ludfordian Lithuania (Musteikis & Cocks 2004) will be further discussed below (see "Lithuania", p. 25).

Further possible misidentifications; Cherns (1983) reported *Ancillotoechia bidenta* from the middle/upper Eke Fm, but this could possibly be an observation of *Ferganella diodonta*. *A. bidenta* was originally described as resembling a juvenile *F. diodonta* (Davidson 1866-1871, p. 150-151). The later species is common in this interval, while Bassett & Cocks (1974) reported *A. bidenta* only from the Mulde and possibly from the Halla beds. To these examples of problematic identifications

Fig. 7. Compiled ranges for brachiopods from Gotland during the Lau Event.

For detailed information on localities compiled as A, B, C....., see App. 1 "Locality correlation", Fig. 4 and Table 1. Arrow - taxon present in older parts of succession at Gotland. Thin line - general report from rock unit, without locality information. Grey line - uncertain report. Rhomb - taxon identified in quantitative study at this level. *Literature reports of *Striispirifer striolatus*, in quantitative study of *Striispirifer* sp. L.



R	Q	P	O	N	M	L	K	J	I	H	G	F	E	D	C	B	A	
Hamra Fm	Burgsvik Fm		U	P	P	e	r	M.	L	o	w	e	r	U	P	P	e	r
						Eke Fm												Hemse Group
L U D F O R D I A N																		

comes that *Delthyris elevata* is easy to confuse with *Howellella elegans* when only the exterior is considered (Bassett & Cocks 1974). *Isorthis crassa*, sporadically reported from the studied interval, was by Bassett & Cocks (1974) considered to have disappeared already before the event.

Especially the inarticulate species synonyms have been hard to connect between them. Due to this, as well as low observation rates, "*Discina striata*" and "*Dinobolus Davidsoni* var. *transversus*" are omitted from Fig. 7. Among the articulate brachiopods, "*Dinorthis rigida*" (Davidson) from Hede 1925ab, *Salopina tubulata* (Lindström) from Bassett & Cocks 1974 and Hurst 1975, *Resserella canalis* (Sowerby) from Bassett & Cocks 1974, *Brachyprion* sp. from Bassett & Cocks 1974 and Hurst 1975, "*Strophomena Orbignyi*" (Davidson) from Munthe 1921 and Hede 1921 and "*Rhynchonella sphaerica*" (Sowerby) from Munthe 1902, have not been possible to identify as synonyms of other names. This generally means few reports and less well restricted ranges.



Fig. 8. Drawings of "*Dinorthis rigida*" to the left, and *Sphaerirhynchia wilsoni* to the right. Modified after Davidson 1866-1871.

A few specimens of "*Dinorthis rigida*" (Fig. 8) and "*Rhynchonella sphaerica*" were nevertheless found in the reference collection at the GeoBiosphere Centre at Lund University. The first closely resembles the "*Orthis rustica*/*Dinorthis rustica*" also found in the collection (cf. Bassett 1970). Bassett & Cocks (1974) referred all specimens of "*D. rustica*" found outside the Slite Group to *Hesperorthis gotlandica*, and they are followed herein. The same authors did also record a species resembling "the British Wenlock Limestone species *Dolerorthis rigida*", but only from the Klinteberg Fm. The specimens of "*Rhynchonella sphaerica*" very much resemble *Sphaerirhynchia wilsoni* (Fig. 8). However, besides "*R. sphaerica*", Munthe (1902) also reports "*Rhynchonella wilsoni*", herein equated with *S. wilsoni* (cf. Davidson 1866-1871). Hence, Munthe regarded them as two separate species, and therefore "*Rhynchonella sphaerica*" is herein retained as a species of its own.

"*Retzia Salterii*" and "*Strophomena* cfr. *imbrex*" is omitted from Fig. 7 because of their low observation rates during this interval and because of difficulties to assign them to the right taxa.

Some observations by earlier writers are completely rejected, at least at the species level. "*Atrypa Barrandei*" because it does not belong to the time period, *Glassia obovata*, *Desquamatia* sp. and *Spinatrypa* sp. because these taxa do not occur at all on Gotland (cf. Bassett & Cocks 1974; Copper 2004).

Results of the literature study

The general results are accounted for in Fig. 7 and the geographical positions of all identified localities are shown in Fig 4. App. 1 contains the locality correlation data used in this

literature study and App. 5 holds the authors' original entries. Selected brachiopod species are listed in App. 6 "Ranges of selected taxa", that shows extended ranges outside the investigated interval. Only a few further notes will be made here.

The early part of the event – the upper Hemse Group and the lower Eke Fm

Two taxa, *Jonesea grayi* and *Atrypa (Atrypa) sowerbyi*, are not seen above the uppermost När Fm. The find of *Atrypina* cf. *gallina* in the upper part of the Hemse Group is only tentative (Copper 2004); most other finds of the species belongs to the Hamra Fm.

At Gotland, "*Lingula Lewisi*" and "*Lingula striata*" disappear from the published record in the lower Eke Fm, somewhere below the Lau Backar 1 horizon (cf. App. 6 "Ranges of selected taxa"). However, the *Lingula* sp. that is reported by Hurst (1975) from younger strata might be referable to one or both of these species. At about the same level as these two lingulids disappear, three new species arrive in the succession: *Atrypa (Atrypa) alata*, *Navispira pusilla* and *Boucotinskia sulcata*. *B. sulcata* is only known from Gotland, ranging the Eke to Hamra Fm (Boucot 1957).

Other taxa appearing for the first time at Gotland in the lower Eke Fm, according to published data, are *Ptychopleurella bouchardi* and *Endrea ekenia*. *P. bouchardi* has also been stated as generally occurring in the Hamra Fm (Munthe 1921; Bassett & Cocks 1974), even if it might have had its acme in the lower Eke Fm.

The intermediate part of the event – Lau Backar 1

Lau Backar 1 represents the uppermost Lower Eke Fm and is the type locality for e.g. *E. ekenia* (Copper 2004). Lau Backar 1 has been thoroughly investigated by several writers during c. 140 years, so that the reported fauna is the most varied of all in the entire here studied succession is not surprising. The encountered diversity is however real.

Five or six species are seen for the last time at this locality. *Janius barrandi*, *E. ekenia* and "*Dinorthis rigida*" have more or less long previous ranges. "*D. rigida*" is reported by Hede (1921) only from the Slite beds, but has also been confirmed from the Hemse Group (Hede 1925b, 1927).

Three taxa seem to make their only appearance at Lau Backar 1: "*Orbiculoidea pilidium*", "*Rhynchonella sphaerica*" and *Rhynchotreta cuneata*. Hede (1925b) mentions the inarticulate "*Orbiculoidea pilidium*" only from "Lau backar". This is in harmony with Lindström (1860), that states "*Discina pilidium*" only from "Lauberg", an older name often used for the locality. Also "*Rhynchonella sphaerica*" is in this study only reported from Lau Backar 1. Munthe (1902) however states its existence from upper Hemse and all the way through lower Eke as well, see "Nomenclature and taxonomy", p. 16. Lindström (1860) had identified "*R. sphaerica*" from Petesvik, i.e. from the lower Hemse Group. Munthe (1902) also identified some rare *Rhynchotreta cuneata* (as "*Rhynchonella cuneata*") at "Lau backar". The species is by Bassett & Cocks (1974) considered to exist in Upper Visby, Högklint, Slite, Halla, Klinteberg and Eke beds; hence it is possible that this is in reality a species group. It is also reported from Lithuania and Podolia, from time intervals earlier than the here

investigated, and from medium deep (BA 3-4) normal turbulence environments (Gritsenko *et al.* 1999; Musteikis & Paškevičius 1999).

Eight taxa, with more or less extended ranges forward in time, occur seemingly for the first time at the Lau Backar 1 level. The majority are Lazarus taxa and only *Boucotinskia? elongata* have no previous records down the column. *B.? elongata* and also *Hesperorthis gotlandica* are by Bassett & Cocks (1974) considered to be confined to the Lau Backar 1 locality or that horizon. Other authors have given *H. gotlandica* (as "*Dinorthis rustica*", and perhaps as "*Schizoramma sp.*") longer ranges, while *B.? elongata* really could be short-ranging. It might however be noteworthy that in the quantitative study herein, *H. gotlandica* could only be identified from Lau Backar 1.

The later part of the event – the middle/upper Eke Fm

Five taxa have their last appearances in the uppermost Eke Fm, while three other taxa seems to have disappeared somewhat earlier. Of them, *Atrypa (A.) alata* only existed in the Eke Fm, while the other have longer preceding ranges.

Resserella canalis is known from the Slite and Eke beds (Walmsley & Boucot 1971; Bassett & Cocks 1974) and is in this study restricted to the upper part of the Eke Fm. *Coolinia pecten* is reported as generally occurring in the Eke Fm, but it is also common in the lower Gotlandic succession (Bassett & Cocks 1974; Hurst 1975). Cherns (1983) reported *Coolinia sp.* from Petsarve in the upper Eke Fm. *Salopina tubulata* is also known from the Hemse Group.

After the event – the Burgsvik and Hamra formations

Lindström (1860) reported *Linoporella punctata* (as "*Orthis punctata*") from localities e.g. around Hoburg and Grumpevik. Nevertheless, Bassett & Cocks (1974) questions the existence of this species higher up in the Gotlandic succession than the Slite Group, and it is possible that authors have different taxa in mind. Earlier, "*Atrypina Barrandii*" was often mentioned from the Burgsvik Fm. It could possibly be a synonym to *Atrypina cf. gallina*, which has been reported from the Hamra Fm, and with less certainty also from the Eke Fm (Copper 2004). Munthe (1921) extends the range of *Gypidula galeata* into the Hamra Fm as well.

Spirigerina quinquecostata has earlier been commonly recorded from the Hamra and Sundre beds (Hede 1921, 1960; Munthe 1921; Bassett & Cocks 1974). Hurst (1975) extended its range back to the upper Burgsvik Fm. Even so, Copper (2004) considers the species to be restricted to the Hamra Fm, in the Hoburgen area, and its longer range could possibly be due to misidentifications. *Atrypa (Atrypa) woodwardi*, a taxon resembling *Atrypa (A.) alata* from the Eke Fm, has its main range in the Hamra Fm, but is possibly also present in the Burgsvik Fm (Copper 2004).

Reticulatrype hamrae is a rare species in the Hamra Fm, often found in the inter-reef grainstone facies, when *S. quinquecosta* thrived in the reefal parts (Copper 2004). "*Strophomena Orbigny*" (probably synonymous with *Morinorhynchus orbigny*) is commonly reported from the

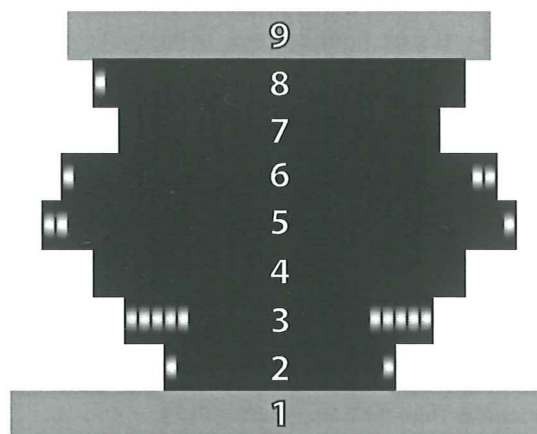


Fig. 9. Number of taxa present during the Lau Event at Gotland. Shadowing indicates taxa identified at that level only through quantitative study. Numbers refer to levels in Fig 7. 1 - Before the event (arrows), 2 - Before the event/När Fm (A-C), 3 - Early event/Botvide Mbr (D-F), 4 - Early event/lower Eke Fm (G-J), 5 - Intermediate event/Lau Backar 1 (K), 6 - Late event/Middle-Upper Eke Fm (L-O), 7 - After the event/Burgsvik Fm (P-Q), 8 - After the event/Hamra Fm (R), 9 - After the event (P-R).

Hamra-Sundre formations (Hede 1921; Munthe 1921). *M. orbigny* has also been stated to occur in the E Baltic Late Ludlow-Pridoli benthic communities, in moderate agitated to rough water (Musteikis & Paškevičius 1999; Männil & Rubel 1999).

Long-ranging species

Dalejina hybrida was reported (as "*Rhipidomella hybrida*") from Hemse strata by Hede (1921, 1925b) only, while Munthe (1921) alone stated its occurrence in the Burgsvik and Hamra formations. *Leptostrophia filosa* has been reported as generally occurring in the whole interval, but no locality has been mentioned (Hede 1921; Munthe 1921), except for the Lau kanalen specimen stated by Hoel (submitted). Elsewhere, it has mainly been reported from Wenlock-Early Ludlow UK and Lithuania (Boucot & Lawson 1999).

Discussion

The sequence of changes through the Lau Event at Gotland

The earliest part of the event – the upper Hemse Group

The lower boundary of Botvide Mbr and the Upper *P. siluricus* Subzone (Fig 1), are coeval with the first faunal changes due to the Lau Event (Jeppsson submitted). Even so, the stepwise extinction within the Botvide Member apparent in the conodont fauna can not be so finely correlated to faunal changes among brachiopods (Fig. 9), mainly due to the generally lesser sample resolution.

The fact that both *Atrypa* (*A.*) *sowerbyi* (Fig. 6, A-B) and *Jonesea grayi* (Fig. 6, W-X) are missing from the uppermost Botvide Mbr, at the high resolved successions at Gannor 1, Hallsarve 1 and Botvide 1 (E, F in Fig 7 and App. 1 "Locality correlation"), is however intriguing, especially since both species occur in strata more generally attributed to the Botvide Mbr (D). It is also noteworthy that even if both taxa were identified in the quantitative study from Mattsarve 1, none of them were identified from Botvide 1.

J. grayi is a small, thin-shelled hard-bottom form, sensitive to excessive clastic sedimentation and high turbidity (Cherns 1999b; Musteikis & Paškevičius 1999). It has been reported as a member of offshore shallow to deep shelf benthic communities from the *Monograptus balticus* Zone and Early Pridoli of SW Byelorussia (Pushkin & Modzalevskaya 1999). It is possible that it disappeared from Gotland due to negative oceanic changes affecting the planktic larvae, supported by negative facies changes affecting the adults. In Lithuania the oldest specimens (early Silurian) are from the shallower E, and the youngest (late Silurian) are from the deeper W facies (Musteikis & Cocks 2004). The stratigraphy of Lithuania will be further discussed below (see "Lithuania", p. 25).

The reason for the absence of *A. (A.) sowerbyi* could partly be due to the recent advancement in nomenclature. Even so, it probably reflects a real disappearance since the literature does not report any atrypids from the very uppermost interval (F in Fig. 7 and App. 1 "Locality correlation"). Nevertheless the quantitative study (Table 3) shows *Endrea ekenia* to be a minor constituent of the uppermost Botvide 1 brachiopod fauna. Adult atrypids had generally lost their pedicle, and only as juveniles needed a hard substrate (Cherns 1983). The more globose varieties sat with their umbo down in relatively soft sediment (Lawson 1999a). The ones with a flat valve, like *A. (A.) sowerbyi*, rested in the surface of the substrate (Fürsich & Hurst 1974). Copper (2004) notices that *A. (A.) sowerbyi* is generally found in biostromal and shallow marginal marine areas. Environments like those can also be found in the Eke Fm. Hence, the disappearance of *A. (A.) sowerbyi* was probably not due only to facies changes.

Following the literature study, also *Mesopholidostrophia laevigata* (Fig. 6, V) became extinct in the upper Hemse strata. However, Bassett & Cocks (1974) consider *M. laevigata* to be restricted to the Mulde beds, and Hede (1925b) reported the same species (as "*Leptaena laevigata*") from the Slite and Mulde beds, well before the here studied interval. A report from Podolia may corroborate this notion (Gritsenko *et al.* 1999). Nevertheless, the species has also been found in drillcores from the Ludfordian Pagėgiai Fm in W Lithuania, i.e. strata that might be comparable to the Eke-Sundre Fm (Musteikis & Cocks 2004), see p. 25. Table 3 states *M. laevigata* to be a minor constituent (less than 1%) of the fauna both at Botvide 1 and Lau Backar 1, giving the taxon a substantially longer range than previously. The species is considered to have preferred quiet water and might have been disturbed by the increased turbulence at Gotland (Hurst 1975; Lawson 1999a). Even so, it had obviously been rare for a long time.

The notion that the När Fm probably was a rather monotonous environment is corroborated by the quantitative study herein, by the clear dominance at Mattsarve 1 of *J. grayi* and at Botvide 1 of *D. navicula*. Nevertheless, several other

taxa occur in small numbers, detectable only by large collections. An example is cf. *Kirkidium knighti*, which was previously unknown in the investigated stratigraphic interval, but was found at Botvide 1. It was probably extinct in the uppermost När Fm, see "Taxa earlier believed...", p. 23.

The early part of the event – the lower Eke Fm

The event strata of the Eke Fm can be subdivided into three parts based on conodonts; the Lower, Middle and Upper Icriodontid Subzones (Fig 1). The extinction of *P. siluricus* was followed by impoverished conodont faunas in the Lower Icriodontid Subzone, the composition changing substantially only at the level of Lau Backar 1, where an additional species returned (Jeppsson submitted).

Atrypa (*A.*) *alata*, *Endrea ekenia* (Fig. 6, D-F) and *Ptychopleurella bouchardi* (Fig. 6, O) are reported from localities comprising, or close to the Hemse-Eke boundary, and might be considered as arising early during the Lau Event. The two latter species are present in small numbers already in the uppermost Botvide Mbr at Botvide 1. *Navispira pusilla* and *Boucotinskia sulcata* are first reported from strata probably somewhat higher in the succession and might therefore have arisen slightly later, however earlier than the Lau Backar 1 horizon (upper Lower Eke). *N. pusilla* is probably an immigrant to Gotland at this time, since it has also been reported from Wenlock in Podolia (Gritsenko *et al.* 1999). It also occurs in the *Ananaspis fecunda* horizon in the Upper Kopanina Fm in Bohemia (Havlíček & Štorch 1990), an interval correlated to the Lau Event and the Eke Fm (cf. Kriz & Schönlaub 1980; Lehnert *et al.* 2003), see below ("Bohemia", p. 31).

P. bouchardi, *A. (A.) alata*, *E. ekenia*, *N. pusilla* and *B. sulcata* have all been reported from a combination of proximal shelf and other environments (Table 1; Cherns 1983; Samtleben *et al.* 2000; Copper 2004). This indicates that facies factors might have a lesser role in their distribution in time and space.

"*Lingula Lewisi*", together with "*Lingula striata*", probably became extinct in the Lower Eke Fm, during the early part of the event (see also App. 6 "Ranges of selected taxa"; Hede 1921). Lingulides can generally be found in all sorts of sediment that is possible to burrow into (Cherns 1999b; Emig 1997), and at Nyan 2 (upper Hemse Group) *Lingula* was even found living in cavities in corals (Richards & Dyson-Cobb 1976). Many lingulid species were probably rather tolerant to low oxygen rates as well (Cherns 1999b). Nevertheless, none of the mentioned taxa are reported from the fossil rich Lau Backar 1, and no lingulides were identified during the quantitative study. Since the lithology do not change significantly through the Eke Fm there are no obvious reasons for the disappearance of these inarticulate taxa at this stratigraphical level, other than the oceanic changes due to the Lau Event.

In the Lower Icriodontid Subzone, but below the Lau Backar 1 level, several species also reappeared after longer absences. Among these Lazarus taxa, *Strophonella euglypha*, *Anastrophia deflexa*, *Ferganella diodonta*, *Homeospira baylei*, *Nucleospira pisum*, *Janius barrandi*, *Striispirifer striolatus* and "*Dinorthis rigida*" have all been reported from a variety of facies (Table 1; Hede 1921, 1925b, 1927; Hurst 1975; Boucot & Lawson 1999; Musteikis & Modzalevskaya 2002).

S. euglypha and *N. pisum* are in the quantitative study found already in the uppermost Botvide 1 strata (Table 3). "*Lingula striata*", cf. *G. laeviscula* and "*Whitfieldella nitida*" seems to have preferred marly substrates, and were not so common in other facies (Hede 1921, 1925b, 1927).

The intermediate part of the event – Lau Backar 1

It is possible that specific oceanic conditions prevailed during the time of deposition of the Lau Backar 1 strata. The fossil record from the locality is substantial and many species return or flourish at this time (Fig. 9). Samtleben *et al.* (2000) regarded Lau Backar 1 as a reef complex environment, and Cherns (1983) interpreted it as low mounds with marlier interareas. Most other localities used in this study are referable to the proximal shelf facies (Table 1; Samtleben *et al.* 2000).

At Lau Backar 1, at least eight species returned after a long absence in the stratigraphical record, and thereafter lived on for shorter or longer times. Of them, *Didymothyris didyma*, *Gypidula galeata* (Fig. 6, Y-Z) and *Sphaerirhynchia wilsoni* were probably less facies dependent (Table 1; Munthe 1910, 1921; Hede 1921, 1925b; Boucot & Lawson 1999). Ratcliffe (1999) interpreted *S. wilsoni* as quasi-infaunal, sitting at the surface of the sediment with the pedicle deep into the substrate, while Cherns (1999b) reckons it to be a co-supportive species, like *Dayia navicula*. *Hesperorthis gotlandica* (as "*Dinorthis rustica*") has been reported from a wide variety of facies as well (Hede 1921).

"*Orbiculoidea* (cf.) *rugata*" and *Salopina tubulata*, seems to have preferred the marlier environments (Hede 1921, 1960), while the preferences of "*Rhynchonella sphaerica*", *Rhynchotrete cuneata* and *Dictyonella capewelli* is unknown. Nevertheless, "*O. rugata*" is reported as a constituent of benthic communities in the Ludfordian of Wales & Welsh Borderland, as well as in the Pridoli of Poland, occurring in rippled calcareous siltstone and limestones with corals (Lawson 1999b; Teller & Boucot 1999). Perhaps the latter is a different species than the Gotlandic one.

"*Orbiculoidea pilidium*", and possibly also *Boucotinskia? elongata*, are short-ranging species only occurring around Lau Backar 1. *Morinorhynchus? sp. B*, identified from Lau Backar 1 and Olsvenne 3, is possibly new at Gotland in the Lower Icriodontid Subzone, as well. It is probably *Morinorhynchus rubeli* (Musteikis & Cocks 2004), a species that has been recorded from e.g. the Ludfordian Pagėgiai Fm in Lithuania.

J. barrandi and "*D. rigida*" became extinct from Gotland near the top of the Lower Icriodontid Subzone. The disappearance of *J. barrandi* is corroborated by the quantitative study herein; it only occurs at Lau Backar 1, where it constitutes less than 1% of the total brachiopod fauna. The species has also been recorded in the Podolian Malinovtsy Fm (Boucot 1962), which has been correlated to the Hemse-Burgsvik units at Gotland (Nikiforova *et al.* 1985), see below ("Podolia", p. 26). Hence it is possible that *J. barrandi* was wiped out over great distances due to the disturbances caused by the Lau Event.

The same might apply to *Mesopholidostrophia laevigata* and *Endrea ekenia*. The latter is restricted to the eastern side of the island and seems to have been actively substituted by *A. (A.) alata* in the SV (Copper 2004). While *A. (A.) alata* existed also in the upper parts of the Eke Fm, *E. ekenia* is not

Table 4. Brachiopod fauna at Lau Backar 1 - comparison between quantitative study herein and Hurst (1975). Adjustments made to achieve a modern nomenclature in both.

	This study		Hurst (1975)	
	(st)	(%)	(st)	(%)
<i>Craniops implicata</i>	14	-		
<i>Hesperorthis gotlandica</i>	3	-		
Orthid indet. sp. K	1	-		
" <i>Dinorthis rigida</i> "	2	-		
<i>Mesopholidostrophia laevigata</i>	15	-		
<i>Leptostrophia filosa</i>	329	8		
<i>Strophonella euglypha</i>	344	8		
<i>Morinorhynchus? sp. B</i>	5	-		
<i>Gypidula galeata</i>	354	8		
<i>Delthyris elevata</i>	8	-		
<i>Ptychopleurella bouchardi</i>	4	-	42	5
<i>Isorthis canaliculata</i>	122	3	6	-
<i>Lepidoleptaena poulsenii</i>	9	-	5	-
<i>Protochonetes striatellus</i>	11	-	1	-
<i>Microsphaeridiorhynchus? nucula</i>	291	7	252	28
<i>Sphaerirhynchia wilsoni</i>	42	-	9	1
<i>Endrea ekenia</i>	149	3	74	8
<i>Dayia navicula</i>	644	15	1	-
<i>Homeospira baylei</i>	558	13	367	41
cf. <i>Glassina laeviscula</i>	23	-	38	4
<i>Nucleospira pisum</i>	677	15	4	-
<i>Janius barrandi</i>	16	-	2	-
<i>Strispirifer sp. L</i>	11	-	3	-
<i>Howellella elegans</i>	680	16	87	10
<i>Dalejina hybrida</i>			4	-

found higher in the succession. As there are no younger Eke Fm strata than the Lau Backar 1 horizon left in the far NE today, it is however hard to say whether *E. ekenia* became extinct straight away or not.

Hede (1921) also claims the death of *Dayia navicula* in the Lower Eke Fm. The number of localities from where it is not reported certainly increases upward in the succession, indicating some sort of influence from the changing oceanic conditions. The quantitative study performed herein could not confirm its existence beyond the Lau Backar 1 strata. The species is otherwise reported outside of Gotland, from a wide range of facies, depths and water circulation modes, before and after the Lau Event (Boucot & Lawson 1999).

Lau Backar 1 – a quantitative studies comparison

Hurst (1975) is the only published quantitative study from Gotland (Table 4). He identified 897 individual brachiopods and 16 species at Lau Backar 1. It can be compared to the 4375 specimens and 26 species identified from the same locality in the present study. One taxon reported by Hurst, *Dalejina hybrida* (Fig. 10), was not recognised in the study herein, however ten other taxa were added instead. Of the latter,

Leptostrophia filosa, *Strophonella euglypha* and *Gypidula galeata* each comprise 8% of the total diversity. The otherwise greatest differences between the studies are that *Microsphaeridiorhynchus? nucula*, *Howellella elegans* and especially *Homeospira baylei* in the Hurst investigation constitutes a far greater part of the total diversity. *H. baylei* constitutes 41% in the Hurst study, compared to 13% herein. On the other hand, *Dayia navicula* and *Nucleospira pisum* comprise less than 1% each in the Hurst study, compared to 15% each in the present study.



Fig. 10. Drawing of *Dalejina hybrida*. Modified after Davidson 1866-1871.

The explanations for the discrepancies are manifold. Obviously, misidentifications are possible. For uncertainties in the present study, see App. 3 "Selected taxonomic remarks". It is however striking that the rather flat, thin and fragile strophomenate taxa seems to be almost missing from the Hurst investigation. An incautious treatment while washing could also explain the much lower number of smooth thin-shelled brachiopods like *G. galeata*, *D. navicula* and *N. pisum*. Even so, slightly different levels might have been sampled for the two studies, since at least one meter of the succession crops out at the geographically rather flat and extensive locality. This means that vertically many 1000 years are represented. Moreover, fluctuations in fauna composition are not far-fetched since there are indications for rapid changes in e.g. isotope curves as well (Jeppsson oral comment).

The later part of the event – the middle/upper Eke Fm

The Middle Icriodontid Subzone is characterised by the return of the conodont *Panderodus equicostatus*, which had been absent since late Wenlock (Jeppsson submitted). The number of localities attributed with certainty to this interval is low. No substantial discussion concerning changes in the brachiopod diversity is possible.

The Upper Icriodontid Subzone is characterised by the total dominance (over 90%) of the single conodont species *Panderodus equicostatus*, a situation resembling the worst parts of the Ireviken and Mulde events (Jeppsson submitted). This is not true for the brachiopods. At Olsvenne 3 *Isorthis canaliculata* is the most common taxon, and constituting c. 29% of the total brachiopod population, far from the situation in the conodont fauna. Also, without attempting any quantification of absolute individual numbers, there are not any substantial differences in number of brachiopod species present in the Upper Eke Fm, when compared to the lower part of Eke Fm (Fig. 9). Moreover, even if the upper Lower Eke Fm Lau Backar 1 locality is included in the comparison, the number of taxa did not decrease by more than 30% in the Upper Eke Fm.

At least eight species are seen for the last time in the Upper Eke Fm. In the more facies dependent group "*Orbiculoidea*

(cf. *rugata*", cf. *Glassina laeviscula* and probably also *Salopina tubulata* disappeared from Gotland at the Eke-Burgsvik boundary. This indicates for them negative facies changes as the main cause of disappearance, even if disturbances due to the event can not be excluded. Another probably facies dependant taxon is *Resserella canalis*. It only occurs in marl units at Gotland and it is part of Lithuanian benthic communities that did not survive excessive silt sedimentation and high turbidity (Musteikis & Paškevičius 1999). *R. canalis* is however also reported from limestone/coral environments in Podolian Wenlock and Polish Pridoli (Gritsenko *et al.* 1999; Teller & Boucot 1999) and it is common in the Wenlock Shale and Limestone of the Welsh Borderland and in some of the mudstones in Wales (Walmsley & Boucot 1971). Even so, at Gotland, none of the mentioned taxa reappeared in the likewise marly environments of the lower Hamra Fm.

Coolinia pecten was possibly finally extinct during the deposition of the Upper Icriodontid Subzone. *C. pecten* had long been rare in the Baltic area, perhaps living on the edge of its existence at Gotland. Elsewhere, *Coolinia* sp. is recorded (rarely) from Ludfordian strata in Lithuanian drillcores (Musteikis & Cocks 2004) and from the coeval Kopanina Fm in Bohemia (Havlíček & Štorch 1990). *C. pecten* occurred in an oxygenated environment with normal turbulence in Lithuania and earlier in Byelorussia, however rather deep (BA 4-5) (Musteikis & Paškevičius 1999; Pushkin & Modzalevskaya 1999). Even so, *Coolinia* has in the past often been confused with *Morinorhynchus* (cf. Davidson (1866-1871; cf. Strusz 2003; cf. Musteikis & Cocks 2004). If the *Coolinia* reported in the literature is identical to the "*Strophomena orbigny*" (= *Morinorhynchus orbigny*?) reported from the Hamra Fm, it did survive the event. It is however possible that the *Morinorhynchus?* sp. B (probably = *M. rubeli*) identified in the quantitative study herein is either equal with the *Coolinia* or with the *M. orbigny*, if they are not one and the same. Either way, *Morinorhynchus?* sp. B (Table 3) comprises less than 1% of the brachiopod fauna at Lau Backar 2 and Olsvenne 3.

Among the less facies dependant taxa described above, only *Atrypa (Atrypa) alata* became extinct for certain at the Eke-Burgsvik boundary. It flourished in the SW Eke oncoid marl region, and disappeared together with the calcareous algae (Copper 2004). *Nucleospira pisum* probably also disappeared at the Eke-Burgsvik boundary, since there are doubts about the identification of the single individual found at Bankvät 1. However, *N. pisum* has also been reported from Lithuania (Musteikis & Modzalevskaya 2002), where it might have an extended range, see below ("Lithuania", p. 25). *Isorthis crassa* seems also to have had a somewhat wider range of habitats (Hede 1921, 1925b, 1927; cf. Gritsenko *et al.* 1999). It occurs in older parts of the succession, as well as sporadically in the När and Eke formations. *I. crassa* did not survive into or beyond the Burgsvik Fm.

Hesperorthis gotlandica, *Strophonella euglypha*, *Anastrophia deflexa*, *Gypidula galeata*, *Ferganella diodonta*, *Sphaerirhynchia wilsoni*, *Homeospira baylei* and *Striispirifer striolatus* all lived through to the Hamra Fm. *Didymothyris didyma* is not found in the Burgsvik Fm, but reappeared in the Hamra Fm.

In conclusion, the majority of brachiopod species that disappeared in or at the top of the Upper Icriodontid Subzone, seems to have been more or less facies dependent and not

necessarily responding to direct event conditions. Only *A. (A.) alata* shows a typical pattern created by oceanic disturbances. On the other hand, the range of "*Whitfieldella nitida*", also presented here as a more or less facies dependant species, extends into the Hamra Fm. No newcomers are recorded at this level, unless Atrypid indet. sp. E (Fig. 6, G-H) and Atrypid indet. sp. D are considered. None of them were identified at any other locality investigated in the quantitative study.

After the event – the Burgsvik and Hamra formations

Almost as many brachiopod species as from the preceding interval are reported from the Burgsvik Fm, despite the fossil scarceness in some parts (Fig. 9). Several of the brachiopods from the Eke Fm, more or less facies dependent, lived through the Burgsvik Fm or returned in the Hamra Fm.

The range of *Brachyprion* sp., that seems to have survived the event, but perished in the Burgsvik Fm, is unfortunately less well restricted. Likewise the ranges of *Linoporella punctata*, *Atrypa (Atrypa) woodwardi*, *Atrypina* cf. *gallina* and *Spirigerina quinquecostata* through or from the Burgsvik Fm seem to have relatively shaky foundations. The very last finds of *Dayia navicula* reported in the literature is from the Burgsvik Fm (Hede 1921; Hurst 1975).

Several of the taxa that survived the Lau Event at Gotland have also been reported from younger or coeval strata in other parts of the world. *Ferganella diodonta* is a constituent in Byelorussian benthic communities from the *Monograptus balticus* Zone, as is *Strophonella euglypha* (Pushkin & Modzalevskaya 1999). *S. euglypha* was rather heavy, had ribs and was probably well equipped with setae to remove silt. Therefore it could live in shallower waters than most strophomenids (Lawson 1999a). It is well known in the whole Baltic (Musteikis & Cocks 2004), however it seems to have had its acme during Wenlock (Pushkin & Modzalevskaya 1999). The quantitative study showed that in the investigated interval, it thrived at Lau Backar 1, where it constitutes c. 8% of the brachiopod fauna.

Homeospira baylei (Fig. 6, K-M) has been reported from Late Ludlow and/or Pridoli strata in Poland, Podolia, Byelorussia and the E Baltic (Gritsenko *et al.* 1999; Musteikis & Paškevičius 1999; Männil & Rubel 1999; Pushkin & Modzalevskaya 1999; Teller & Boucot 1999). However, Nikiforova *et al.* (1985) points out that there are a considerable external homoeomorphy in the *Homeospira* group, and that several species might be hidden in at least the Podolian material. There are also some stratigraphical uncertainties, see below ("Lithuania", p. 25, and "Podolia", p. 26).

The geographical distribution of *Sphaerirhynchia wilsoni* resembles that of *H. baylei*, except for the absence in the E Baltic (Gritsenko *et al.* 1999; Pushkin & Modzalevskaya 1999; Teller & Boucot 1999). *Didymothyris didyma* is common throughout Baltica (Modzalevskaya & Wenzel 2003) and is e.g. also reported from Podolia (Gritsenko *et al.* 1999) and the Paadla beds in the E Baltic (Männil & Rubel 1999). The later interval has been correlated with the Hemse to Burgsvik Fm at Gotland (Baarli *et al.* 2003). However, Jeppsson *et al.* (1994) showed considerable gaps in the Estonian succession, so the later correlation might be overoptimistic.

Other brachiopod responses to the Lau Event at Gotland

One way to cope with low primary production is to reduce the population size; however at the same time becoming prone to extinction (Twitchett 2001). Lazarus taxa are the survivors from this group, suffering only apparent extinction and reappearing later (Twitchett 2001). A sparse population also risks a situation where immigrants settle vacant niches when conditions ameliorate (Urbanek 1993). A post-event radiation from the old species is then also hampered. Another response is the lilliput effect, when certain species, sometimes only in certain areas, (temporary) decreases in size, due to stunting or dwarfing (Urbanek 1993; Price-Lloyd & Twitchett 2002). If this strategy work, they are likely to mass-occur, since the competition decreases by the loss of other species during the event (Urbanek 1993). The size reduction is related to both rates of growth and the length of the life span (Price-Lloyd & Twitchett 2002). During the End-Permian extinction, the size changes mirrors the fluctuating $\delta^{13}\text{C}$ curve, and are unrelated to benthic oxygen levels, according to Price-Lloyd & Twitchett (2002).

Taxa earlier believed to have disappeared before the Lau Event

Together with several other taxa, as mentioned above, cf. *Kirkidium knighti* (Fig. 6, U) has earlier been considered extinct at Gotland already before the start of the Lau Event (cf. Bassett & Cocks 1974). Pentamerids are often considered depth dependant (Johnson 1997). Even so, substrate is not unimportant. At Gotland *K. knighti*, as well as another pentamerid species, *Antirhynchonella linguifera*, seems to have preferred environments with a higher amount of carbonate than the mainly marly upper Hemse strata could provide (cf. Johnson 1997). However, combined with reports from slightly younger strata in other parts of the world (Boucot & Johnson 1979; Gritsenko *et al.* 1999), the identification of cf. *K. knighti* from Gotland is significant in an international context. Talent *et al.* (1993) described the Lau Event as "the Pentamerid Event" based on the notion that the pentamerid brachiopods, common in most Ludlow strata of the world, are almost gone in the Pridoli parts. Even if no high resolved stratigraphical data existed, they assumed that the extinction might have coincided with the isotopic excursion.

Pentamerids in general are adapted for turbulent environments (e.g. Boucot & Johnson 1979), however possibly not for algal encrustation. The extinction of (cf.) *K. knighti* due to the Lau Event is therefore likely. Moreover, even if *A. linguifera* did disappear in a somewhat earlier interval and the other pentamerid taxon in this study, *Gypidula galeata*, probably lived right through, it is also possible that a low-numbered *G. galeata* sensu stricto was terminated in the (upper) Hemse Group along with *K. knighti*, and that a modified form of that taxon is found in the Eke Fm (cf. Bassett & Cocks 1974). In connection to this, it is also noteworthy that only juvenile individuals represent both cf. *Kirkidium knighti* and *Gypidula galeata* in the quantitative study herein.

Morinorhynchus crispus is another taxon that has earlier been considered extinct before the onset of the event (Bassett & Cocks 1974). Nevertheless, the *Morinorhynchus?* sp. A specimen from Botvide 1 closely resembles *M. crispus*.

Together with the extended range of *Mesopholidostrophia laevigata*, the additional taxa identified herein reflect the importance of large collections.

Lilliput effects

Microsphaeridiorhynchus? nucula (Fig. 6, S-T) seems to have its acme from the Eke Fm and forward, indicating for it improving environmental conditions during the event and afterwards, at least when compared to the upper Hemse Group. It seems to have benefited from an eventual reduced competition. It is also possible that this distribution is related to the lilliput effect. The relative frequency of smaller sized individuals in the population of *M.? nucula* is higher at Olsvenne 3 than at Lau Backar 1. At both localities the species comprises about 10% of the preserved brachiopod fauna. *M.? nucula*, with its strong pedicle, ribs and thick shell, was adapted for turbulent environments (Fürsich & Hurst 1974; Hurst 1975; Lawson 1999a). Moreover, it is in the East Baltic known to have mass occurred if higher than normal turbulence caused stress in the more diverse benthic communities (Musteikis & Paškevičius 1999). Therefore it might seem contradicting that *M.? nucula* comprises over 90% of the brachiopod fauna at Bankvät 1, in a calm and sheltered environment. On the other hand, Price-Lloyd & Twitchett (2002) observed prolonged lilliput effects in the benthic fauna some time after the End-Permian event, due to the disturbances in the ecological structure. This is corroborated by the sedimentary wrinkle structures found in the Burgsvik Fm (Calner 2005). Calner (2005) argues that these structures are related to the more or less undisturbed growth of thin microbial mats and that their presence indicates a prolonged period of reduced infaunal activity continuing some time after the event as well.



Fig. 11. Drawing of *Protochonetes striatellus*. Modified after Davidson 1866-1871.

The concept of lilliput faunas might also be applied to two other species. *Isorthis canaliculata* (Fig. 6, I-J) and *Protochonetes striatellus* (Fig. 11) apparently decreased in size from the Hemse Group into the Hamra Fm (Böger 1968; Hurst 1975), even if the *P. striatellus* populations did include a few larger specimens in the Eke Fm as well (Böger 1968). When it comes to *I. canaliculata*, this conclusion is corroborated by the quantitative study herein. Unfortunately the *P. striatellus* material from the quantitative study is too small to permit any firm conclusions.

Both species were robust and might be considered to have been adapted to the kind of shallow water depths interpreted for the event and post-event strata at Gotland. In the Polish Pridoli, Teller & Boucot (1999) places *I. canaliculata* in moderate turbulence limestone/coral environments, and *P. striatellus* is in the E Baltic a part of the rough water to shoal living *Didymothyris-Salopina* community (Männil & Rubel 1999). *I. canaliculata* could in the Hemse beds be connected to the agitated *Dayia navicula* biofacies (Hurst 1975). Thus, the size

reduction could indicate a response to changing chemistry of the ocean water, i.e. the Lau Event. However, a size reduction mainly due to constraints induced by the shallowing can not be excluded, since the mentioned authors do not provide information about the size distribution. Besides, *I. canaliculata* has also been reported as a constituent in quiet water and marly offshore shallow shelf benthic communities from the Pridoli in SW Byelorussia (Pushkin & Modzalevskaya 1999). Further, a weak turbulence setting is postulated for the Podolian *Dayia navicula* and *Didymothyris didyma* communities, carrying *P. striatellus* as well (Gritsenko *et al.* 1999).

Lastly, there is another group of brachiopods that might show lilliput effects due to the Lau Event, the pentamerids. *Gypidula galeata* and cf. *Kirkidium knighti* are both represented only by juvenile individuals in the quantitative study herein, as discussed above, p. 23.

Relative frequency

The quantitative study (Table 3) shows that *Craniops implicata* is most common at Olsvenne 3, a locality extremely rich in calcareous algae. It also occurs in rather great numbers, together with *Microsphaeridiorhynchus? nucula*, in the probably restricted environment at Bankvät 1. It is possible that *C. implicata* exploited niches that had become vacant due to the event or an adverse environment in general. Further, the competition between filtrating organisms must have been greater at Lau Backar 1 than at Olsvenne 3. Even so, recent calcareous algae are considered to exploit vacant niches (Whalen *et al.* 2002), and this might also be valid for the brachiopod species thriving at Olsvenne 3. The relative frequencies of taxa at different localities also imply that *Isorthis canaliculata* and *Shaleria (S.) ornatella* were in general probably less sensitive to algal overgrowths than *Howellella elegans* and *Homeospira baylei*. Another taxon belonging to the former group is probably also *Gypidula galeata*, while *Nucleospira pisum* might belong to the latter.

S. (S.) ornatella (App. 3, Fig. 18) and *Dayia navicula* (Fig. 6, P-R), major constituents of upper Hemse strata, continue into the Eke Fm. Earlier writers have reported that the numbers of these species decline substantially above the boundary (cf. Cherns 1983 discussing Malm 1 and Burgen 4; Hede 1925b). This notion is partly true when it comes to *D. navicula*, in the quantitative study constituting 73% of the total brachiopod fauna at Botvide 1, and decreasing to 15% at Lau Backar 1. On the other hand, one should keep in mind that the Botvide 1 sample is from the uppermost *Dayia-coquina* of that locality. While no further *D. navicula* were found in younger strata, the quantitative study herein shows that the number of *S. (S.) ornatella* increased to a maximum at the Upper Eke locality Olsvenne 3. To this comes, that the *Strophodonta (Strophodonta) hoburgensis* (Fig. 6, N; Hoel submitted) found at Bankvät 1 is certainly the species previously reported as *S. (S.) ornatella*. *Shaleria (S.) ezerensis* is another species previously often reported as *S. (S.) ornatella* and could possibly have wrongly extended its range.

In conclusion, both *S. (S.) ornatella* and *Dayia navicula*, sometimes considered opportunistic and otherwise proven to be very hardy, decreased in numbers or disappeared during periods of amelioration. It is possible that the strophomenide *S. (S.) ornatella* became extinct due to the clastic input during

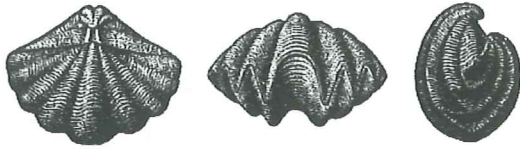


Fig. 12. Drawing of *Howellella elegans*. Modified after Davidson 1866-1971.

the deposition of the Burgsvik Fm and that *D. navicula* were sensitive to algal overgrowth. Moreover, opportunistic taxa are seldom competitive in a mature system. Hence, it is possible that the substantial presence of *D. navicula* at Lau Backar 1 falsifies the hypothesis made herein, that the locality represents a part of the event where brachiopods thrived again after an initial setback.

Dalejina hybrida seems generally to have become less common after the event, pointing to facies factors, even if it could also be partly the result of the skewness in reports due to the lesser amount of published data from southernmost Gotland. According to Ratcliffe (1999) the genus *Dalejina* preferred soft muds and could have been rhizopedunculate. Nevertheless, *Dalejina hybrida* occurs in both marl and limestone in e.g. the East Baltic and Byelorussia, where it is reported from quiet to normal turbulence, nearshore to offshore strata, dated from Wenlock to Pridoli (Männil & Rubel 1999; Musteikis & Paškevičius 1999; Pushkin & Modzalevskaya 1999).

Another peculiarity concerning ranges, is that even though three representatives of the Superfamily Orthoidea occur in the Lower Eke Fm, none are present in the upper Eke Fm. "*Dinorthis rigida*" was extinct during the intermediate part of the event, but both *Hesperorthis gotlandica* and *Ptychopleurella bouchardi* reappeared after the event, at least according to some literature. In the quantitative study herein, none of them were found above the Lau Backar 1 horizon. The orthids had only a relatively weak pedicle, a small mantel cavity and a relatively underdeveloped lophophor apparatus (Fürsich & Hurst 1974). Hence, it is possible that excessive silt and detritus brought in by the ongoing shallowing disturbed them. Tychsen & Harper (2004: fig. 1) describe a sudden decline in diversity among the Orthida of Baltica and Avalonia Major during the Ludfordian. This might be connected to the Lau Event. Even so, other investigated terranes (e.g. Siberia, Bohemia, Laurentia) do not show such features. Other explanations are that both Baltica and Avalonia experienced shallowing during this time, and the disappearances might have environmental reason. It might also be due to a deficiency in the database.

The same Upper Eke absence is by the way also true for *Dictyonella capewelli* and *Sphaerirhynchia wilsoni*, even if finding these rather rare species is to a large extent due to the size of collections.

Long-ranging species

The nine or ten species that ranges through the whole interval (Fig. 7; Table 3) were probably not adapted to a particular living environment; they were generalists. An example is *Howellella elegans* (Fig. 12), which had a cosmopolitan distribution during the Silurian (Ratcliffe 1999). Its shell form enhanced the water circulation, helping it make better use of

available food particles, as well as deflect silt (Lawson 1999a). It also had a strong pedicle and could stand turbulence well (Fürsich & Hurst 1974; Lawson 1999a). The species did however not constitute any significant part of the fauna at any herein quantitatively studied locality, except for Lau Backar 1, where it comprises c. 16% of the identified brachiopods.

Another example is *Craniops implicata*, a real all-round brachiopod, occurring in benthic communities from Wenlock to Pridoli in Great Britain and the Baltic Basin, in quiet to rough water, at almost all depths and on all sorts of substrate (Boucot & Lawson 1999; Emig 1997).

Lau Event and brachiopods from selected parts of the world

Surface currents have been proposed as a reason for similarities in lithology and fauna between certain Silurian continents (Kriz *et al.* 2003). The following brief exposé covers geological successions from the same basin as that Gotland was a part of, from another part of Baltica, from the same Silurian equatorial setting and from a cooler water setting.

The same basin - Lithuania and Ukraine

Lithuania

Two studies of brachiopods from Lithuanian drillcores have recently been published. Musteikis & Modzalevskaya (2002) describe mainly smooth atrypids, athyridids and rhynchonellids. Musteikis & Cocks (2004) investigate plectambonitoidean, strophomenoidean and orthotetoidean brachiopods.

Both works covers facies types from the pelagic to the lagoonal and are based on the same stratigraphical correlation (Fig. 13). The Dubysa Regional Stage comprises in its uppermost part the *Polygnathoides siluricus* Zone, and is followed by the Pagėgiai Regional Stage. Even if these authors use a somewhat different conodont zonation (cf. Musteikis & Modzalevskaya 2002: fig. 2-3; Musteikis & Cocks 2004: fig. 2-3), it can be roughly correlated to the one used for Gotland. *R. dubia* has also been reported from the uppermost Hemse Group at Hallsarve 1 and higher, an *O. s. scanica* fauna is found in the Eke Fm and the *O. wimani* Zone can be correlated to post-event strata (Jeppsson 1975, submitted). To this comes that Kaljo *et al.* (1997) record a substantial $\delta^{13}\text{C}$ isotope excursion in the upper part of the Dubysa Fm in Latvia, at the top of the Nova beds. These beds are also connected to a sea-level drop. Hence, even if resolution is very low, these studies do reflect the ranges of brachiopods living during the Lau Event in Lithuania. The uncertainties of ranges are added to by the fact that collections from drillcores generally are rather small.

Based only on the information in Fig. 13, the interpretation must be that the Lithuanian brachiopods were more or less unaffected by the Lau Event. Out of the 22 existing taxa in the studied interval only two or possibly three arise or become extinct during the entire proposed time of the event. The great-

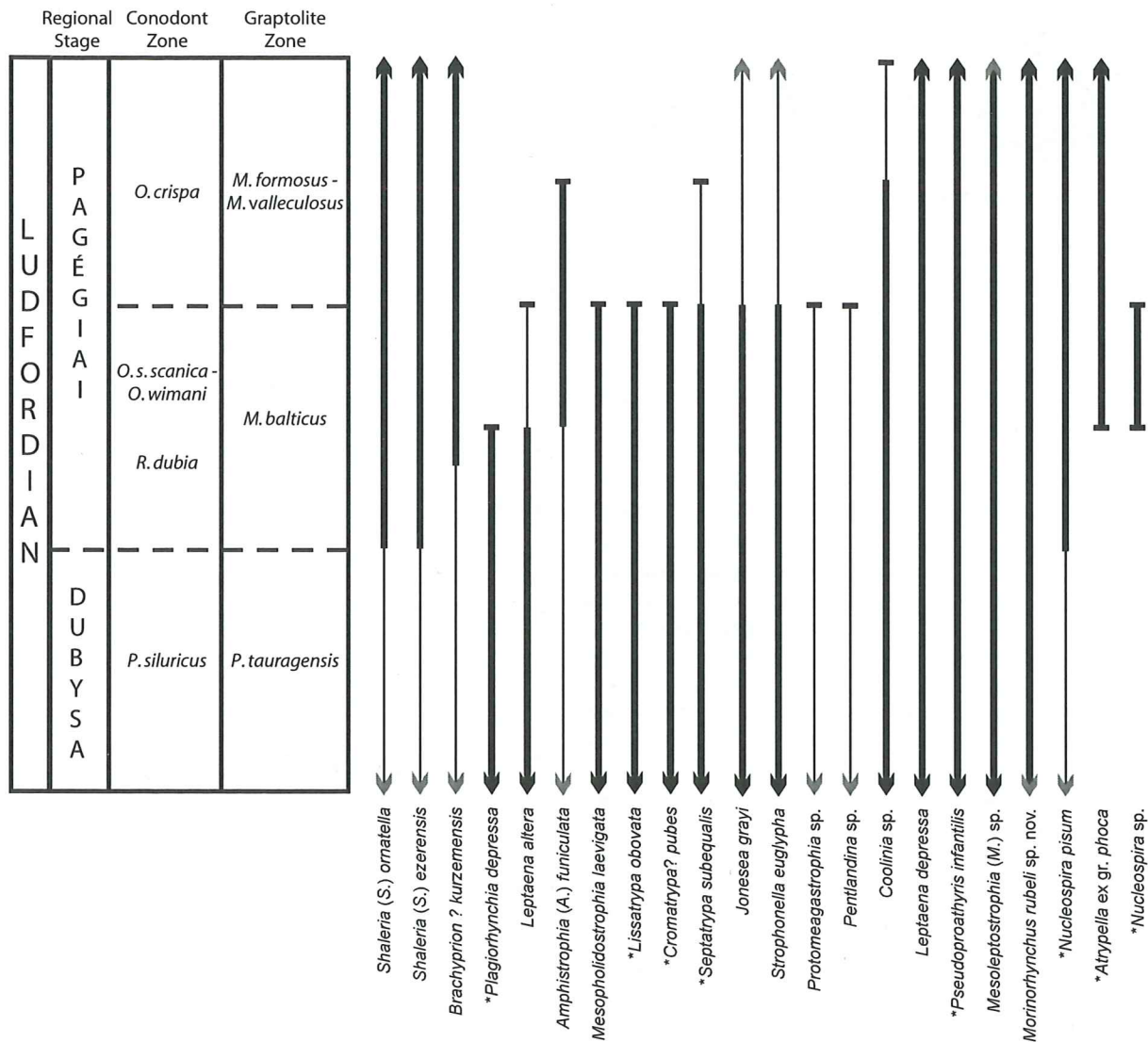


Fig. 13. Ranges for selected brachiopod taxa during the Lau Event, from Lithuanian drillcores. Thickness of stratigraphical units is not to scale. Thin line - gap in reports/uncertain boundaries. Black arrow - taxa exist immediately below/ above interval, grey arrow - taxa exists after gap in reports. Modified after *Musteikis & Modzalevskaia (2002) and Musteikis & Cocks (2004).

est extinction seems instead to coincide with the boundary towards the *O. crispa* Zone. Two of the then affected taxa, *Jonesea grayi* and *Mesopholidostrophia laevigata*, are known to disappear early or rather early during the Lau Event at Gotland. To this comes, that *S. (S.) ornatella* at Gotland becomes less common during the event than before, the opposite of the Lithuanian report. *Nucleospira pisum*, that on Gotland disappear or at least becomes much less common at the end of the event, has an extended range in Lithuania. Since the faunas at Gotland and Lithuania most certainly were in close contact, and when all data is taken together, this is rather peculiar.

A suspicion arises, that the stratigraphic constraints for the Lithuanian brachiopod ranges are not as good as would be desirable. It is unclear whether the stratigraphical data based on conodonts were obtained from the same drillcores as the brachiopod data. Another problem is that the on-going shallowing during the Late Silurian forced depth-related communities towards the west. Hence the youngest finds of

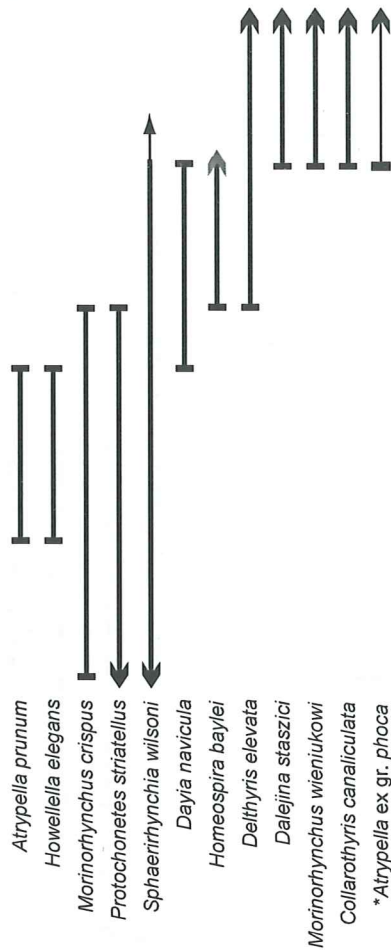
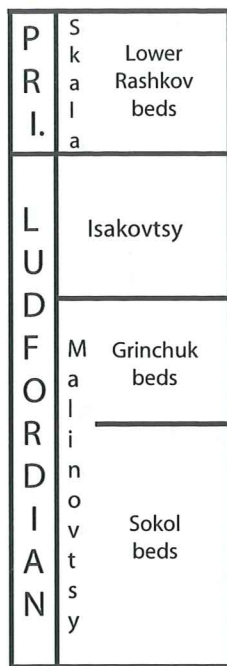
most taxa are from W Lithuania (cf. Musteikis & Modzalevskaia 2002; cf. Musteikis & Cocks 2004). By this follows that if W Lithuania has not been as extensively investigated in conodont studies as in brachiopod studies, and facies associations have been the main tool for correlation, there might be an age discrepancy. Zones erected on Lithuanian conodont data might then be too short, allowing for an adjustment downward of true brachiopod ranges in Fig. 13.

Therefore, the present author argues that the Lau Event in Lithuania **did** affect the brachiopods substantially. Out of the 22 described taxa, seven were extinct and frequencies of at least six additional taxa were affected.

Podolia

Even though Podolia and the Dnestr River sections are famous among palaeontologists, the published material on the stratigraphical relationships is confusing. The brachiopod

Stratigraphy and rock units according to Nikiforova *et al.* 1985.



Stratigraphy proposed herein

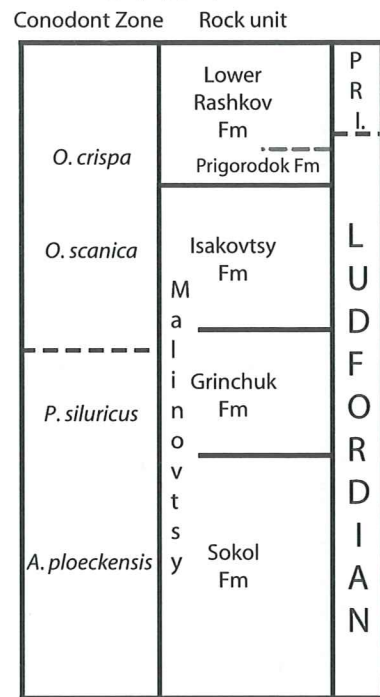


Fig. 14. Brachiopod ranges during the Lau Event in Podolia.

Thickness of stratigraphical units is not to scale. Thin line - gap in reports. Black arrow - taxa exist immediately below/ above interval, grey arrow - taxa exists after gap in reports. Range data from Nikiforova *et al.* (1985) and *Abushik *et al.* (1985). Modified after Abushik *et al.* (1968); Nikiforova *et al.* (1968); Drygant 1984; Abushik *et al.* (1985); Nikiforova *et al.* 1985; Paris & Grahn (1996); Huff *et al.* (2000); le Hérisse *et al.* (1997) and le Hérisse (2002).

records from Podolia are therefore hard to evaluate. Nikiforova *et al.* (1985) reported the existence of eight upper Ludlow brachiopod species (Fig. 14). However, when comparing additional research in brachiopods, as well as in conodonts, chitinozoas and bentonite horizons (Nikiforova & Predtechenskij 1968; Drygant 1984; Abushik *et al.* 1985; Paris & Grahn 1996; Huff *et al.* 2000; cf. le Hérisse *et al.* 1997; cf. le Hérisse 2002) it is clear that Nikiforova *et al.* (1985) drew the Ludlow-Pridoli boundary to low. When adjusting for this, three additional taxa are included, as well as one taxon reported by Abushik *et al.* (1985).

The Sokol Fm was considered coeval with the Hemse Group at Gotland and comprises mainly nodular limestones, with thin marl bands (Nikiforova *et al.* 1985). Based on the first appearance of *Kirkidium knighti*, Abushik *et al.* (1985), place the Gostian-Ludfordian boundary near the top of the Fm. According to Nikiforova *et al.* (1985), *Kirkidium knighti sensu stricto* became extinct in the Sokol Fm, however Nikiforova *et al.* (1968) report it (as "*Conchidium knighti*") from younger strata as well. There might be an evolution line. Huff *et al.*

(2000) refer the upper parts of the Sokol Fm and most of the succeeding Grinchuk Fm to the *Polygnathoides siluricus* Zone. Even so, according to Drygant (1984), that taxon has not been found in Podolia.

The Grinchuk Fm, by Nikiforova *et al.* (1985) considered comparable in age to the Eke-Burgsvik formations, has a marly bottom part, a middle limestone part and a top part of marly limestones (Nikiforova *et al.* 1985). Abushik *et al.* (1985) related the find of *Neobeyrichia lauensensis* from the upper Grinchuk Fm, equating it in age with the Leintwardine Fm in Great Britain. At Gotland, that ostracode taxon became extinct during the deposition of the Eke Fm (Martinsson 1962). Besides *Atrypella prunum* and *Morinorhynchus crispus*, also *Atrypa sowerbyi* and *Janius barrandi* have earlier been reported from the Grinchuk Fm (Nikiforova *et al.* 1968). At Gotland *A. prunum* disappeared before the onset of the Lau Event, possibly due to facies changes; Nikiforova *et al.* (1985) explicitly mentions the correlation between the areas. *A. (A.) sowerbyi* and probably *M. crispus* (as *Morinorhynchus?* sp. A herein) became extinct during the early part of the event, slightly

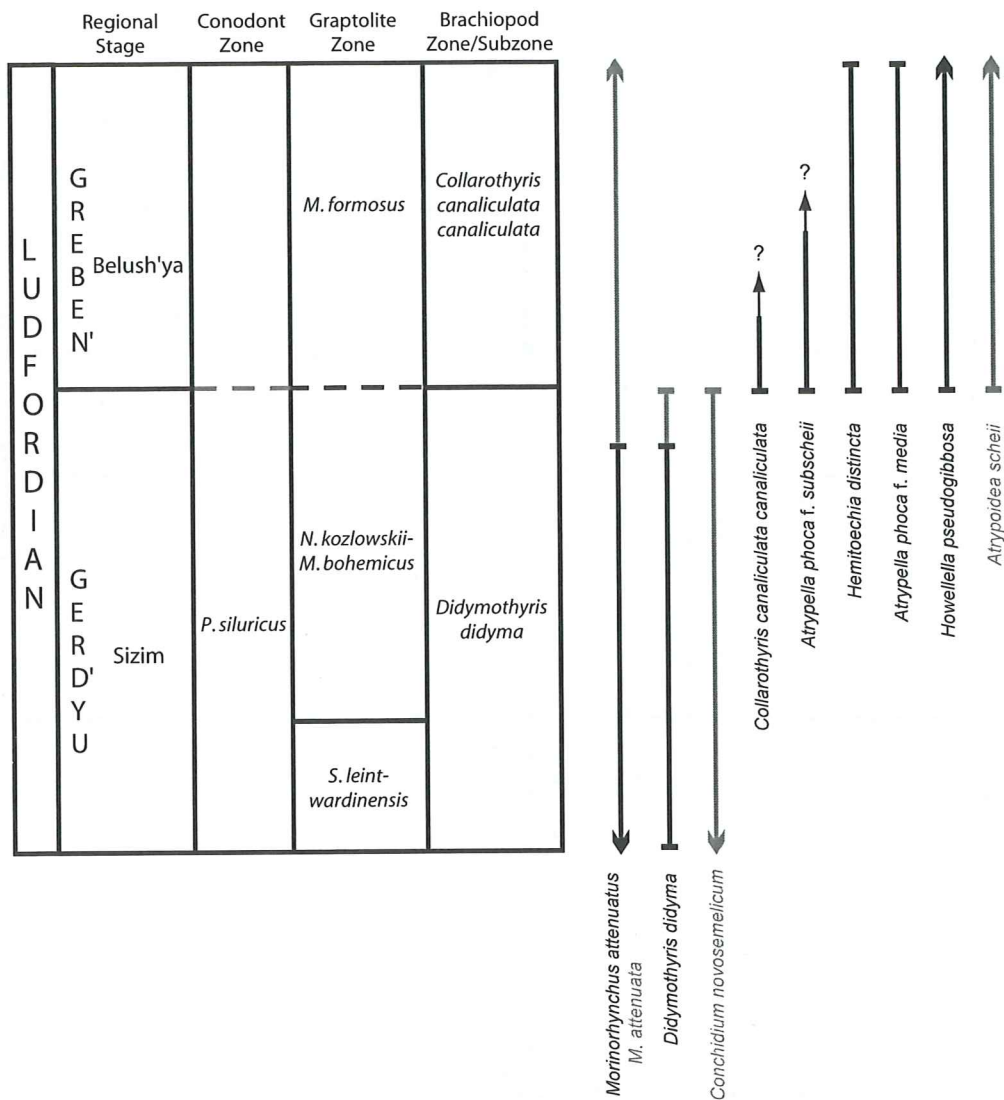


Fig. 15. Brachiopod ranges during the Lau Event in Timan-Pechora region, Russia. Thickness of stratigraphical units is not to scale. Thin line - gap in reports. Black arrow - taxa exist immediately below/ above interval. Modified after Antoshkina (2000); Modzalevskaya & Wenzel (1999) and Beznosova (2000) (grey lines).

before the return of *J. barrandi*. Based on the above, it is probable that the upper Grinchuk Fm is contemporaneous with the upper När and lower Eke formations.

The lithologies of the Isakovtsy Fm mainly consist of dolomitic marls and limestones, deposited in an inner shelf to shoal setting (Nikiforova *et al.* 1985; Paris & Grahn 1996), indicating a sea-level drop. Algae are common and the fauna is dominated by brachiopods and ostracods (Paris & Grahn 1996), except for the uppermost dolomitic marl horizon, where brachiopods are almost absent (Abushik *et al.* 1968). Isakovtsy Fm was by Nikiforova *et al.* (1985) considered to be coeval with the Burgsvik-Hamra formations. Nevertheless, Abushik *et al.* (1985) states (rightly) that the presence of *Homeospira baylei* rather is characteristic for the Eke-Hamra formations. Huff *et al.* (2000) use *O. scanica* as a tentative zone fossil in the interval. That conodont taxon is on Gotland found in the Eke Fm (Jeppsson 1975, submitted). The last find of *Dayia navicula* on Gotland is from the Burgsvik Fm. Hence, it is

herein proposed that the Isakovtsy Fm in Podolia is contemporaneous with the upper Eke and possibly lower Burgsvik formations at Gotland.

The lithologies of the Rashkov Fm incorporates nodular dolomites, limestones and sandstones, deposited in an inner shelf to open shelf setting, and the fauna is mainly composed of stromatoporoids, corals and ostracods (Paris & Grahn 1996). The Rashkov Fm was by Nikiforova *et al.* (1985) considered to be lower Pridoli. However, the first find of *O. crispera*, at Gotland reappearing in the upper part of the Hamra Fm, is from *c.* 5 m above the base of lowermost Rashkov, in the Prigorodok Fm (Drygant 1984; Abushik *et al.* 1985). Chitinozoas partly corroborates this notion (Paris & Grahn 1996), while le Hérissé (2002), based on acritarch studies, states that (lower) Rashkov Fm is coeval with the Burgsvik Fm and the Hoburgen Secundo episode. *Morinothyris wieniukowi* has herein been discussed as a possible synonym for *M. rubeli* (Musteikis & Cocks 2004) or/and for *M. orbigny*,

the later reported from the Hamra Fm. *Collarothyris canaliculata* and *Atrypella* (ex gr.) *phoca* both occur late during the event, or possibly slightly after the event, (see "Lithuania", p. 25 and "Russia").

In conclusion, with some stratigraphical adjustments, the Podolian brachiopod ranges as well show a surprisingly good correspondence to the ranges from Gotland.

The same continent - Russia

The Timan-Pechora region in Russia is situated at the (north)easternmost edge of Baltica, slightly N of the Silurian paleoequator (Fig. 3; Copper & Brunton 1991). The Upper Silurian strata here are composed of a continuous succession of carbonates with biostromal and stromatolitic horizons (Modzalevskaya & Wenzel 1999; Antoshkina 2000). During the Ludlow a rimmed shelf with shallow water low-energy conditions was produced and the taxonomic diversity among brachiopods became rather low. Athyridids of a relatively small size dominated (Modzalevskaya & Wenzel 1999), later to be replaced by mainly monospecific *Greenfieldia* or *Didymothyris* brachiopod coquinas (Antoshkina 2000).

During the Early Ludfordian *Didymothyris didyma* Zone, the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ isotopic values were stable, however decreasing upwards, possibly as a result of slight diagenetic alteration (Modzalevskaya & Wenzel 1999). The lithology is mainly composed of marlstones, followed by an increasing amount of stromatolites towards the top. At the reference localities along the Kozhym River, the very uppermost layers are somewhat terrigenous and lack fossils (Antoshkina *et al.* 2000). From this zone, Modzalevskaya & Wenzel (1999) report only two brachiopod species: the common index fossil *D. didyma* and the rarer *Morinorhynchus attenuatus*. Both disappeared near the top of the zone, according to these authors (Fig. 15).

Modzalevskaya & Wenzel (1999) show *M. attenuatus* as the only survivor of nine Gorstian species and point out that it is also known from North America. Bassett & Cocks (1974) mentions that *M. attenuatus* is approximately the same age as the Gotlandic *Morinorhynchus crispus*. Beznosova (2000), also working in the Timan-Pechora-northern Ural area, report "*Morinorhynchus attenuata*" with an extended range, well into Pridoli (Fig. 15). Musteikis & Cocks (2004) doubt the records of *M. (cf.) attenuata* from this area and suggest that it is instead *Morinorhynchus rubeli*, which they describe from Ludfordian and Pridoli Lithuania as well.

Beznosova (2000) instead adds *Conchidium novosemelicum* as a Ludlow brachiopod species terminating at the end of the *D. didyma* Zone. This pentamerid taxon mainly occurred in reefal facies, together with other large-shelled brachiopods for which she gives no ranges. Antoshkina *et al.* (2000) also mentions *Atrypodea lingulata* as occurring in the interval, unclear at what level.

Immediately at the base of the Late Ludfordian *Collarothyris canaliculata canaliculata* Subzone, the lithology in the northern sections shifts to shale, with only a minor later interruption of marlstone (Modzalevskaya & Wenzel 1999: fig. 2). Further, a substantial isotopic shift is recorded within this subzone, however not as great as in the strata from Gotland. A short-term regression interval is interpreted as well (Antoshkina 2000). Five new brachiopod species appeared; one of them continued into the succeeding Pridoli *Collarothyris canalicu-*

lata trapezoideus brachiopod Subzone (Modzalevskaya & Wenzel 1999). In that later Subzone the lithology remains the same and six new brachiopod species are added. Antoshkina *et al.* (2000) remarks that, at the Kozhym River reference localities at least, these two subzones are dominated by smooth-shelled brachiopods, often occurring in concentrated lenses.

The *D. didyma* Zone seems to be possible to correlate to the Hemse Group at Gotland and the *C. c. canaliculata* Subzone to the Eke-Hamra formations (cf. Antoshkina 2000: fig 3; cf. Modzalevskaya & Wenzel 1999: fig 2). Besides the isotopic signatures and abrupt changes in sea-level, lithology and brachiopod fauna (Nekhorosheva & Patrunov 1999; Modzalevskaya & Wenzel 1999), the interval is correlated to the Baltic Basin Lau Event strata also by other faunal elements, e.g. the osteichthyan fish *Andreolepis hedei* (cf. Fredholm 1988; cf. Wigforss-Lange 1999; Modzalevskaya & Wenzel 1999; Vergoossen 1999). Beznosova (2000) mentions the presence of *Polygnathoides siluricus* in the *D. didyma* Zone strata.

The described faunal development has been recorded in several sections in the Urals-Novaya Zemlya area (Modzalevskaya & Wenzel 1999). Needless to say; several features have parallels in the Gotlandic strata. The only major divergence seems to be that in Russia the stromatolitic facies was more common before than during the event. Obviously, during and following the event was a time of rapid evolution, in response to something outside of facies changes. Intervals of clastic sedimentation had occurred earlier, in the *D. didyma* Zone, without any extinction (Modzalevskaya & Wenzel 1999: fig. 2). There is an evolutionary succession from *Didymothyris* to *Collarothyris*, as well as within *Atrypella*; on the whole evolution generally mainly affected internal structures.

The same equatorial setting - Australia

Like Baltica, the Australian Plate was situated at or close to the paleoequator during the Silurian. The position is often reconstructed as far to the E of Baltica (Fig. 3). Based partly on data from this continent Talent *et al.* (1993) describes "the Pentamerid Event", occurring in the *P. siluricus* Zone. A general brachiopod diversity decline is stated, as well as a short-term regression. These authors also connect their findings to "the *Cardiola* Event" in the Carnic Alps in Austria (cf. Schönlaub 1986).

Strusz (2002, 2003) describes the Protorthida, the Orthida, and the Strophomenata of the Yass Syncline succession in New South Wales, SE Australia. During the Silurian this was a shallow water shelf setting with occasional silicic volcanism. Rickards and Wright (1999), working with graptolites in the same area, points out that most of their material is excellently preserved and more or less undeformed.

Six orthid and seven strophomenate species existed during the Lau Event interval (Strusz 2002, 2003). Five out of the eleven taxa living at the time of the deposition of the upper *P. siluricus* Zone strata became extinct somewhere at the top of that zone (Fig. 16). Strusz do not report any brachiopods from the *B. cornutus* graptolite Zone strata. Even so, Rickards & Wright (1999) report the presence of "small brachiopods" there and a distinctive layer rich in graptolites, i.e. mainly *M. bohemicus*, tops the Black Bog Shale Fm (Link & Druce 1972; Strusz 2002).

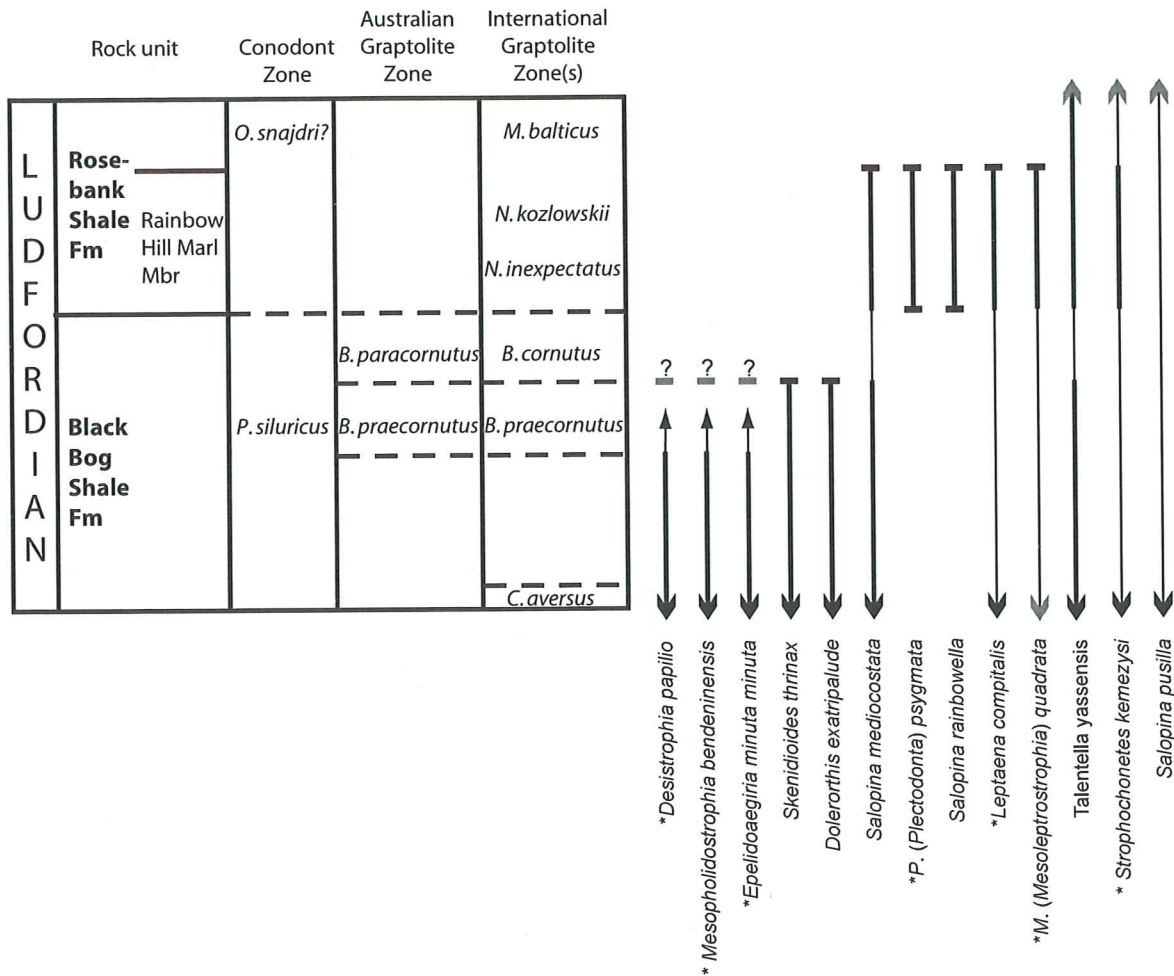


Fig. 16. Ranges for strophomenate and orthide brachiopods during the Lau Event in the Yass Syncline, Australia. Thickness of stratigraphical units is not to scale. Thin line - gap in reports. Black arrow - taxa exist immediately below/above interval, grey arrow - taxa exists after gap in reports. *Strophomenates (Strusz 2003). Modified after Strusz (2002, 2003); Rickards & Wright (1999); Link & Druce (1975) and Urbanek (1970).

Three out of the eleven mentioned brachiopod taxa from the Black Bog Shale Fm survived into the Rosebank Shale Fm and terminated at the top of the silty Rainbow Hill Marl Mbr. Two of them were probably more or less facies dependent, since they do not occur at shale localities anywhere in the succession. Rainbow Hill Marl Mbr also carries two short ranging species. This unit has previously been called "The Middle Trilobite Bed" and is 1-3 m thick (Link & Druce 1972; Rickards & Wright 1999). The same level was indicated as "Pentamerid Event" strata by Talent *et al.* (1993: fig 2).

The three remaining taxa pass into the Pridoli. *Salopina pusilla* and *Strophochonetes kemezysi* were probably facies dependent, since they occur in siltstones and (silty) marlstones before and after the studied interval. In general, in the shale facies immediately preceding the event, the strophomenates do not seem to be common either.

The top of the *P. siluricus* Zone has not been defined in the Yass Syncline. In the pioneer work on conodont stratigraphy by Link & Druce (1972), no fauna compositions are reported from the part of the succession considered here (except from the Yarwood Siltstone Mbr), probably due to the low element yield from shales. Even so, Rickards & Wright (1999) considers

the *B. praecornutus* graptolite zone to be possible to correlate to the upper *L. scanicus*, *S. leintwardinensis* and *P. podoliensis* Biozones in central Asia. Strusz (2002) however states that the Yarwood Siltstone Mbr, or "The Lower Trilobite Bed" is possibly referable to the upper *S. leintwardinensis* and more probably to the *C. aversus* Zones, limiting the range of the *B. praecornutus* Zone considerably.

Obviously, also the Yass Syncline strata contain some parallels to the scenario at Gotland. Besides the extinction of the five mentioned brachiopod species early during the event, a facies shift towards marlier environments, probably due to the event and indicating shallower water, favoured new species. These, together with some longer-range brachiopod species survived the event but not the return to normal, possibly due to substantial population decreases during the event. It is interesting that *Salopina rainbowella*, restricted to the event strata, is expressively said to be externally similar to *Salopina tubulata* (Strusz 2002), one of the species at Gotland that in the studied interval only occurs in the Eke Beds. Further, there was a multi-adapted brachiopod species, not disturbed by the event and a Lazarus taxon reappearing after a long absence from the stratigraphical record.

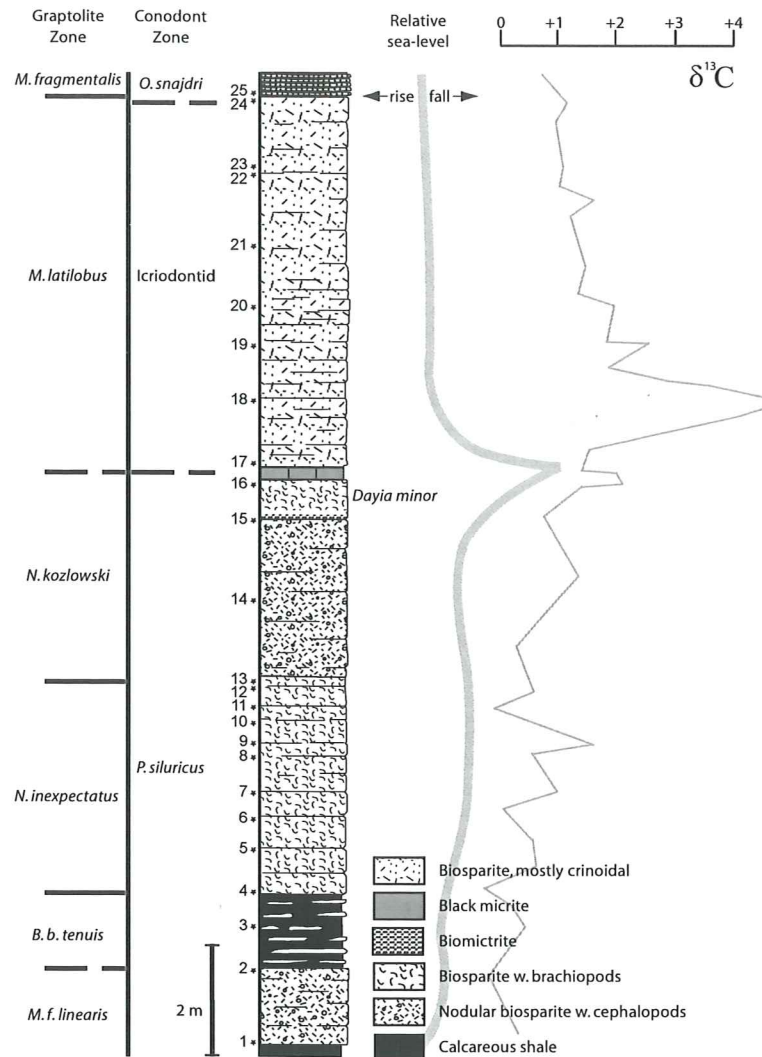


Fig. 17. The Lau Event in Bohemia.

Modified after Kriz & Schönlaub (1980); Lehnert *et al.* (2003) and references therein and Jeppsson oral comment.

Graptolites apparently mass-occurred in connection with the boundary between the two main rock units. This feature could be in analogy with the *Dayia* and *Shaleria* coquinas at Gotland. This discussion is however hampered by the fact that, according to Strusz (2002), the succeeding silty marl unit might be the result of a slump or turbidity current. Urbanek (1970), who once named the *B. praecornutus* and the *B. cornutus* Zones, remarks that the latter only has a very short range, in a "highly characteristic horizon" in Poland. It is possible that this reflects more or less anomalous event strata.

The cooler water setting - Bohemia

The Lau Event in the Prague Basin (Fig. 3) presents a cooler water setting, but still with several similarities to the course of events at Gotland. The Mušlovka Quarry section in the Daleje valley is the basis for the information presented here (Kriz & Schönlaub 1980; Lehnert *et al.* 2003).

The first faunal change slightly preceded the first shift in stable isotopes, which occurs in a part of the section containing

abundant *Dayia minor*, strongly reminding of the upper Hemse *Dayia navicula* coquinas (Fig. 17). Beds 15-16 is here tentatively correlated to the Botvide Mbr at Gotland, mainly based on the conodont zonation (cf. Kriz & Schönlaub 1980; Jeppsson oral comment).

Dark argillaceous limestone, very poor in fossils, follows. It is related to erosion or a hiatus in the basin, as well as a brief sea-level drop, resembling the situation at E Gotland, during the early part of the event.

The interval corresponding to the Eke Fm is composed of crinoidal limestones, as is e.g. the lowermost Eke Fm part of the section at Botvide 1. New brachiopod, cephalopod and trilobite taxa appear, e.g. *Navispira pusilla*, a species that has also been reported as a newcomer at the same stratigraphical level at Gotland.

The maximum $\delta^{13}\text{C}$ isotopic excursion is found in bed 18, which is here correlated to the Lower Eke Fm, based on the conodont assemblage occurring in the section (Jeppsson oral comment). At Gotland the maximum excursion is found higher up in the succession (Fig 1).

Conclusions

1. At Gotland, brachiopod diversity did not plunge in the same dramatic fashion as the conodont diversity. However, a considerable brachiopod faunal re-organisation took place during and due to the Lau Event.
2. The early part of the event can be subdivided according to lithology. In the uppermost Botvide Mbr *Atrypa (A.) sowerbyi* and cf. *Kirkidium knighti* became extinct and *Jonesea grayi* disappeared. *Endrea ekenia* and *Ptychopleurella bouchardi* also first appeared (in small numbers) and several Lazarus taxa reappeared. In the lowermost Eke Fm ten Lazarus taxa, the majority less facies dependent, reappeared and "*Lingula Lewisi*" and "*Lingula striata*" probably became extinct. There are perhaps two distinguishable times of changes. *Atrypa (A.) alata* appeared during the first and *Navispira pusilla* and *Boucotinskia sulcata* during the second.
3. The intermediate part of the Lau Event seems to have allowed for the greatest diversity. The time for the reappearance of the nine Lazarus taxa at Lau Backar I was not facies controlled, since there are more or less marly and oncoidal environments through the entire Eke Fm. This part of the event ended with the extinction of "*Dinorthis rigida*", *Endrea ekenia*, *Mesopholidostrophia laevigata* and *Janius barrandi*. The heydays of *Dayia navicula* were over as well.
4. During the later part of the event only a very low diversity conodont fauna existed. However, among brachiopods, range changes are only proven at the Eke-Burgsvik boundary, where lithology also changes considerably. Of the eight disappearing taxa, *Atrypa (A.) alata*, and possibly *Nucleospira pisum*, were for certain extinct due to direct event conditions.
5. The most severe times for brachiopods were before and early during the event. Out of the 63 listed taxa, 42 occur before the investigated interval. However, only 18 are reported from localities containing strata deposited right before the onset of the event. Out of the 42 pre-event taxa, 31 occur at Lau Backar I, together with six taxa first appearing during the event. During the later part of the event, 28 of the pre-event taxa occur, together with six taxa first appearing during the event. At least 25 of the 42 pre-event taxa survived the event. Among taxa that first appeared during the event, at least two, *Navispira pusilla* and *Boucotinskia sulcata*, also survived and occur in the Burgsvik and Hamra formations.
6. Among the only nine or ten taxa that have more or less continuous ranges through the whole event, *Isorthis canaliculata*, *Protochonetes striatellus* and *Microsphaeridiorhynchus? nucula* show distinct Lilliput effects, and the pentamerids may also have been affected.
7. Re-organisation patterns are also detectable among published brachiopod faunas from Lithuania, Ukraine, Russia, Australia, and probably also from Bohemia.
8. Large collections are essential to even begin to reach the true ranges of taxa only occurring in small numbers.

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Appendix 1. Locality correlation

The stratigraphic placement of the localities follows Laufeld (1974a), Jeppsson & Jerre (ms) and Jeppsson (submitted), and the latest work is used when contradictions are encountered. Most of the datings are conodont based. *Further comments on grouping, see below. Taxa present at each locality are shown in Fig. 7 and original entries in App. 5.

Hemse Group

A. Lower När Fm, Hemse Marl, SE part, *P. siluricus* Zone. Gogs 1

1. Hede 1960, p. 80, lines 4-9: "Loc. 41. Ditch about 350 m NW by N of Gogs".
2. Hurst 1975, p. 251, 258-259, Table 3: "G-22.1".
3. Harper & Boucot 1978b, p. 161: "*Shaleriella delicata*, USNM loc. 10039".

B. När Fm, main part? Hallsarve 2 and Fie 1

4. Hede 1921, p. 58, bottom 3 lines - p. 59, top 15 lines: "SO om L. Bjerges i Lau socken". Hallsarve 2.
5. Hede 1925b, p. 24, bottom 9 lines - p. 25, top 9 lines: "200 m NV om vägskalet Koparve-gårdarna i Lau socken". Hallsarve 2.
6. Copper 2004, pp. 39-42: "*Atrypa (Atrypa) sowerbyi*. Fie 1".

C. När Fm in general (Main part and/or Botvide Mbr)

7. Hede 1919, pp. 43-44: "Tabellarisk översikt över Burgsviksborrningens fossil, Dayia-skiffer".
8. Hede 1927, p. 27, lines 7-19: "200 m SSO om Binge i Alva".
9. Hurst 1975, pp. 251, 258-259, Table 3: "G-19, G-19.1". Gannor 3.
10. Copper 2004, pp. 39-42, 79: "*Atrypa (Atrypa) sowerbyi*, *Atrypina cf. gallina*, Bomunds, Burgen".

*D. När Fm, Botvide Mbr

11. Munthe 1910, pp. 1420-1422: "Dayia flag". Table.
12. Munthe 1910, p. 1409, lines 4-14: "Dayia flags".
13. Hede 1919, pp. 25-30: The Burgsvik core, the interval 63.6 - 68.6 m.
14. Munthe 1921, pp. 69-70: "Tabell över en del fossils... uppträdande..., Dayia-fliskalk".
15. Munthe 1921, p. 26, lines 3-7: "Dayia-fliskalken".
16. Hede 1960, p. 80, line 30 - p. 81, line 13: "Loc 42. Section about 50 m SSW of Botvide (southern) farm". Botvide 1. (Locality with the Hemse-Eke boundary).
17. Hurst 1975, pp. 251, 258-259, Table 3: "G-60.1". Botvide 1.
18. Hurst 1975, pp. 251, 258-259, Table 3: "G-58.1, G-58.2". Nyan 2. (Locality with the Hemse-Eke boundary).
19. Copper 2004, pp. 39-42: "*Atrypa (Atrypa) sowerbyi*. Lau kanal".
20. Harper & Boucot 1978b, p. 161: "*Shaleriella delicata*, USNM loc. 10026". Hågvide 1.

*E. När Fm, Botvide Mbr. "Lag a". (Localities with the Hemse-Eke boundary)

21. Hede 1925b, p. 37, lines 25-42: "Lau-kanalen, ca 1,7 km SV om Lau kyrka, lag a". Gannor 1.
22. Munthe 1902, p. 231, lines 13-32: "Lau-kanalen, ca 1,7 km SV om Lau kyrka, lag c. Gannor 1.
23. Hede 1925b, p. 44, bottom 5 lines: "I Litorinahavets översta erosionsterrass V om Hallsarve-gårdarna, V om och intill vägen till Alskog, lag a". Hallsarve 1.
24. Hede 1925b, p. 45, lines 28-30: "strax SV om Botvide-gårdarna, lag a". Botvide 1.
25. Munthe 1902, p. 259, bottom 2 lines - p. 260, top 3 lines: "SV om Botvide, lag c". Botvide 1.

*F. När Fm, Botvide Mbr. "Lag b". (Localities with the Hemse-Eke boundary)

26. Hede 1925b, p. 38, lines 17-29: "Lau-kanalen, ca 1,7 km SV om Lau kyrka, lag b". Gannor 1.
27. Munthe 1902, p. 232, lines 12-20: "Lau-kanalen, ca 1,7 km SV om Lau kyrka, lag d₁. Gannor 1.
28. Munthe 1902, p. 232, lines 21-28: "Lau-kanalen, ca 1,7 km SV om Lau kyrka, lag d₂. Gannor 1.
29. Hede 1925b, p. 44, lines 40-44: "I Litorinahavets översta erosionsterrass V om Hallsarve-gårdarna, V om och intill vägen till Alskog, lag b (*Leptostrophia impressa*-rikt)". Hallsarve 1.
30. Hede 1925b, p. 44, lines 34-38: "I Litorinahavets översta erosionsterrass V om Hallsarve-gårdarna, V om och intill vägen till Alskog, lag b (*Dayia navicula*-späckat)". Hallsarve 1.
31. Munthe 1902, p. 258, lines 25-29: "I Litorinahavets markerade erosionsterrass V om Hallsarve-gårdarna, V intill vägen åt Alskog, lag d_{2,1} (margelkalk)". Hallsarve 1.
32. Munthe 1902, p. 258, lines 21-24: "I Litorinahavets markerade erosionsterrass V om Hallsarve-gårdarna, V intill vägen åt Alskog, lag d_{2,1} (*Strophomena impressa*-rikt)". Hallsarve 1.
33. Munthe 1902, p. 258, lines 17-20: "I Litorinahavets markerade erosionsterrass V om Hallsarve-gårdarna, V intill vägen åt Alskog, lag d_{2,1} (*Dayia navicula*-späckad)". Hallsarve 1.
34. Hede 1925b, p. 45, lines 22-26: "strax SV om Botvide-gårdarna, lag b". Botvide 1.
35. Munthe 1902, p. 259, lines 29-34: "SV om Botvide, lag d". Botvide 1.

Eke Fm

*G. Lower Eke Fm. "Lag c". (Localities with the Hemse-Eke boundary)

36. Hede 1925b, p. 38, bottom 6 lines - p. 39, top 18 lines: "Lau-kanalen, ca 1,7 km SV om Lau kyrka, lag c". Gannor 1.
37. Munthe 1902, p. 235, lines 1120: "Lau-kanalen, ca 1,7 km SV om Lau kyrka, lag d₁. Gannor 1.
38. Hede 1925b, p. 44, lines 27-32: "I Litorinahavets översta erosionsterrass V om Hallsarve-gårdarna, V om och intill vägen till Alskog, lag c". Hallsarve 1.
39. Munthe 1902, p. 258, lines 12-16: "I Litorinahavets markerade erosionsterrass V om Hallsarve-gårdarna, V intill vägen åt Alskog, lag d₃. Hallsarve 1.

***H. Lower Eke Fm. "Lag d". (Localities with the Hemse-Eke boundary)**

40. Hede 1925b, p. 39, lines 19-36: "Lau-kanalen, ca 1,7 km SV om Lau kyrka, lag d". Gannor 1.
41. Munthe 1902, p. 236, bottom 7 lines - p. 237, top 11 lines: "Lau-kanalen, ca 1,7 km SV om Lau kyrka, lag e. Gannor 1.

***I. Lower Eke Fm. "Lag e". (Localities with the Hemse-Eke boundary)**

42. Hede 1925b, p. 44, lines 17-25: "I Litorinahavets översta erosionsterrass V om Hallsarve-gårdarna, V om och intill vägen till Alskog, lag e". Hallsarve 1.
43. Hede 1925b, p. 40, lines 6-10: "Lau-kanalen, ca 1,7 km SV om Lau kyrka, lag e^m₁. Gannor 1.
44. Hede 1925b, p. 40, lines 11-19: "Lau-kanalen, ca 1,7 km SV om Lau kyrka, lag e^k₁. Gannor 1.
45. Hede 1925b, p. 41, lines 3-10: "Lau-kanalen, ca 1,7 km SV om Lau kyrka, lag e^k₂-e^m₂. Gannor 1.
46. Munthe 1902, p. 246, lines 4-17: "Lau-kanalen, ca 1,7 km SV om Lau kyrka, lag f^k₂-f^m₂. Gannor 1.

***J. Lower Eke Fm**

47. Copper 2004, pp. 51-53: "*Atrypa (Atrypa) alata*, Bodudd 1".
48. Copper 2004, pp. 70-71: "*Endrea ekenia*, Burgen 4".
49. Hede 1921, p. 67, line 25 - p. 68, line 11: "1,8 km öster om L. Dippen och 2 km N om Näs' kyrka... även... 300 m NO om Skåls på Näsudden; 1,2 km NNV om Näs' kyrka; i närheten av Magnuse och Ålarve i Rone socken samt 3,5 km Ö om Rone kyrka".
50. Copper 2004, pp. 51-53: "*Atrypa (Atrypa) alata*, Näs 1".

K. Upper lower Eke Fm. Lau Backar 1. (Type locality for the *Rhizophyllum* Limestone)

51. Lindström 1860, pp. 358-371: "Lau backar, Lauberg".
52. Munthe 1902, p. 249, bottom 8 lines - p. 250, top 2 lines: "Laubackar".
53. Hede 1921, p. 68, bottom 4 lines - p. 69, line 18: "Lau backar".
54. Hede 1925b, p. 46, lines 9-38: "strax innanför Ancylus-gränsvallen 1,2 km NO om Lau kyrka".
55. Hede 1960, p. 81, bottom 10 lines - 82, top 2 lines: "Loc. 43. Lau backar, 1,25 km ENE of church of Lau".
56. Hurst 1975, pp. 251, 258-259, Table 3: "G-E". Lau backar 1.
57. Bassett & Cocks 1974: mentions several species as originally found at "Lau backar, Lauberg".
58. Copper 2004, pp. 70-71: "*Endrea ekenia*, Lau backar 1".
59. Hoel, in press, p. 15: "Lau backar".
60. Harper & Boucot 1978b, p. 161: "*Shaleriella delicata*, USNM loc. 10038".

L. Middle Eke Fm. Halor 2

61. Hurst 1975, pp. 251, 258-259, Table 3: "G-35".
62. Harper & Boucot 1978b, p. 161: "*Shaleriella delicata*, USNM loc. 10015".

M. Middle/Upper Eke Fm

63. Hurst 1975, pp. 251, 258-259, Table 3: "G-57.4". Kullunde 4 according to Hurst, however not at the same coordinates as Larsson 1979, who originally described the locality Kullunde 4.
64. Hurst 1975, pp. 251, 258-259, Table 3: "G-57.2, G-57.3". Kullunde 3 according to Hurst, however not at the same coordinates as Larsson 1979, who originally described the locality Kullunde 3.
65. Hede 1960, p. 82, bottom 6 lines - p. 83, top 3 lines: "Loc. 45. Digging on north-eastern side of main road 2 km N by W of church of Grötlingbo". Lingvide 1.
66. Walmsley & Boucot 1971, p. 499, lines 12-16: "north-east of the main road 2 km north of Grötlingbo church". Lingvide 1.
67. Hede 1927, p. 35, lines 12-28: "kanalen omedelbart NO om Eke kyrka". Eke 2.

N. Upper Eke Fm

68. Chems 1983, p. 24, lines 17-25: "oncolitic strata, Bodudd 2".
69. Hurst 1975, pp. 251, 258-259, Table 3: "G-AX". Kullunde 2.
70. Copper 2004, pp. 51-53: "*Atrypa (Atrypa) alata*, Kullunde 4".
71. Chems 1983, p. 24, bottom 9 lines - p. 25, top 4 lines: "Petsarve".
72. Hoel, submitted, p. 16-17: "*Shaleria (Shaleriella) ezerensis*, Petsarve 4".
73. Munthe 1910, p. 1410, top 6 lines: "the *Sphaerocodium* marl... uppermost part".

***O. Uppermost Eke Fm, Ronehamn 2**

74. Hede 1921, p. 68, lines 11-37: "500 m SV om Ronehamns hamn".
75. Hede 1925b, p. 27, line 4 - p. 28, line 5: "500 m SV om Ronehamns hamn".
76. Copper 2004, pp. 51-53: "*Atrypa (Atrypa) alata*, Ronehamn 2".

Burgsvik Fm

***P. Lower Burgsvik Fm in general**

77. Hede 1925b, p. 32, bottom 9 lines - p. 33, top 11 lines: "strax NNV om Kapelluddens fiskläge". Kapellet 1.
78. Hede 1927, p. 35, bottom line - p. 36, top 5 lines: "sandstenen".

***Q. Upper Burgsvik Fm in general**

79. Munthe 1910, p. 1412, lines 17-24: "passage bed between the sandstone and the oolite".
80. Munthe 1910, p. 1413, lines 9-19: "the oolite".
81. Hede 1919, pp. 16-18: The Burgsvik core, the upper 7 m of the Burgsvik Beds (partly oolitic).
82. Hede 1921, p. 73, line 26 - p. 74, line 14: "400 m V om Bobbenarve i Burgsvik". Oolite.
83. Hede 1925b, p. 32, lines 23-37: "skiktkomplexet... å Burgenområdet och å Närsholm".
84. Hede 1925b, p. 32, bottom 9 lines - p. 33, top 16 lines: "strax Ö om punkt 28 överst å Burgen". Oolite.
85. Hede 1925a, p. 27, bottom 15 lines - p. 28, top 4 lines: "ledets yngsta delar, samt ooliten".
86. Hede 1960, pp. 83-84: Loc. 46. "Quarry 200 m SSE of Uddvide (southern) farm, Burgsvik Sandstone and Oolite". Uddvide 1. (Locality with the Burgsvik-Hamra boundary).
87. Hurst 1975, pp. 251, 258-259, Table 3: "G-33.1, G-33.2". Uddvide 2. (Locality with the Burgsvik-Hamra boundary).
88. Hurst 1975, pp. 251, 258-259, Table 3: "G-1.1, G-1.2, G-1.3, G-1.4". Hoburgen 2. (Locality with the Burgsvik-Hamra boundary).
89. Hoel, submitted, p. 16-17: "*Shaleria (Shaleriella) ezerensis*, upper part of the Burgsvik Fm, Kätteviken".

Hamra Fm

R. Lower Hamra Fm

90. Munthe 1910, pp. 1420-1422: "Sphaerocodium limestone." Table.
 91. Munthe 1910, p. 1413, bottom 7 lines - p. 1414, top 28 lines: "Sphaerocodium limestone, and the "marly reef-limestone" replacing it.
 92. Hede 1919, pp. 43-44: "Tabellarisk översikt över Burgsviksborrningens fossil, Sphaerocodium-kalksten".
 93. Hede 1919, pp. 14-16: The Burgsvik core, top part (ca 2 m) of drillcore, Hamra beds.
 94. Munthe 1921, pp. 69-70: "Tabell över en del fossils... uppträdande..., Sphaerocodiumkalk".
 95. Munthe 1921, p. 45, lines 12-23: "Sphaerocodium-kalken".
 96. Munthe 1921, p. 47, lines 10-16: "Sphaerocodium-kalkens... ekvivalent den m. el. m. leriga revkalken".
 97. Hede 1921, p. 75, bottom 8 lines - p. 76, top 5 lines: "Hamra-kalkstenens *understa* del... utbildad i Burgsviksborrningens profil".
 98. Hede 1925a, p. 28, bottom 4 lines - p. 29, top 8 lines: "Sphaerocodium-kalken".
 99. Hede 1960, p. 83: Loc. 46. "Quarry 200 m SSE of Uddvide (southern) farm, Hamra Group. Uddvide 1.
 100. Hede 1960, p. 84 - p. 85, top 14 lines: Loc 47. "Hoburgen (Storburg)".
 101. Copper 2004, pp. 72-73: "Reticulatrypea hamrae, Husryggen 1, ca. 2 m above Burgsvik Sandstone."
 102. Copper 2004, p. 79: "Atrypina cf. gallina, Kättelviken 1."
 103. Copper 2004, pp. 53, 72-73, 79, 104-106: "Atrypa (Atrypa) woodwardi, Reticulatrypea hamrae, Atrypina cf. gallina, Spirigerina quinquecostata, Hoburgen, V-sidan".
 104. Hoel, in press, pp. 15-16: "Burgsvik Öja parish/ Gansviken Grötlingbo parish".

Reports of taxa generally occurring in Eke, Burgsvik and Hamra Fm, respectively

*S. Eke Fm in general

105. Munthe 1910, p. 1409, bottom 8 lines: "the *Sphaerocodium* marl".
 106. Munthe 1910, pp. 1420-1422: "Sphaerocodium marl". Table.
 107. Hede 1919, pp. 43-44: "Tabellarisk översikt över Burgsviksborrningens fossil, Sphaerocodium-märgelsten".
 108. Munthe 1921, p. 29, bottom 7 lines - p. 30, top 5 lines: Eke in general.
 109. Munthe 1921, pp. 69-70: "Tabell över en del fossils... uppträdande..., *Ekemärgelsten*".
 110. Hede 1921: "Tavla 1: Grafisk tabellframställning..., Eke-märgelsten".
 111. Hede 1921, pp. 91-94: "Tabellarisk fossilöversikt, Brachiopoda, Eke-märgelsten".
 112. Hede 1921, p. 66, line 33 - p. 67, line 13. Eke in general.
 113. Hede 1925b, pp. 48-49: "Tabell... Armfotingar, Eke-gruppen".
 114. Hede 1925b, p. 25, bottom 17 lines. Eke in general.
 115. Hede 1925a, p. 26, lines 4-23: Eke in general.
 116. Hede 1927, p. 34, bottom 9 lines - p. 35, top 11: Eke in general.
 117. Hede 1927, pp. 52-54: "Tabell... Armfotingar (Brachiopoda), Eke-märgelsten".
 118. Bassett & Cocks 1974, pp. 42-44: "Table 1. Summary of distribution..., Eke Beds".
 119. Cherns 1983, p. 22, lines 17-20: "Common brachiopods of the Eke Fm".

*T. Burgsvik Fm in general

120. Munthe 1910, p. 1411, lines 1-14: "the lowest and the uppermost parts of the sandstone".
 121. Munthe 1910, pp. 1420-1422: "Sandstone and Clay-marl, Oolite". Table.
 122. Hede 1919, pp. 43-44: "Tabellarisk översikt över Burgsviksborrningens fossil, Sandsten med lersten och oolit".
 123. Munthe 1921, p. 38, bottom 7 lines - p. 40, top 38 lines: "sandstenslagrets översta delar".
 124. Munthe 1921, pp. 69-70: "Tabell över en del fossils... uppträdande..., *Burgsviks-sandsten* (Oolit och sandsten)".
 125. Hede 1921: "Tavla 1: Grafisk tabellframställning..., Burgsvik-sandsten och -oolit".
 126. Hede 1921, pp. 91-94: "Tabellarisk fossilöversikt, Brachiopoda, Burgsvik-sandsten o. -oolit".
 127. Hede 1921, p. 73, line 26 - p. 74, line 14: "400 m V om Bobbenarve i Burgsvik". The upper sandstone.
 128. Hede 1925b, p. 30, lines 16-21: Burgsvik in general.
 129. Hede 1925a, p. 27, lines 22-30: "sandstenslagrets undre och mellersta delar".
 130. Hede 1925b, pp. 48-49: "Tabell..., Armfotingar, Burgsvik-sandsten och oolit".
 131. Hede 1927, pp. 52-54: "Tabell... Armfotingar (Brachiopoda), Burgsvik-sandsten".
 132. Bassett & Cocks 1974, pp. 42-44: "Table 1. Summary of distribution..., Burgsvik Beds".
 133. Copper 2004, p. 16, p. 53: "Burgsvik Formation, *Atrypa (Atrypa) woodwardi*".

U. Hamra Fm in general

134. Munthe 1921, p. 44, lines 23-38: Hamra in general.
 135. Munthe 1921 Burgsvik, p. 48, line 22 - p. 49, line 11: Hamra in general.
 136. Munthe 1921 Burgsvik, p. 49, line 13 - p. 50, line 40: Hamra in general.
 137. Munthe 1921, pp. 69-70: "Tabell över en del fossils... uppträdande..., *Hamrakalk*".
 138. Munthe 1921, p. 51, lines 4-9: "södra delen av Grötlingboud".
 139. Hede 1921, p. 76, lines 11-29: "...lagrets *undre* del... södra stranden av Grötlingboud". Bankvät 1.
 140. Hede 1921, p. 77, lines 2-26: "...lagrets *undre* del... västsidan av sydligaste Hoburgsudden".
 141. Hede 1921, p. 77, bottom 2 lines - p. 78, top 10 lines: "lagrets mellersta... 1.1 km N om Hamra ka och 500 m rakt västerut från Norrgårda". Middle Hamra.
 142. Hede 1921: "Tavla 1: Grafisk tabellframställning..., Hamra-kalksten".
 143. Hede 1921, pp. 91-94: "Tabellarisk fossilöversikt, Brachiopoda, Hamra-kalksten".
 144. Hede 1925b, pp. 48-49: "Tabell..., Armfotingar, Hamra-kalksten".
 145. Hede 1925b, p. 34, bottom 3 lines - p. 35, top 4 lines: "Hamra-kalkstenen".
 146. Hede 1925a, p. 29, line 9-43: "revkalkstenen, Hamra-kalkstenen, märglig kalksten".
 147. Hede 1960, p. 85, bottom 14 lines - p. 86. Upper Hamra.
 148. Bassett & Cocks 1974, pp. 42-44: "Table 1. Summary of distribution..., Hamra Beds".

Comments on grouping of localities and references

D.

All references are probably referable to the upper part of Botvide Mbr, above the disappearance of *Panderodus panderi* (cf. Jeppsson submitted). Most of these fossil lists are labelled "Dayia flags", which is equal to the upper part of Botvide Mbr. Hurst visited the Botvide 1 locality in the 1970-ties, when it was greatly deteriorated and the bottom parts were inaccessible. This assumption is less secure when it comes to Nyan 2, Lau kanal och Hågvide 1, even if the short section at Nyan 2 would indicate its validity. Nevertheless, it is only the fossil list from Nyan 2 that are substantial, containing many species. The differences between Nyan 2 and Botvide 1 are that Hurst (1975) reports *Shaleria* (*Shaleria*) *ornatella* from Nyan 2 but not from Botvide 1, and vice versa when it comes to *Brachyprion* sp. Since already Munthe (1902) pointed out that the uppermost strata containing *S. (S.) ornatella* is missing at Botvide 1, this is not surprising. The *Shaleria* (*Shaleriella*) *ezerensis*, reported from Lau kanal (as *Shaleriella delicata*), is also found in both older and younger strata, while Hågvide 1 is the locality with the last appearance of *Atrypa* (*Atrypa*) *sowerbyi*. Even so, the ranges of the two later species are generally less well restricted.

E. and F.

These fossil lists are referable to the topmost decimetres of the Botvide Mbr.

G., H. and I.

This is the continuation of the successions treated in E. and F. Nevertheless, since the Hemse and Eke Beds are separated by a discontinuity surface, there is a time lapse. How great have not yet been determined, but Jeppsson (submitted) postulates the absence of only a few decimetres at Botvide 1.

J.

Copper (2004) gives no absolute measurements, only locality names. The other reference (Hede 1921) is also rather vague, stratigraphically speaking. Lower Eke Fm is the closest designation possible to use, even if both Bodudd 1 and Burgen 4 are localities comprising the Hemse-Eke boundary.

O.

The Eke-Burgsvik boundary is present at Ronehamn 2. Only a restricted amount of strata are exposed at the locality. A preserved piece of argillaceous limestone with the notation "500 m SV om Ronehamns hamn", kept at the GeoBiosphere Centre at Lund University, shows that the lithology is strongly dominated by calcareous algae.

P. and Q.

Most fossil lists from the past specify only the upper parts of the Burgsvik Fm or the whole Fm as one, as fossils are scarce especially in the lower parts.

P.

The fossil list from the Burgsvik drillcore (Hede 1919) is excluded from this interval, due to uncertainties with where the Eke-Burgsvik boundary should be drawn (cf. Jeppsson submitted). There are no possibilities to resample either, since the drillcore was destroyed during investigation. Even so, all species from the core, except *Dayia navicula*, are represented by the other references here given.

Q.

Hurst (1975) reports 2 st *Dayia navicula* from Hoburgen 2. The reference is included here, despite the uncertainties with the range of that species, since this is a locality possible to resample.

S. and T.

All reported species retained, also *Dayia navicula*, since they are only generally reported and no closer stratigraphic inferences can be made.

Appendix 2. Locality data

The localities are presented in stratigraphical order after Laufeld (1974a), Jeppsson & Jerre (ms) and Jeppsson (submitted). The interval of a single sample is given as, e.g. -0.3/-0.2 m; i.e. with the lower boundary first.

Mattsarve 1

GPS coordinates N6355475 O1669998, 1100 m NE (and slightly N) of Lau church, Hemse Group, När Fm. *P. siluricus* Zone (Jeppsson submitted).

Locality description – The locality is reached by a field road, starting immediately N of the Mattsarve farm and going NW-wards. To the NE of the field road a permanent pasture with juniper and blackthorn is separated from a levelled grazed field by a shallow ditch, trending NE-wards. The sample spot is situated where a cowtrail crosses the ditch, c. 50 m N of field road.

Field sample description – Sample G03-007LG, from -0.4/-0.3 m below ground surface, mainly consists of a c. 5 centimetres thick pure marl layer formed below a distinct continuous limestone layer. A minor part of the sample was collected immediately above that limestone layer. Other distinct limestone layers existed at c. -0.15 m and at -0.4 m below ground level; the first was underlain by another thick marl layer as well. An intermediate position at c. -0.25 m below ground surface were occupied by minor marly horizons formed between 2-3 thin, more or less lens shaped limestone layers.

Washed sample description – The tiny residue after washing consists of calcareous marlstone with a minor clastic component (Table 2). The preserved macroscopic fauna is generally poor and the brachiopods are also quite small, except for the atrypids.

Botvide 1

GPS coordinates N6355804 O1671532, c. 2530 m NE of Lau church and c. 170 m NE of the triangulation point 17.36, with the boundary horizon between the Hemse and Eke units. For a detailed description, see Munthe (1902) and Hede (1925b, 1960).

Locality description – Roadside section W of the road, c. 50 m SSW of the southern house at Botvide. The Hemse strata (Botvide Mbr) in the lower part of the section comprise stratified dolomite-rich limestone lenses and thinner marls. Accumulations of *Dayia navicula* occur in the limestone. The Eke strata in the upper part of the section are represented by crinoid limestone scattered with stromatoporoids and oncolites. The locality contains a large-scale antiform structure, and at the highest point the Hemse-Eke boundary is 2.25 m above the bottom of the ditch, but 7 m further to the north it is only 0.5 m above the ditch.

Field sample description – Sample G03-019LG was collected in a marly layer in the uppermost decimetre of the Hemse strata, starting at the highest point of the antiform, and continuing towards the north. The marly layer seems to laterally grade into a shell laden limestone layer. Even so, the marl, which thins substantially at places, probably overlies the limestone. In the collected marly material two or more 0.5-1.5 centimetres wide, flat pebbly conglomerate also existed (cf. Calner 2005). These often had a very rusty appearance.

Washed sample description – The residue after washing consists mainly of dolomitic marlstone with a fair amount of clastic material, together with chips of tightly cemented *coquinas* of dominantly *Dayia navicula* (Table 2).

Lau Backar 1

GPS coordinates N6354836 O1670836, c. 1250 m ENE of Lau church and c. 1000 m SW of the triangulation point near Botvide, Eke Fm, *Rhizophyllum* Limestone, probably the upper part of the Lower Eke Beds (Jeppsson submitted). For a detailed description, see Hede (1960).

Locality description – The locality is reached by following the power-line poles WNW-wards from the solitary white house at the sharp bend of the private road. Lau Backar 1 is a surface exposure with more or less waterfilled clay pits, surrounded by bushes. A marl sample was taken in a vegetationless, c. 10 m² wide, area on the far side of the crescent shaped clay pit closest to the road.

Field sample description – Sample G03-004LG, from -0.32/-0.15 m below ground surface, encompasses 0.5-5 centimetres thick marl layers. 1-3 centimetres thick carbonate-richer harder parts consisting of more or less lens shaped layers and individual concretions intercalated these marl layers. The amount of concretions possibly decreased deeper down. At the -0.15 m level below ground surface a c. 0.5 centimetres thick fine-grained grey layer of unknown origin, however resembling a bentonite layer, was encountered.

Washed sample description – The residue after washing consists mainly of fossils from a wide variety of groups, with a minor part calcareous and relatively hard marlstone, incorporating unidentifiable brachiopod shells. The soft calcareous marl also stuck rather hard to the individual valves, making the interior features of shells hard to evaluate. Nevertheless, the brachiopod fauna is very diverse and individuals are often quite big compared to the other localities. Only 1/6 of the smallest fraction (1-2 mm) was picked, due to the large number of already identified valves/individuals in coarser fractions. The whole 1-2 mm residue sample weighed 270 g, before picking.

Olsvenne 3

GPS coordinates N6331131 O1647101, c. 3600 m SSV of Näs church and c. 2870 m NE of the triangulation point 7.4, Eke Fm (Laufeld 1974b). Laufeld (1974b) considered Olsvenne 3 to be referable to the Eke Fm, lowermost part. However, due to the high amount of oncolids, the geographical position and yet unpublished conodont data (Jeppsson oral comment) this locality is regarded to represent the middle or upper Eke beds.

Locality description – Olsvenne 3 has been described as a "ditch exposure at the cattle-grid in the field road" (Laufeld 1974b). Today the ditch is overgrown and the cattle grid was removed over 15 years ago. The field road could nevertheless be identified, serving fields ESE of the road. A sample of heavily weathered marl was taken at the SW field, c. 1 m from the field road and c. 11 m from the edge of the main road.

Field sample description – Sample G03-017LG, consisting of oncoidal marl from -0.5/-0.35 m below ground surface, was underlain by a very hard marl surface.

Washed sample description – Due to the high oncoidal content, the residue after washing is relatively substantial (Table 2). Even so, the fauna seems to have been rich, with brachiopods comprising a substantial part. Obviously, identification of the encrusted specimens is impossible. Only 1/6 of the smallest fraction (1-2 mm) was picked, due to the large number of already identified valves/individuals in coarser fractions. The whole 1-2 mm residue sample weighed 850 g, before picking.

Bankvät 1

GPS coordinates N6334552 O1657713, c. 4680 m SE of Grötlingbo church and c. 1 km V of the NW-most point of the islet of Tuttar, Hamra Fm, unit b (Laufeld 1974b; Jeppsson submitted). For a detailed description, see Munthe (1921).

Locality description – Bankvät 1 is reached by walking through a permanent pasture, overgrown with blackthorn and juniper. From the gate in the fence, close to the sharp bend in the road SW of Kauparve, a stone fence is followed on its eastern side, towards the coast. At the coast, there is an irregular shaped vernal pool ("vät"), with the smaller part towards land. The greater outer one has a distinct edge. To the SV a high stone fence continues out in the sea and has a small square ruin close by it. The sample spot is situated in the vegetationless area between the pools, approximately 20 m from the closest edge of the outer pool and 80 m from the high stone fence in the NE.

Field sample description – Sample G03-374LJ, from -0.4/-0.3 m below ground level, consists of marl. In this, more or less concretionary and partly fossil rich limestone layers were also encountered.

Washed sample description – Only c. 5 kg was washed, due to the high content of brachiopods (Table 2). The residue consists of more or less calcareous micritic marlstone, often with a high crinoidal content. No attempt to identify the few brachiopods in the concretionary limestone pieces has been made.

Appendix 3. Selected taxonomic remarks

Inarticulate brachiopods

During the study, no other inarticulate species than *Craniops implicata* were identified. There is nevertheless a certain amount of variability within the *C. implicata* at Mattsarve 1 and Botvide 1, and this is not observed at the other localities. It is possible that more than one species is represented here. If so, then one species disappeared early during the event.

Orthids

Only one specimen of Orthid indet. sp. K and two of "*Dinorthis rigida*" was found. The first slightly resembles *Hesperorthis davidsoni*, by Bassett & Cocks (1974) considered to be confined to the Lower Visby Fm. The latter is represented in the early 20th century reference collection kept at the BioGeosphere Centre at Lund University, where it is labelled "*Dinorthis rigida*" (cf. Bassett 1970). No clear connection between that and the supposedly resembling *Hesperorthis martinssoni* sp. nov. described by Bassett & Cocks (1974) and can be made.

It is possible that a few individuals of *Salopina tubulata*, *Isorthis crassa* or *Dalejina hybrida* were identified as *Isorthis canaliculata*, due to disturbing matrix and pressure distortions. At Botvide 1 it is possible that part of the identified *I. canaliculata* is in reality *I. crassa*. The main internal identification features are obscured, however the c. 1/5 of the individuals that have a more arched commissure and a somewhat more globose form than the majority might be referable to *I. crassa*. It is also possible that *Isorthis crassa* in reality disappeared already before the Lau Event (cf. Bassett & Cocks 1974).

Strophomenoids

Strophomenid indet. sp. G is represented by only one shell, found at Botvide 1. It is possible that it is referable to *Brachyprion* sp.

In the cases when specimens with wide, rather flat and often thin shells lacked the taxonomic characters used in the literature, the ornamentation had to be considered. A faint pattern was equated with *Leptostrophia*, a coarse, even pattern with *Strophonella*, and an unequally parvicostellate pattern with *Shaleria*. The geniculate profile of *Shaleria* (*Shaleriella*) *ezerensis* and *Strophonella* (*Strophonella*) *euglypha*, compared to the more straight profile of the *Shaleria* (*Shaleria*) *ornatella* and *Leptostrophia filosa* provided further guidance.

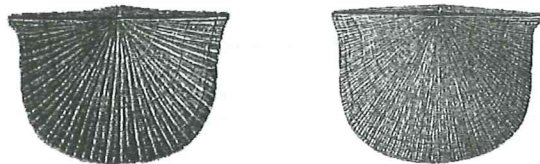


Fig. 18. *Shaleria* (*S.*) *ornatella* to the left, *Leptostrophia filosa* to the right. Modified after Davidson 1866-1871.

The Strophomenoids found at Bankvät 1 could very well belong to *Strophodonta* (*Strophodonta*) *hoburgensis* Hoel (submitted). The material is however rather small and only two out of five specimens clearly exhibits the described features; the rest resembles *Shaleria* (*S.*) *ornatella*. Even so, the whole population at Bankvät 1 is reported as *Strophodonta* (*S.*) *hoburgensis* in the quantitative study.

Morinorhynchus? sp. A and B

Morinorhynchus? sp. A at Botvide 1 is represented by one single specimen and might possibly be referable to *M. crispus*. *Morinorhynchus?* sp. B, identified from Lau Backar 1 and Olsvenne 3, is probably close to or identical to *M. rubeli* sp. nov., recently described by Musteikis & Cocks (2004) from Lithuania. It is also possible that single individuals of *Coolina* were identified as *Morinorhynchus?* sp. B at Olsvenne 3.

Pentamerids

The whole population of the *Gypidula galeata* is juvenile. Therefore the commissure is rather straight, or slightly wavy, not undulating at a greater scale as at e.g. the specimen figured as *G. galeata* by Bassett & Cocks (1974: Pl. 5:8a-d). The beak is in the most cases not as incurved either. It is possible that a few here identified *G. galeata* is in reality juvenile *Howellella elegans*. Moreover, Bassett & Cocks (1974) mentions that it is possible that the Eke *Gypidula* sp. is a modified form.

Microsphaeridiorhynchus? nucula

It is possible that a few specimens of *Anastrophia deflexa* or much less probably *Sphaerirhynchia wilsoni* were identified as *Microsphaeridiorhynchus?* *nucula*, due to disturbing matrix and pressure distortions.

The collection of *Sphaerirhynchia wilsoni* from Lau Backar 1 is very much affected by pressure distortions and most looks like "dehydrated" *N. pisum*. It is therefore possible that a few *S. wilsoni* were wrongly identified as *N. pisum*.

Atrypids

The collection of Atrypid indet. sp. F from Mattsarve 1 consists of rather small individuals. At the same time *Atrypa* (*A.*) *sowerbyi* from the same locality consists of fully grown individuals. The easy conclusion would be that they are all representatives of the same species. However, Atrypid indet. sp. F do not resemble the figured *A.* (*A.*) *sowerbyi* in Coppers monograph (2004), due to its more rugged surface.

The atrypid species expected at the stratigraphical level at Olsvenne 3 is *Atrypa* (*Atrypa*) *alata* (Copper 2004). Even so, the common Atrypid indet. sp. E does not seem to be possible to equate with that species, nor with any other atrypid taxa of widely comparable age, represented in Copper's monograph. It is however possible that the less common Atrypid indet. sp. D is really *A.* (*A.*) *alata*.

Athyridids

It is possible that a few individuals of "*Whitfieldella nitida*" or less probably *Didymothyris didyma* have been identified as cf. *Glassina laeviscula* due to the lack of visible internal features. It is also possible that some cf. *G. laeviscula* were wrongly identified as *Nucleospira pisum*.

Spiriferids

The here identified *D. elevata* mainly differs from *Howellella elegans* in the greater width of the interarea, since no internal features were possible to investigate.

The whole identified collection of *Striispirifer* sp. L consists of juveniles. Nevertheless, it could probably be equated with *Striispirifer striolatus*, previously reported from the studied interval. It is however also a slight possibility that they are juveniles of *H. elegans*.

Appendix 4. A selection of species name synonyms

Groupings in superfamilies mainly according to Treatise on Invertebrate palaeontology, Pt H (Brachiopoda) (Williams *et al.* 1965, revised 2000-2002). Updates names used herein in bold.

Bassett & Cocks 1974	Hede 1960	Hede 1920-ties	Munthe 1921	Munthe 1902 / Munthe 1910	Lindström 1860	Notes and explanations
[Superfamily CRANIOPSOIDEA]						
	<i>Craniops implicata</i>	<i>Pholidops implicata</i>		<i>Pholidops implicata</i> / -	<i>Discina implicata</i>	Lindström 1860, 375. Davidson 1866-1871 Vol. III Pt. VII, p. 80, pl. viii, 13-18: <i>Crania implicata</i> . Cocks 1978, 20: <i>Craniops implicatus</i> . Popov & Holmer 2000, 164-165: <i>Craniops implicata</i> (Sowerby 1839).
[Superfamily ORTHACEA [ORTHOIDEA]						
<i>Hesperorthis gotlandica</i> (Schuchert & Cooper 1932)	<i>Schizorammina gotlandica</i>	<i>Dinorthis rustica</i> (Sow)	<i>Dinorthis rustica</i> (Sow)	<i>Orthis rustica</i>	<i>Orthis rustica</i>	Lindström 1860, 370. Davidson 1866-1871 Vol. III Pt. VII, p. 238, pl. xxiv, 13-17. Bassett & Cocks 1974, 6. Only tentative correlation to <i>Dinorthis rustica</i> .
<i>Ptychopleurella bouchardi</i> (Davidson 1847)	<i>Ptychopleurella bouchardi</i>	<i>Orthis Bouchardi</i>		<i>Orthis Bouchardi</i> / -	<i>Orthis Bouchardi</i>	Davidson 1866-1871 Vol. III Pt. VII, p. 209, pl. xxvi, 16-23. Bassett & Cocks 1974, 8. Cocks 1978, 49.
[Superfamily ENTELEACEA [ENTELETOIDEA]						
<i>Salopina tubulata</i> (Lindström 1860)					<i>Orthis tubulata</i>	Lindström 1860, 367-368. Bassett & Cocks 1974, 9.
<i>Linoporella punctata</i> (de Vermeuil 1848)	<i>Linoporella cf. punctata</i>	<i>Orthis punctata</i>	<i>Orthis punctata</i>	- / <i>Orthis punctata</i>	<i>Orthis punctata</i>	Bassett & Cocks 1974, 12. Cocks 1978, 81.
[Superfamily DALMANELLOIDEA]						
<i>Isorthis canaliculata</i> (Lindström 1860)	<i>Levenea canaliculata</i>	<i>Dalmanella canaliculata</i>		<i>Orthis canaliculata</i> / -	<i>Orthis canaliculata</i>	Davidson 1866-1871 Vol. III Pt. VII, p. 218, pl. xxvii, 12-13. Bassett & Cocks 1974, 10. Walmsley & Boucot 1975, 93: <i>Levenea canaliculata</i> .
<i>Isorthis crassa</i> (Lindström 1860)	" <i>Orthis</i> " <i>crassa</i>	<i>Dalmanella crassa</i>			<i>Orthis crassa</i>	Davidson 1866-1871 Vol. III Pt. VII, p. 213, pl. xxvii, 17-19. Bassett & Cocks 1974, 10. Walmsley & Boucot 1975, 80: <i>Isorthis (Arcuella) crassa</i> .
<i>Delejina hybrida</i> (Sowerby 1839)	<i>Rhipidomella cf. hybrida</i>	<i>Rhipidomella hybrida</i>		<i>Orthis hybrida</i> / -	<i>Orthis hybrida</i>	Davidson 1866-1871 Vol. III Pt. VII, p. 214, pl. xxvii, 15-16. Bassett 1972, 62-64. Bassett & Cocks 1974, 11. Cocks 1978, 71.
[Superfamily EICHWALDIACEA [EICHWALDIOIDEA]						
<i>Dictyonella capewellii</i> (Davidson 1848)		<i>Dictyonella Capewelli</i>		- / <i>Eichwaldia Capewelli</i>	<i>Porambonites? Capewelli</i> (Dav)	Davidson 1866-1871 Vol. III Pt. VII, p. 193, pl. xxv, 12-15 (<i>N.b.</i> not fig. 13 acc. to Cocks 1978). Bassett & Cocks 1974, 12. Cocks 1978, 90.
[Superfamily PLECTAMBONITACEA [PLECTAMBONITOIDEA]						
<i>Aegirita grayi</i> (Davidson 1849)	<i>Chonetoidea grayi</i>	<i>Plectambonites? inconstans</i> (Haupt)	<i>Plectambonites? inconstans</i> (Haupt)			Bassett & Cocks 1974, 13. Cocks 1978, 104. Musteikis & Cocks 2004, 469-470: <i>Jonesea grayi</i> Only tentative correlation to <i>Plectambonites? inconstans</i> .
[Superfamily STROPHOMENACEA [STROPHOMENOIDEA]						
<i>Leptostrophia filosa</i> (Sowerby 1839)		<i>Leptostrophia filosa</i>	<i>Leptostrophia filosa</i>		<i>Strophomena filosa</i>	Davidson 1866-1871 Vol. III Pt. VII, p. 307, pl. xiv, 14-20. Bassett & Cocks 1974, 15. Cocks 1978, 126-127. Musteikis & Cocks 2004, 464-465: <i>Mesoleptostrophia (Mesoleptostrophia) filosa?</i>
<i>Shaleria aff. ornatella</i> (Davidson 1871)	<i>Shaleria? impressa</i>	<i>Leptostrophia impressa</i>	<i>Leptostrophia impressa</i>	<i>Strophomena impressa</i>		Davidson 1866-1871 Vol. III Pt. VII, p. 309, pl. xii, 16-20. Bassett & Cocks 1974, 17. Cocks 1978, 129. Cocks & Rong 2000, 300-301: <i>Shaleria (Shaleria) ornatella</i> .
<i>Strophonella (Strophonella) euglypha</i> (Dalman 1828)	<i>Strophonella euglypha</i>	<i>Strophonella euglypha</i>		- / <i>Strophomena euglypha</i>	<i>Strophomena euglypha</i>	Davidson 1866-1871 Vol. III Pt. VII, p. 288, pl. xj, 1-5. Bassett & Cocks 1974, 17. Cocks 1978, 131. Harper & Boucot 1978a, 95-97: <i>Strophopron euglypha</i> . Musteikis & Cocks 2004: <i>Strophonella euglypha</i>
[Superfamily DAVIDSONIACEA [ORTHOTETOIDEA]						
<i>Morinorhynchus crispus</i> (Lindström 1861)		<i>Strophomena crispata</i>		<i>Strophomena serrulata</i> / -		Bassett & Cocks 1974, 20. cf. Bassett 1977, 98
[Superfamily CHONETACEA [CHONETOIDEA]						
<i>Protochonetes striatellus</i> (Dalman 1828)	<i>Chonetes striatellus</i>	<i>Chonetes striatellus</i>	<i>Chonetes striatellus</i>	<i>Chonetes striatella</i>	<i>Chonetes striatella</i>	Davidson 1866-1871 Vol. III Pt. VII, p. 331, pl. xlix, 23-26. Bassett & Cocks 1974, 22. Cocks 1978, 135.
[Superfamily PORAMBONITACEA]						
<i>Anastrophia deflexa</i> (Sowerby 1839)	<i>Anastrophia deflexa</i>	<i>Anastrophia deflexa</i>	<i>Anastrophia deflexa</i>	- / <i>Rhynchonella deflexa</i>	<i>Rhynchonella deflexa</i>	Davidson 1866-1871 Vol. III Pt. VII, p. 178, pl. xxi, 24-27. Bassett & Cocks 1974, 22. Cocks 1978, 139.
[Superfamily PENTAMERACEA]						
<i>Gypidula galeata</i> (Dalman 1828)	<i>Gypidula galeata</i>	<i>Gypidula galeata</i>		- / <i>Pentamerus galeatus</i>	<i>Pentamerus galeatus</i>	Davidson 1866-1871 Vol. III Pt. VII, p. 145, pl. xv, 13-23. Bassett & Cocks 1974, 24. Cocks 1978, 144.
[Superfamily RHYNCHONELLACEA]						
<i>Rhynchotreta cuneata</i> (Dalman 1828)				<i>Rhynchonella cuneata</i>	<i>Rhynchonella cuneata</i>	Davidson 1866-1871 Vol. III Pt. VII, p. 164, pl. xxi, 7-11. Bassett & Cocks 1974, 25-26. Cocks 1978, 146.
<i>Ferganella diodontia</i> (Dalman 1828)		<i>Camarotoechia diodontia</i>		- / <i>Rhynchonella diodontia</i>	<i>Rhynchonella borealis</i> var. <i>diodontia</i>	Davidson 1866-1871 Vol. III Pt. VII, p. 174, pl. xxi, 21-23 (<i>N.b.</i> not fig. 21 acc. to Cocks 1978). Bassett & Cocks 1974, 26. Cocks 1978, 148: <i>Stegerhynchus diodontia</i> .
<i>Microsphaeridiorhynchus? nucula</i> (Sowerby 1839)	<i>Camarotoechia nucula</i>	<i>Camarotoechia nucula</i>		<i>Rhynchonella nucula</i>	<i>Rhynchonella nucula</i>	Davidson 1866-1871 Vol. III Pt. VII, p. 181, pl. xxv, 14. Kozłowski 1929, 150: <i>Camarotoechia nucula</i> . Bassett & Cocks 1974, 27. Cocks 1978, 150.

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<i>Sphaerirhynchia wilsoni</i> (Sowerby 1816)	<i>Sphaerirhynchia wilsoni</i> (<i>Sphaerirhynchia wilsoni</i>)	<i>Wilsonia Wilsoni</i>		<i>Rhynchonella Wilsonii</i>	<i>Rhynchonella Wilsoni</i>	Davidson 1866-1871 Vol. III Pt. VII, p. 167, pl. xx4, 7-11. British Museum 1964, 90. Bassett & Cocks 1974, 27. Cocks 1978, 152-153.
Superfamily ATRYPACEA						
<i>Spirigerina quinquecostata</i> (Munthe 1910)	<i>Plectatrypa marginalis quinquecostata</i>	<i>Atrypa marginalis 5-costata</i>	<i>Atrypa marginalis 5-costata</i>	- / <i>Atrypa marginalis</i> nov. var. <i>5-costata</i>		Lindström 1860, 363 mentions a var. of <i>Spirigerina marginalis</i> (Dalman). Bassett & Cocks 1974, 30. Copper 2004, 104-106.
Superfamily DAYIACEA						
<i>Dayia navicula</i> (Sowerby 1839)	<i>Dayia navicula</i>	<i>Dayia navicula</i>	<i>Dayia navicula</i>	<i>Dayia navicula</i>	<i>Rhynchonella navicula</i>	Davidson 1866-1871 Vol. III Pt. VII, p. 190, pl. xxi, 20-23. Davidson 1882-1883, 96-97, pl. v, 1-4. Kozłowski 1929, 179-181. Bassett & Cocks 1974, 31. Cocks 1978, 167. Havlicek & Storch 1990, 205-206.
<i>Coelospira pusilla</i> (Hisinger 1837)	"A." <i>pusilla</i>	<i>Atrypa? pusilla</i>	<i>Atrypa? pusilla</i>	- / <i>Atrypa? pusilla</i>	<i>Spirigerina? pusilla</i>	Bassett & Cocks 1974, 32. Havlicek & Storch 1990, 207: <i>Navispira pusilla</i>
Superfamily RETZIAEACEA						
<i>Homoeospira baylei</i> (Davidson 1848)	<i>Rhynchospirina baylei</i>	<i>Retzia Baylei</i>	<i>Retzia Baylei</i>	<i>Retzia Salteri</i> var <i>Baylei</i>	<i>Retzia Baylei</i>	Davidson 1866-1871 Vol. III Pt. VII, p. 127, pl. xii, 23-25, 27. Kozłowski 1929, 212-213: <i>Rhynchospirina Baylei</i> . Bassett & Cocks 1974, 33. Cocks 1978, 161. Rubel 1982: <i>H. baylei</i> = <i>Rhynchospirina baylei</i> . Nikiforova et al. 1985, 55-56.
Superfamily ATHYRIDACEA						
<i>Didymothyris didyma</i> (Dalman 1828)	<i>Protathyris didyma</i>	<i>Whitfieldella didyma</i>		<i>Meristina didyma</i>	<i>Spirigera didyma</i>	Bassett & Cocks 1974, 34. Cocks 1978, 207: <i>Meristina didyma</i> in the Davidson collection = <i>Whitfieldella</i> sp. Tentative correlation only.
		<i>Whitfieldella nitida</i>		<i>Meristina cfr nitida</i> / -	<i>Spirigera? nitida</i>	Cocks 1978, 207, 208: <i>Meristina nitida</i> Hall in Davidson's monograph = <i>Whitfieldella nitida</i> (Hall 1843). Tentative correlation only.
cf. <i>Glassina laeviuscula</i> (Sowerby) <i>sensu</i> Davidson 1867		cf. <i>Athyris?</i> <i>laeviuscula</i>				Davidson 1882-1883, 101-103, pl. 1v, 24-26. Bassett & Cocks 1974, 34. Cocks 1978, 164.
<i>Nucleospira pisum</i> (Sowerby 1839)		<i>Nucleospira pisum</i>		<i>Nucleospira pisum</i> / -	<i>Spirigera? pisum</i>	Davidson 1866-1871 Vol. III Pt. VII, p. 106, pl. x, 16-20. Bassett & Cocks 1974, 35. Cocks 1978, 167.
Superfamily CYRTIACEA						
<i>Janius barrandi</i> (de Vemeuil 1848)	<i>Janius schmidti</i>	<i>Spirifer Schmidti</i>		<i>Spirifera Schmidti</i> / -	<i>Spirifera Schmidti</i>	Hedström 1923, pl. 4, 10-14. Bassett & Cocks 1974, 36. Boucot 1962, 698-700: <i>Janius schmidti</i> .
<i>Strispirifer striolatus</i>	" <i>Eospirifer</i> " <i>striolatus</i>	<i>Spirifer striolatus</i>	<i>Spirifer striolatus</i>	<i>Spirifera striolata</i>	<i>Spirifera striolata</i>	Bassett & Cocks 1974, 37.
Superfamily SPIRIFERACEA						
<i>Delthyris elevata</i> (Dalman 1828)	<i>Delthyris elevata</i>	<i>Spirifer elevatus</i>		<i>Spirifera elevata</i> / -	<i>Spirifera elevata</i>	Davidson 1866-1871 Vol. III Pt. VII, p. 95, pl. x, 7-11 (<i>N.b. not D. elevata</i> acc. to Bassett & Cocks 1974. Davidson's figs. 7, 8, 10, 11 assigned to <i>Howellella subsignis</i> by Cocks 1978. However, the two genera may be externally homeomorphic). Kozłowski 1929, 185-187: <i>Spirifer (Delthyris) elevatus</i> . Bassett & Cocks 1974, 37.
<i>Howellella elegans</i> (Muir-Wood 1925)	<i>Howellella</i> cf. <i>elegans</i>	<i>Spirifer crispus</i>				Davidson 1866-1871 Vol. III Pt. VII, p. 97, pl. x, 13-15: <i>Spirifera crispus</i> . Kozłowski 1929, 190-191: <i>Spirifer (Crispella) crispus</i> . Bassett & Cocks 1974, 38. Cocks 1978, 162-163.
<i>Boucotinskia sulcata</i> (Hisinger 1831)	<i>Hedeina crista</i>	<i>Spirifer sulcatus</i>	<i>Spirifer sulcatus</i>	<i>Spirifera sulcata</i> / -	<i>Spirifera sulcata</i>	Davidson 1866-1871 Vol. III Pt. VII, p. 91, pl. x, 4-6 (<i>N.b. not B. sulcata</i> acc. to e.g. Boucot 1957 and Cocks 1978, but <i>Kozłowskiella strawi</i>). However, the two genera are externally homeomorphic and only <i>B. sulcata</i> is known from Ludlow and Gotland). Boucot 1957, 324-326, 330-331, pl. 2. Brunton et al. 1967, 179-180. Bassett & Cocks 1974, 38-39.
<i>Boucotinskia? elongata</i> (Munthe 1910)	" <i>Spirifer</i> " <i>insignis</i> <i>minor</i>	<i>Spirifer insignis</i> cf. <i>minor</i>		<i>Spirifera Schmidti</i> var. <i>elongata</i> / <i>Spirifera sulcata</i> var. <i>elongata</i>		Hedström 1923, 13-15, pl. 5. Boucot 1962, 698-700: <i>Janius insignis</i> . Bassett & Cocks 1974, 39.

Appendix 6. Ranges of selected taxa

Munthe (1910, 1921) described only Hemse-Sundre beds, Hede (1921) lacked the Halla beds, Hede (1925b) only treated the Hemse-Hamra beds, Hede (1927) dealt with Slite-Burgsvik and Hurst with Lower Visby-Burgsvik. Bassett & Cocks (1974) = their "Table 1: Summary".

x - reported, (x) - uncertain report, - reference work do not cover the stratigraphic interval, ?/aff. - as indicated by quoted author. Updated names used herein in bold. *Author not worked with material from Gotland.

Species	Reference	L. Visby Marl	U. Visby Marl	Hogklint Lst	Tofta Lst	Slite Gr	Halla Lst	Mulde Marl	Klinteberg Lst	Hemse Gr	Eke Marl	Burgsvik Sst	Hamra Lst	Sundre Lst
INARTICULATES														
<i>Lingula "Lewisi"</i>	Hede 1921									x	x			
<i>Lingula Lewisi</i>	Hede 1925b	-	-	-	-	-	-	-	-	x				-
<i>Lingula Lewisi</i>	Hede 1927	-	-	-	-			(x)		x			-	-
<i>Lingula striata</i>	Hede 1921									x	x			
<i>Lingula striata</i>	Hede 1927	-	-	-	-			(x)		x			-	-
<i>Orbiculoidea rugata</i>	Hede 1921					x	-		x	x	x			
<i>Craniops implicata</i>														
<i>Pholidops implicata</i>	Hede 1921		x	x		x	-	x	x	x	x	x	x	x
Superfamily ORTHACEA [ORTHOIDEA]														
<i>Hesperorthis gotlandica</i>	Bassett & Cocks 1974											x		
<i>Dinorthis rustica</i>	Hede 1921								x	x		x		x
<i>Dinorthis rustica</i>	Munthe 1921	-	-	-	-	-	-	-	-	-	-	x	x	x
<i>Ptychopleurella bouchardi</i>	Bassett & Cocks 1974					x			x	x	x		x	x
<i>Orthis Bouchardi</i>	Hede 1921								x	x	x			
Superfamily ENTELETACEA [ENTELETOIDEA]														
<i>Linporella punctata</i>	Bassett & Cocks 1974			x		x							?	
<i>Orthis punctata</i>	Munthe 1921	-	-	-	-	-	-	-	-	-	-	x	x	
[Superfamily DALMANELLOIDEA]														
<i>Isorthis canaliculata</i>	Bassett & Cocks 1974									?	x	x	x	x
<i>Dalmanella canaliculata</i>	Hede 1921					x	-	x	x	x	x	x	x	x
<i>Isorthis crassa</i>	Bassett & Cocks 1974						?	x		x				
<i>Dalmanella crassa</i>	Hede 1921					x	-	x	x	x	x			
<i>Dalmanella crassa</i>	Hede 1927	-	-	-	-	(x)		x	x	x	x		-	-
<i>Dalejina hybrida</i>	Bassett & Cocks 1974			x		x	x	x		x	x			
<i>Rhipidomella hybrida</i>	Hede 1921		x			x	-	x		x	x			
Superfamily EICHWALDIACEA [EICHWALDIOIDEA]														
<i>Dictyonella capewellii</i>	Bassett & Cocks 1974		x	x		x	x		aff.	aff.	x			
<i>Eichwaldia Capewellii</i>	Munthe 1910	-	-	-	-	-	-	-	-	-	-		x	
Superfamily PLECTAMBONITACEA [PLECTAMBONITOIDEA]														
<i>Jonesea grayi</i>	*Musteikis & Cocks 2000													
<i>Aegiria grayi</i>	Bassett & Cocks 1974									x				
<i>Plectambonites? inconstans</i>	Hede 1921									x				
Superfamily STROPHOMENACEA [STROPHOMENOIDEA]														
<i>Lepidoleptaena poulsoni</i>	Hoel in press									x	x		x	x
<i>Leptostrophia filosa</i>	Bassett & Cocks 1974		x	x					aff.	x				
<i>Leptostrophia filosa</i>	Hede 1921						-	x	x	x			x	
<i>Shaleria (S.) ornatella</i>	*Cocks & Rong 2000													
<i>Shaleria aff. ornatella</i>	Bassett & Cocks 1974									x	x	x		
<i>Leptostrophia impressa</i>	Hede 1921									x	x	x	x	
<i>Strophonella (S.) euglypha</i>	Bassett & Cocks 1974							x		x	x			
<i>Strophonella euglypha</i>	Hede 1921					x	-	x	x	x	x	x		
<i>Strophomena euglypha</i>	Munthe 1910	-	-	-	-	-	-	-	-		x	x	x	
Superfamily DAVIDSONIACEA [ORTHOTETOIDEA]														
<i>Coolinia pecten</i>	Bassett & Cocks 1974	x	x	x		x			x		x			
<i>Coolinia pecten</i>	Hurst 1974	-	x	x							-	-	-	
Superfamily CHONETACEA [CHONETOIDEA]														
<i>Protochonetes striatellus</i>	Bassett & Cocks 1974									x	x	x	x	
<i>Chonetes striatellus</i>	Hede 1921									x	x	x	x	

Species	Reference	L. Visby Marl	U. Visby Marl	Hogskind Lst	Tofta Lst	Slite Gr	Halla Lst	Mulde Marl	Klimateberg Lst	Hense Gr	Eke Marl	Burgsvik Sst	Hanna Lst	Sundre Lst
Superfamily PORAMBONITACEA														
<i>Anastrophia deflexa</i>	Bassett & Cocks 1974				x	x			x	x	x		x	
<i>Anastrophia deflexa</i>	Hede 1921						-				x		x	
<i>Anastrophia deflexa</i>	Hede 1925b	-	-	-	-	-	-	-	-		x	x		-
Superfamily PENTAMERACEA														
<i>Gypidula galeata</i>	Bassett & Cocks 1974					x	x	x	x	x	aff.			
<i>Gypidula galeata</i>	Hede 1921					x	-			x				
<i>Gypidula galeata</i>	Hede 1927	-	-	-	-	(x)	?	(x)	x	x				
<i>Gypidula galeata</i>	Munthe 1921											x	x	
Superfamily RHYNCHONELLACEA														
<i>Ferganella diodonta</i>	Bassett & Cocks 1974			?		x			x	x				
<i>Camarotoechia diodonta</i>	Hede 1921				x	x	-	x		x	x	x		
<i>Rhynchonella diodonta</i>	Munthe 1910	-	-	-	-	-	-	-	-		x	x	x	
<i>Microsphaeridiorhynchus? nucula</i>	Bassett & Cocks 1974		x	x		x	x	x	x	x	x	x	x	
<i>Camarotoechia nucula</i>	Hede 1921			x	x	x	-	x	x	x	x	x	x	x
<i>Sphaerirhynchia wilsoni</i>	Bassett & Cocks 1974								x		x			
<i>Wilsonia wilsoni</i>	Hede 1921						-	x	x	x				
<i>Rhynchonella wilsoni</i>	Munthe 1910													x
Superfamily DAYIACEA														
<i>Dayia navicula</i>	Bassett & Cocks 1974									x	x			
<i>Dayia navicula</i>	Hede 1921						-			x	x			
<i>Navispira pusilla</i>	*Havlicek & Štorch 1990													
<i>Coelospira pusilla</i>	Bassett & Cocks 1974										x	x	x	
<i>Atrypa? pusilla</i>	Hede 1921						-				x	x	x	
Superfamily RETZIACEA														
<i>Homoeospira baylei</i>	Bassett & Cocks 1974						x				x		x	
<i>Retzia Baylei</i>	Hede 1921						-				x	x	x	
Superfamily ATHYRIDACEA														
<i>Didymothyris didyma</i>	Bassett & Cocks 1974							?	?	x	?			
<i>Whitfieldella didyma</i>	Hede 1921					x	-	x		x				
<i>Whitfieldella didyma</i>	Hede 1925b	-	-	-	-	-	-	-	-	x	x			-
<i>Meristina didyma</i>	Munthe 1910	-	-	-	-	-	-	-	-				x	
cf. <i>Glassina laeviscula</i>	Bassett & Cocks 1974								x	x				
cf. <i>Athyris? laeviscula</i>	Hede 1925b	-	-	-	-	-	-	-	-		x			-
<i>Nucleospira pisum</i>	Bassett & Cocks 1974			x		x		x			x			
<i>Nucleospira pisum</i>	Hede 1921	x				x	-	x		x	x			
Superfamily CYRTIACEA														
<i>Janius barrandi</i>	Bassett & Cocks 1974									x	x			
<i>Spirifer Schmidtii</i>	Hede 1921						-			x	x			
<i>Spirifer Schmidtii</i>	Hede 1927	-	-	-	-				(x)	x			-	-
<i>Strispirifer striolatus</i>	Bassett & Cocks 1974								x		x	x	?	?
<i>Spirifer striolatus</i>	Hede 1921						-				x		x	
Superfamily SPIRIFERACEA														
<i>Delthyris elevata</i>	Bassett & Cocks 1974							x		?	?		?	
<i>Spirifer elevatus</i>	Hede 1921					x	-	x		x	x	x	x	x
<i>Spirifer elevatus</i>	Hede 1927	-	-	-	-	-	x	x	x	x	x		-	-
<i>Howellella elegans</i>	Bassett & Cocks 1974	x	x	x		x	x	x		x			x	x
<i>Spirifer crispus</i>	Hede 1921		?			x	-	x	x	x	x		x	
<i>Spirifer crispus</i>	Hede 1927	-	-	-		x		x		x			-	-
<i>Boucotinskia sulcata</i>	Bassett & Cocks 1974										x	x	x	
<i>Spirifer sulcatus</i>	Hede 1921						-				x		x	
<i>Boucotinskia? elongata</i>	Bassett & Cocks 1974										x			
<i>Spirifer insignis</i> cf. <i>minor</i>	Hede 1925b	-	-	-	-	-	-	-	-		x			x
<i>Spirifera sulcata</i> var. <i>elongata</i>	Munthe 1910	-	-	-	-	-	-	-	-		x			

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