Changes in beyrichiid ostracode faunas during the Late Silurian Lau Event on Gotland, Sweden

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Department of Earth- and Ecosystem Sciences Division of Geology Lund University 2010

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Cover Picture: A selection of beyrichiid specimens, recorded from Late Silurian strata at Gotland. From the upper left, to the lower right; *Beyrichia (Simplicibeyrichia) globifera, Sleia equestris, Neobeyrichia (Nodibeyrichia) scissa, Hemsiella loensis, Neobeyrichia (Nodibeyrichia) regnans* and *Neobeyrichia (Neobeyrichia) ctenophora.*

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Abstract: This paper deals with how palaeocope ostracodes of the family Beyrichiidae, from the Silurian strata at Gotland were affected by the Late Silurian Lau Event. The Lau Event is associated with a positive carbon isotope excursion, lithology changes and faunal changes in accumulated strata related to sea-level changes and a glaciation in the Late Ludlow. In order to find out how the beyrichiid faunas where affected by the event, fossils have been studied through samples collected from five different localities on Gotland, exposing pre-Lau Event, Lau Event, and post-Lau Event strata. A total of 633 beyrichiid specimens representing 22 different taxa were identified in the samples. Based on literature studies on the beyrichiid biostratigraphy on Gotland, an additional 15 taxa were included in this study, and an additional 27 localities. Subfamilies of Beyrichiidae treated herein are; Craspedobolbininae, Amphitoxotidinae, Treposellinae, Beyrichiinae and Hexophthalmoidinae. Except Hexophthalmoidinae, which disappears before the event, all subfamilies have been affected by the Lau Event. Several taxa were negatively affected, reported as e.g. 11 last appearance datums (LAD:s), four Lazarus taxa and three Lilliput taxa. Taxa that have been negatively affected by the Lau Event are e.g. Neobeyrichia (Neobeyrichia) lauensis and Neobeyrichia (Nodibeyrichia) scissa which occurs frequently in pre-event strata, but diminishes in frequency in middle event strata, to eventually disappear in upper event strata. The lineages of taxa such as Hemsiella anterovelata, Calcaribeyrichia bicalcarata, Hoburgiella tenerrima and Plicibeyrichia ornatissima have gaps through extensive portions of the event strata, and reappear again in post-event strata. Other taxa show a positive response to the event reflected by frequent occurrences and high abundances in relation to other taxa in the Lau Event strata. Neobeyrichia (Neobeyrichia) ctenophora occurs scarcely in pre-event strata, but is very frequent in event strata. The lineage of N. (Ne.) ctenophora continues into post-event strata where it is less frequent. Similarly, Hemsiella loensis and *Sleia equestris* occur frequently in event strata compared to many other taxa which are rare, occur as Lazarus taxa or have their LAD: s in Lau Event strata. A recovery of the beyrichiid faunas is apparent in the Hamra Fm., where the fauna is characterized by a moderate diversity and with reappearing Lazarus species and recovered Lilliput species. Based on the faunal changes, it can be concluded that a re-organisation among beyrichiids did occur during the Lau Event.

Keywords: Gotland, Late Silurian, Lau Event, ostracodes, Beyrichiidae, faunal turnovers.

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Förändringar i beyrichiida ostrakodfaunor under den sensiluriska Laukatastrofen på Gotland

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Abstrakt: Den här uppsatsen behandlar hur palaeocopa ostrakodfossil av familjen Beyrichiidae, avsatta i sensilurisk lagerföljd på Gotland, påverkades av den så kallade Laukatastrofen som ägde rum i sen Ludlow. I lagerföljd avsatt under Laukatastrofen har bland annat positiva kolisotopanomalier, litologiförändringar och faunaförändringar påvisats, vilka är relaterade till globala havsnivåförändringar och en glaciation i sen Ludlow. För att ta reda på hur beyrichiidfaunan påverkades av katastrofen, har prover insamlade från fem olika lokaler på Gotland studerats. För att jämföra pre-katastrof fauna, katastroffauna och post-katastrof fauna, har proverna insamlats från lagerföljd avsatt innan-, under-, och efter Laukatastrofen. Totalt har 633 beyrichiidfossil fördelat på 22 skilda taxa identifierats med hjälp av provmaterialet. Dock behandlas ytterligare 15 taxa baserat på litteraturstudier av beyrichiidernas biostratigrafi på Gotland, och 27 övriga lokaler med pre-katastrof fauna, katastrof fauna och post-katastrof fauna. Underfamiljer till Beyrichiidae, som har påträffats i det aktuella tidsintervallet är; Craspedobolbininae, Amphitoxotidinae, Treposellinae, Beyrichiinae och Hexophthalmoidinae. Med undantag för Hexophthalmoidinae som försvinner innan Laukatastrofen, har alla underfamiljer visat sig påverkas av katastrofen. I Laukatastroflager har bland annat 11 utdöenden, fyra Lazarustaxa och tre Lilliputfaunor påträffats. Exempel på taxa som påverkats negativt av katastrofen är Neobeyrichia (Neobeyrichia) lauensis och Neobeyrichia (Nodibeyrichia) scissa, vilka förekommer frekvent i prekatastroflager och äldre katastroflager, men vilka uppträder endast sällan i övre katastroflager där arterna så småningom dör ut. Lazarusfaunor i katastroflager har påvisats bland arterna Hemsiella anterovelata, Calcaribeyrichia bicalcarata, Hoburgiella tenerrima och Plicibeyrichia ornatissima. Viss taxa har gynnats positivt av katastrofen då de dominerar markant över andra arter i fråga om frekvens eller abundans i katastroflager. Neobeyrichia (Neobeyrichia) ctenophora, Hemsiella loensis och Sleia equestris förekommer frekvent i Laukatastroflager, i motsats till andra taxa som förekommer mycket sällan eller dör ut i katastroflager. S. equestris och H. loensis förekommer också i ett högt antal exemplar i de prover som har insamlats från katastroflager. Vidare påträffas uppkomst av nio nya taxa i katastroflager. En återhämtning av beyrichiidfaunan påvisas i postkatastrof lager där Lazarustaxa återkommer, Lilliputfaunor återhämtas och en mer divers fauna förekommer. Baserat på förändringarna som påvisats bland studerade beyrichiidtaxa, kan det konstateras att det har skett en omorganisation av beyrichiidfaunan under Laukatastrofen.

Nyckelord: Gotland, Sensilur, Laukatastrofen, ostrakoder, beyrichiider, faunaförändringar.

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1 Introduction

The Late Ludlow Lau Event had a profound impact on the marine realm. The event is associated with lithology changes and alterations in the positive $\delta^{13}C$ isotope composition and $\delta^{18}O$ composition (see e.g. Jeppsson 1990, 1998; Jeppsson & Aldridge 2000; Talent et al. 1993; Eriksson & Calner 2008). The Lau Event is also associated with profound faunal turnovers in the marine realm. Extinctions, faunal turnovers and Lilliput patterns have been recognised among clades such as e.g. conodonts, polychaetes and graptolites in Lau Event strata (see e.g. Urbanek & Teller 1997; Jeppsson & Aldridge 2000; Eriksson et al. 2004; Jeppsson 2006). The objective of this study was to investigate if a response to the event is detectable also among beyrichiids. The study is focusing on the family Beyrichiidae from the Silurian strata of Gotland, Sweden. The biostratigraphy on the beyrichiids on Gotland has been studied in detail by Martinsson (1962). Data of Martinsson (1962) is herein integrated with data obtained from microscopy work on five samples collected from Ludlow strata on Gotland to evaluate possible responses to the event.

2 Beyrichiidae

2.1 Classification of the Beyrichiidae

A large-scale faunal radiation occurred during the Middle Ordovician which brought about all recent and fossil orders of class Ostracoda by the end of the Late Silurian (Braddy *et al.* 2002). Five ostracode orders, namely; Archaeocopida, Leperditicopida, Palaeocopida, Podocopida and Myodocopida are recognised by Benson *et al.* (1961). During the Early Ordovician,

Palaeocopida and its suborder Beyrichicopina appeared (Scott 1961a). The latter is the most abundant fossil ostracode suborder recognised thus far. Family Beyrichiidae described by Matthew (1886) originated from Beyrichicopina during the Middle Ordovician and disappeared in Upper Devonian or Lower Permian strata (Scott 1961a). Martinsson (1962) described seven subfamilies within the family Bevrichiidae: Craspedobolbininae (Martinsson 1962), Treposellinae (Henningsmoen 1954), Amphitoxotidinae (Martinsson 1962), Zygobolbinae (Ulrich & Bassler 1923), Beyrichiinae (Matthew 1886), Kloedeniinae (Ulrich & Bassler 1923) and Hexophthalmoidinae (Martinsson 1962). Genera belonging to the subfamilies Craspedobolbininae, Amphitoxotidinae, Beyrichiinae, Treposellinae and Hexophthalmoidinae are treated herein. The classification of ostracodes presented by Scott (1961a) differs in some respect from the classification presented by Martinsson (1962). Martinsson presents the following classification: from order Ostracoda derives suborder Palaeocopa (Henningsmoen 1953) [nom. correct. (Jaanusson 1957)]. From suborder Palaeocopa derives superfamily Beyrichiacea (Matthew 1886) and family Beyrichiidae (Matthew 1886).

Beyrichiids were first identified as ostracodes by Beyrich (1845). Yet, M'Coy (1846) conferred the family its taxonomical nomenclature, Beyrichia, after studies on fossil ostracodes in Llandoverian sandstones and slates in County Galway, Ireland (Martinsson 1962). As the chief part of the literature study herein is based on Martinsson (1962) his classification is adopted herein.



Fig. 1. Nomenclature of selected external features of beyrichiids and other palaeocope ostracodes. Modified after Scott (1961b).

2.2. Morphology, ontogeny and sexual dimorphism

The ostracode exoskeleton, also called carapace, is bivalved and is generally elliptical or ovate. The carapace has a varying length ranging from c. 0.5 mm to 30 mm, and is encrusted with two layers, consisting of CaCO₃ coated with a smooth or ornamented layer of chitin (C₈H₁₃O₅N)_n (Scott 1961b; Brusca & Brusca 2003). Cephalon and thorax are fused to form a cephalotorax, a feature seen on no other crustacean groups than Ostracoda and Remipedia (Scott 1961b; Brusca & Brusca 2003). Among various beyrichiid characteristics are: well developed carapace lobations, noticeable sexual dimorphism in adult individuals, straight articulating hinge lines, and salient ornamentations (Scott 1961b). Lobation (Figs. 1 and 2) is developed either as convex bulges, syllobiums or nodes, separated by concave sulcules, which are characteristic for beyrichiids. Ornamentation (Fig. 2) is recognised as a variety of features; such as granulation, tuberculation and spinosity (Scott 1961b; Martinsson 1962). Despite common features among the family, the morphology of different beyrichiid genera varies markedly (Figs. 3 and 4). The male individuals (herein referred to as heteromorphs) do not display clear morphological differentiation from juveniles apart from carapace size. Adulthood in ostracodes is therefore easiest recognised in female heteromorph individuals, which differ from both juveniles and males (Braddy 2002). Within the family Beyrichiidae, sexual dimorphism is distinguished by cruminas (Fig. 2), a storage of larvae (Scott 1961b), which are present only in adult females (herein referred to as heteromorphs). Male individuals



Fig. 2. SEM photographs. Morphology of selected beyrichiid specimens. **A**. *Sleia equestris*, heteromorph specimen, dorsal view, Olsvenne 3, Eke Fm. Cruminas are displayed on the anterior-ventral sides to the right. The articulating hinge-line is demonstrated on the central part on the dorsal side of the specimen. **B**. *Neobeyrichia* (*Nodibeyrichia*) *scissa*, tecnomorph specimen, lateral view, Botvide 1, När Fm. The specimen is displaying ornamentations such as spines along the ventral side (present on both left and right valve), and warts on the posterior-lateral side.

might appear to be over represented in a community at a first glance, which is explained by the preadult heteromorph carapaces having similar morphology as tecnomorph beyrichiids (Martinsson 1962).

2.3. Habitats

Ostracodes are adapted to all aquatic environments on earth. The most common habitats are shallow marine shelf areas in which the greatest varieties of species are recognised (Scott & Wainwright 1961; Brusca & Brusca 2003). Recent ostracode faunas are living at an extensive marine depth range, with diversities and abundances depending on factors such as bottom substrate, nutrient supply, water turbulence, light penetration and vegetation. At tropical latitudes, faunas are generally the most diverse, although abundances are



Fig. 3. SEM photographed specimens of beyrichiids from Gotland, which are frequent in one or more samples. **A.** *Beyrichia* (*Simplicibeyrichia*) globifera, heteromorph, Lau Backar 1, lateral view. **B**. *Sleia equestris*, tecnomorph, Olsvenne 3, lateral view. **C**. *Neobeyrichia* (*Nodibeyrichia*) scissa, tecnomorph, Botvide 1, lateral view. **D**. *Hemsiella loensis*, tecnomorph, Olsvenne 3, lateral view. **E**. *Neobeyrichia* (*Nodibeyrichia*) regnans, tecnomorph, Bankvät 1, lateral view. **F**. *Neobeyrichia* (*Neobeyrichia*), tecnomorph, Lau Backar 1, lateral view.



Fig. 4. SEM photographed specimens of selected Ludfordian beyrichiids from Gotland which are less frequent in the studied samples. A. *Retisacculus semicolonatus*, tecnomorph, Olsvenne 3, lateral view. B. *Gannibeyrichia biplicata*, tecnomorph, Lau Backar 1, lateral view. C. *Aitilia calcarulata*, heteromorph, Lau Backar 1, lateral view. D. *Calcaribeyrichia bicalcarata*, heteromorph, lateral view, Bankvät 1.

not necessarily higher (Benson 1961). Beyrichiids in specific were generally syngamic as tecnomorph and heteromorph individuals commonly inhabited the same environment. Beyrichiids also lived in the same environment through all stages of ontogeny (Martinsson 1962). Their sensitivity to bottom substrates make them well suited as paleo-environmental tools. Species adapted to a coarse-grained substrate generally are crawlers, and has highly ornamented and rigid exoskeletons. Species adapted to fine-grained substrates has small-sized and smooth carapaces (Benson 1961).

3 Geological setting and stratigraphy

The Silurian of Gotland was formed on the shelf of a low-latitude epicontinental sea. Part of this sea was the Baltic Basin, which covered a great part of today's southern Scandinavia and the eastern Baltic region (Fig. 5). The strata of Gotland were deposited at the eastern part of the Baltic Basin and constitute a series of stacked carbonate platforms separated by discontinuity surfaces (Jeppsson et al. (2006). The entire exposed Silurian succession on Gotland (Fig. 6) has an estimated thickness of ca. 750 m (Jeppsson et al. 2006) and has a supposed age range of ca. 10 Ma (Calner et al. 2004). Located at the NW part of the island are the oldest exposed strata of latest Llandovery, which are overlain by successively younger beds towards the SE with the youngest exposed strata, deposited during the latest Ludlow.

- 3.1 The Ludfordian succession on Gotland
- 3.1.1 The När Formation

The När Formation is $\geq 65m$ thick and consists of aggrading very sparsely graptolitiferous marls, interbedded with argillaceous limestone (Jeppsson 2006). The formation is the youngest of three units in the Hemse Group which is a > 200m thick association deposited during early through mid Ludlow (Jeppsson 2006). In the north-eastern part of the exposed När Fm., the formation is thinner than towards the southwest, and three outliers of the succeeding Eke Fm. cover parts of the När Fm. The facies of the När Fm., up to the upper 2.15 m of the unit, are indicative of a platform environment, ranging from different depths seaward of a reef barrier (Eriksson & Calner 2008). The uppermost ca. 2.15 m of the När Fm. displays a distinct fauna, and is referred to as the Botvide Member. The member is equivalent to the Upper Polygnathoides siluricus conodont Subzone (Jeppsson 2006). The base of the Botvide Mbr. marks a significant decline of P. siluricus which otherwise occurs regularly in the När Fm. (Jeppsson et al. 2007). The lithofacies of the Botvide Mbr. also differs from that of the När Fm., alternating between limestone, mudstone packstone and grainstone (Munthe 1910; Cherns 1983). The packstone beds yield extraordinary high abundances of the brachiopod Davia navicula (Munthe 1910; Hede 1921; Spjeldnaes 1950). Other mass occurrences are also present, such as the brachiopod Shaleria aff. ornatella (Munthe 1902) as well as Lilliput faunas, e.g. of the conodont Ozarkodina excavata (Jeppsson & Calner 2003). The upper boundary of the member is exposed as an erosional hardground surface at various localities on Gotland (Spjeldnaes 1950). The facies of the Botvide Mbr. are associated with a subtidal to peritidal setting and a shallowing environment (Eriksson & Calner 2008).



Fig. 5. Map of Gotland, the localities of the five studied samples herein, and study area and palaeogeography of the Baltic Basin. The numbers on the map of Gotland represent the location of: 1= Botvide 1, 2= Burgen-1 drillcore, 3= Ronehamn 1 core, 4= Grötlingbo 1 core, 5= Uddvide 1 core, 6= Burgsvik 1 core. After Calner & Eriksson (2006), modified from Baarli *et al.* (2003).

3.1.2 The Eke Formation

The Eke Fm. is divided into three informal units, associated with the Lower-, Middle-, and Upper- Icriodontid conodont Zone, respectively. The formation has varying facies SW and NE of the Burgen outlier in the NE (Fig. 7). To the SW of the outlier, the succession has been studied through the Burgsvik-1, Grötlingbo-1, Ronehamn-1, and Uddvide-1 cores (Fig. 5 and 7) each core displaying both common and varying facies (see e.g. Hede 1919; Laufeld 1974; Snäll 1977; Eriksson & Calner 2008). However, the strata display major facies such as packstone and grainstone, all of progradational facies. The grainstone contains very high abundances of oncoids, which is characteristic for the Eke Fm. (Calner & Eriksson 2006). A ca 10 m thick Eke Fm. association is present in the Lau outlier, NE of the Burgen outlier. Here, a blackened flat-pebble conglomerate rests on the hardground atop of the Botvide Mbr. Above the conglomerate rests beds of crossbedded crinoidal grainstone to floatstone facies, with occurrences of stromatoporoid reefs, algae and corals (Munthe 1902; Manten 1971; Eriksson & Calner 2008). On top of this are marls and reefs, which constitutes the main part of the Eke Fm. (Munthe 1902; Eriksson & Calner 2008). The conodont fauna of Upper Eke Fm. is of low diversity and dominated by Pan*derodus equicostatus,* which comprises > 90 % of the conodont fauna (Jeppsson et al. 2007).

3.1.3 The Burgsvik Formation

The Burgsvik Fm. comprises two distinct units, the Burgsvik Sandstone and the Burgsvik Oolite, separated by a flooding surface (Munthe 1921; Hede 1921; Stel & de Coo 1977; Long 1993; Eriksson & Calner 2008). The lower boundary of the Burgsvik Sst. marks the beginning of the stable Hoburgen Secundo Episode and the Ozarkodina snajdri conodont Zone, described in Jeppsson (2006). The unit has a thickness of 40.11 m according to measurements of the Burgsvik-1 core (Hede 1919, 1921; Eriksson & Calner 2008). The strata of the older Burgsvik Sst. Mbr. are composed of mud-, silt- and sand- facies, being partly hummocky cross-stratified, and intercalated with sandy claystones (Hede 1919, 1921). A feature characterising the member is the absence of various benthic fossil groups, such as ostracodes, and a diminishment of the brachiopod diversity (Stel & de Coo 1977; in Eriksson & Calner 2008). The upper boundary of the member is exposed in the SW part of Gotland and is normally seen as massive to hummocky cross-stratified strata (Calner et al. 2004). The depositional environment is interpreted by Eriksson & Calner (2008) as reflecting a prograding delta. The Burgsvik Oolite Mbr. is composed of a few metres thick oolite and oncoidal rudstone, with a grainstone matrix and occurrences of bivalves as common features (Calner et al. 2004). Abraded bioclasts in the oolite indicate a peritidal depositional environment, whereas the Burgsvik Sst. reflects a depositional environment below fair weather wave base (Calner et al. 2004). The beginning of the O. snajdri Zone marks an abrupt faunal change among conodonts, changing to a diverse fauna, different from the low diversity fauna of Upper Icriodontid Zone (Jeppsson *et al.* 2007).

3.1.4 The Hamra Formation

The Hamra Fm. is primarily composed of marly limestone with reefal strata, which are well exposed in the southern parts of Gotland. In the lowermost Hamra Fm., the exposed strata are oolitic with oncolitic shoal deposits. On top of this follows marls, marly limestone, reefs, and reef associated sediments (Jeppsson *et al.* 2007). The succession proceeds with facies similar to that of the När Fm., below the Botvide Mbr. (preevent strata) (Calner 2005; Jeppsson *et al.* 2007), and is associated with shallow subtidal depositional environments (Eriksson & Calner 2008). New conodont taxa are reported by Jeppsson *et al.* (2006) as well as reappearances of taxa which are absent in the Lau Event strata (Lazarus taxa).

4 The Late Silurian Lau Event

During the Silurian; the Ireviken Event, the Mulde Event and the Lau Event, affected the lithology and the ecology on Gotland. The Lau Event, which is the youngest of the three, extends from the lower boundary of the Upper *P. siluricus* Subzone to the upper boundary of the Upper Icriodontid Subzone (Jeppsson & Aldridge 2000; Jeppsson 2006). The event was first described by Jeppsson (1990, 1993) and is named after the Lau parish on Gotland. The initiation of the event

is associated with a global Late Ludlow positive carbon isotope excursion (CIE) starting right below the Last Appearance Datum (LAD) of P. siluricus. The Late Ludlow CIE is the most substantial positive carbon excursion of the Phanerozoic and is correlated to a glaciation (see e.g. Eriksson & Calner 2008). Late Silurian sea level changes are reflected in the depositional sequences as systems tracts (see e.g. Eriksson & Calner (2008). The facies of the Upper P. siluricus Subzone in the Botvide Mbr. are related to deep platform environments and are suggested to constitute a High Stand Systems Tract (HST). The lithofacies of the rest of the Botvide Mbr., are associated with a forced regression and a Falling Stage Systems Tract (FSST). The initiation of the FSST coincides with the lower boundary of the Botvide Mbr.

An ordinary δ^{13} C value in the Late Silurian succession was defined by Samtleben *et al.* (2000) as < 0.5 ‰. This value increased significantly during the Lau Event. A δ^{13} C value of 1.24 ‰ in the Botvide Mbr. was measured through the Burgen-1 core (Eriksson & Calner 2008). Data from Jeppsson *et al.* (2007) reveal an increase to *c.* 3.5 ‰ in the conglomerate layer, separating the Upper *P. siluricus* Subzone and the Lower Icriodontid Zone. The FSST continues into the lower part of the Eke Fm. In the upper part of Lower Eke Fm. at Lau Backar 1, a 6.30 ‰ value was reported by Jeppsson *et al.* (2007). The associated facies characterises a Low Stand Systems Tract (LST), and a possible interglacial paleoenvironment. The LST is followed by a Transgressive Systems Tract (TST) in

CONODONT ZONES AND SUBZONES		CONODONT FAUNAS	GRAP- TOLITES	OCEANIC STATE (SEVERITY)	LITHOSTRATI- GRAPHY		SEDIMEN NE (proximal)	FS SW (distal)	THICKNESS metres NE SW	
<i>O. snajdri</i> Zone (lower part)		moderate	Pm.	Hoburgen	Hamra Fm (lower part)		oncolitic lst., marl		Hamra + Sundre c.100 (88-124)	
		diversity	sity lobus Episode		Burgsvik Fm		oolite sandstone		29.83? 47.22	
l cr don n t i d	Upper Icrio- dontid Subzone	one species strongly dominating	im-	im- over- shed uuna E V (4)		upper Eke	oncolitic Ist. + marl	oncolitic mudstone	10?	
	Middle Icriodontid Subzone	low diversity with P. equicostatus	pover- ished		Eke Fm	middle Eke	oncolitic lst. + marls	oncolitic mudstone, rare lst. beds	L+M+U Eke 31.3? 13.90 L+M Eke	
	Lower Icrio- dontid Subzone	low diversity	fauna			lower Eke	oncolitic marl oncolitic crinoid lst.	dolomitic mudstone, rare lst. beds	>10 2.55	
P. iZ lo un re i c us	O. excavata fauna	rapid	e n t		e	H e	Botvide	Shaleria coquinas	mudstone	0.21
	Upper P. siluricus Subzone	stepwise extinctions		n (3) t (2)	m s När ^e Fm G	Member	Dayia coquinas, dolomitic dolo lst. and marl	Dayia coquinas, omitic mudst., rare lst. beds	2.1	
	Main part of the Zone	very diverse; platform conodonts	diverse, with <i>N.</i> kozlowski	Havdhem Primo Episode	o u p	main part of the När Fm Millklint Lst. Mbr	crinoid marl Ist. alt.	mudstone, marl, rare Ist. beds	30+ 65+ Hemse c. 200 (250?)	

Fig. 6. Correlation of lithostratigraphy, biostratigraphy and oceanic state of the Ludfordian on Gotland. Modified after Jeppsson (2006) after which the conodont and graptolite zonation are revised from Urbanek (1997), the oceanic state from Jeppsson & Aldridge (2000) and Jeppsson (1998) and after which lithologies are modified after Hede (1919, 1921).



Fig. 7. Lithological units on Gotland studied herein, illustrated as a transect. The numbers corresponds to: 1. Botvide 1 (locality), 2. Burgen-1 drillcore and Burgen outlier, 3. Ronehamn 1 core, 4. Grötlingbo 1 core, 5. Uddvide 1 core and 6. Burgs-vik 1 core. After Calner & Eriksson (2006).

the Middle Eke Fm. The boundary to the Upper Eke Fm. coincides with the onset of a HST and a CIE peak (Eriksson & Calner, 2008). Jeppsson et al. (2007) reported a value of 9.17 ‰ from Ronnings 1. The transition from the HST to the following FSST coincides with the lower boundary of the Burgsvik Sst. and the O. snajdri Zone, the onset of the Hoburgen Secundo Episode, and a glaciation. The FSST is associated with a drastic decline in level bottom biota (Eriksson & Calner 2008). Still, high ratios of δ^{13} C are detectable, e.g. in a sample from Glasskär 3 with a reported value of 10.54 ‰ (Jeppsson et al. 2007). The beginning of the LST is related to the lower boundary of the Burgsvik Oolite and the onset of a greenhouse period (Calner & Eriksson 2008). Associated lower δ^{13} C values are measured. A δ^{13} C increase is reported in the transition from the LST to the following TST (Calner & Eriksson 2008). Through the Hamra Fm. and the lower TST the δ^{13} C ratio declines again. Values up to 5.87 ‰ were reported by Samtleben et al. (2000) at Bankvät 1. The δ^{13} C value declines to almost pre-event ratios of 0.52 ‰ measured by Samtleben et al. (2000) at Klehammarsård 3, Sundre Fm. (Jeppsson et al. 2007). Eriksson & Calner (2008) discussed two separate explanations for the δ^{13} C excursion. One explanation is based on Kump et al. (1999) suggesting that glacio-eustacy caused carbonate platforms at low latitudes to be subaerially exposed, which lead to changes in riverine carbon influx to the sea. The second explanation is based on Wigforss-Lange's (1999) suggestion that an increase in $\delta^{13}C$ was a result of increased photosynthetic activity by benthic cyanobacteria.

5 Materials and Methods

The material used for this study consists of data recorded from the published literature and five samples collected by Lena Gustavsson and Lennart Jeppsson in 2005 (see Gustavsson 2005), from marly strata deposited during the late Ludfordian on Gotland. The samples were collected at Mattsarve 1, Botvide 1, Lau Backar 1, Olsvenne 3, and Bankvät 1 (see Table 1, or Laufeld, 1974 for detailed descriptions of the localities). Each sample was treated with a sodium carbonate solution (Gustavsson 2005) and, to reduce the pick-

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ing time, the sample residues were then split up to four times with a standard sample divider, with the number of splits depending on the original sample weight (Table 1). This was followed by sieving of the residues into size fractions 0.5-1.0 mm and 1.0-2.0 mm (see Table 1). Material below 0.5 mm and above 2.0 mm was not studied in detail. The fractions were picked under a binocular light microscope. All ostracode specimens were collected and sorted into micropalaeontological slides for detailed studies. The specimens were counted, and when possible, assigned to genus or species. Identification of specimens was based on morphology and size. Specimens with only a left or a right valve present were counted as one, as with specimens with both valves articulated. The number of beyrichiid specimens per sample varies between 14 and 285. Selected specimens of interest were photographed with a scanning electron microscope (SEM). The samples were integrated with analyses of published literature on Silurian ostracodes from Gotland (Martinsson 1962) allowing systematic identifications of the specimens

6 Results

The results herein are based on the published data presented by Martinsson (1962) and on my sampled material. The results are summarised also in Fig. 8, which demonstrates beyrichiid lineages ranging through 32 localities on Gotland. The localities in Fig. 8 are arranged in ascending stratigraphical order. The quantitative results of my study are illustrated in detail in Table 2. A total of 37 species were identified by Martinsson (1962) at one or more localities on Gotland. Altogether I have recorded 633 specimens which could be taxonomically assigned to family Beyrichiidae. Following to the classification, it could be concluded that these specimens represent 22 species. Data from Mattsarve 1, Olsvenne 3 and Bankvät 1 derive from my sampled material only. Additionally, Beyrichiidae faunas of Botvide 1 and Lau Backar 1 were studied also by Martinsson (1962). Data from the remaining 27 localities are based solely on Martinsson (1962). Also, the sampled material from Mattsarve 1, Lau

Table 1. Sample details.

Sample id.	Locality	Weight (g)	Fractions (mm)	Splits	Number of Beyrichiidae specimens
G03-007LG	Mattsarve 1	410	0.5-1.0	x 1	7
			1.0-2.0	x 1	7
G03-09LG	Botvide 1	11 630	0.5-1.0	x 2	13
			1.0-2.0	x 4	14
G03-004LG	Lau Backar 1	11 020	0.5-1.0	x 3	21
			1.0-2.0	x 3	111
G03-017LG	Olsvenne 3	21 980	0.5-1.0	x 2	174
			1.0-2.0	x 3	27
G03-374LJ	Bankvät 1	1 020	0.5-1.0	x 1	66
			1.0-2.0	x 1	193

Backar 1, Olsvenne 3 and Bankvät 1 yields ostracode specimens which I could not confidently assign to accurate taxa. Brief data about these specimens, such as number of specimens per sample, are however dealt below.

6.1 The pre-event faunas

Mattsarve 1 (G03-007LG) (Fig. 5) is the only sample herein which yields a pre-event fauna. The sample yields 14 specimens which can be assigned to various beyrichiid species. Furthermore, the sample yields four ostracode specimens of other affinities than the Beyrichiidae. The amount of recorded specimens of fraction 0.5-1.0 mm and 1.0-2.0 mm is at an even ratio as the fractions yield seven specimens respectively.

The Mattsarve 1 sample yields five species. *Hemsiella hemsiensis* encompasses five specimens. *Neobeyrichia (Nodibeyrichia) scissa* (Fig. 3) and *Neobeyrichia (Neobeyrichia) nutans* are represented by three specimens each. Further, *Lophoctenella* cf. *scanensis* and *Hammariella pulchrivelata* are represented by one and two specimens respectively (Table 2). Mattsarve 1 marks the First Appearance Datum (FAD) for *L.* cf. *scanensis*. The pre-event taxa recorded by Martinsson (1962) from Hammars 1 to Fie 1, and the sampled material from Mattsarve 1 altogether comprise a total of 17 species (Fig. 8). Two additional species show Lazarus patterns in the upper När Fm. and these reappear first in the Eke Fm.

Neobeyrichia is the most frequent genus throughout the När Fm. Neobeyrichia (Neobeyrichia) lauensis and N. (No.) scissa are recorded at six and eight of the pre-event localities respectively (Fig. 8). Neobeyrichia (Neobeyrichia) ctenophora (Fig. 3) occurs at three pre-event localities. The lineages of N. (Ne.) lauensis, N. (No.) scissa and N. (Ne.) ctenophora continue into the Botvide Mbr. Also, H. pulchrivelata is fairly frequent in pre-event strata, as it is recorded at six localities. The lineage of H. pulchrivelata ends in pre-event strata as the LAD of H. pulchrivelata is recorded at Fie 1, slightly below the Botvide Mbr. Fie 1 also marks the LAD of Atterdagia paucilobata which appears rather scarcely in the När Fm. The lineage of H. hemsiensis also ends in pre-event strata, and its LAD is recorded at Hulte 1 (Fig.8). Conversely, Hulte

1 marks the FAD of *Hoburgiella tenerrima* and *Sleia equestris* (Fig. 3) of which lineages continue into Lau Event strata.

The lineages of certain taxa are interrupted by gaps through sections of the När Fm. *Kolmodinia* cf. *grandis* has a fairly extensive gap throughout the upper När Fm. and reappears first in the Eke Fm. *Hamulinavis pirulifera* is similarly absent in all När Fm. localities treated herein, and reappears in the Eke Fm. *Beyrichia (Simplicibeyrichia) globifera* (Fig. 3, Fig 8.), is absent through an extensive part of the upper När Fm., but is recorded again at the Eke Fm. Also, the lineage of *N. (Ne.) ctenophora* has a gap through a section of the uppermost När Fm., but reappears in Eke Fm.

Summarised; N. (Ne.) nutans, N. (Ne.) lauensis, N. (No.) scissa, L. cf. scanensis, A. paucilobata, H. hemsiensis, H. tenerrima, S. equestris and H. pulchrivelata occur in the pre-event strata from Mattsarve 1 to Fie 1. The lineages of N. (Ne.) nutans, A. paucilobata, H. hemsiensis and H. pulchrivelata disappear in pre-event strata. L. cf. scanensis, N. (Ne.) lauensis, N. (No.) scissa, H. tenerrima and S. equestris continue into event strata. K. cf. grandis, H. pirulifera, B. (S.) globifera and N. (Ne.) ctenophora have gaps through various sections of the pre-event strata, but reappear again in the Botvide Mbr. N. (Ne.) lauensis and N. (No.) scissa dominate the pre-event fauna, regarding frequency and dominates the Mattsarve 1 sample considering abundance.

6.2 The early event faunas

The Botvide 1 sample (G03-09LG) (Fig.5) is weathered and contains numerous ostracodes that are worn, fragmented and not suitable for identification. I recorded 27 beyrichiid specimens in the sample and no ostracode specimens of other affinities. 13 specimens derive from the 0.5-1.0 mm fraction, and 14 specimens derive from the 1.0-2.0 mm fraction. Three genera could be identified in the sample; *Neobeyrichia*, *Lauella* and *Lophoctenella*. As in the Mattsarve 1 sample, the great majority of specimens are represented by *Neobeyrichia*. The most abundant species of the Botvide 1 sample are decisively *N. (Ne.) lauensis* and *N.*



Table 2. Identified taxa in the studied samples.

(No.) scissa, similar to the pre-event faunas. N. (Ne.) lauensis and N. (No.) scissa are also the most frequently occurring taxa of the Botvide Mbr. as Martinsson (1962) recorded the taxa at both Botvide 1 and Gannor 1. I recorded 12 specimens of N. (Ne.) lauensis and 13 specimens of N. (No.) scissa. I also recorded one specimen each of Lauella uncinata and L. cf. scanensis in the sample. Moreover, Botvide 1 marks the FAD of L. uncinata and the LAD of L. cf. scanensis. Martinsson (1962) also recorded the LAD of L. cf. scanensis at Botvide 1, but recorded the FAD of L. uncinata in the Eke Fm. Furthermore, Martinsson (1962) recorded S. equestris at Botvide 1. The gaps in the lineages of H. pirulifera, K. cf. grandis, B. (S.) globifera and N. (Ne.) ctenophora continue still throughout the Botvide Mbr. Likewise, the lineage of *H. tenerrima* has a gap which is ranging through the Botvide Mbr.

6.3 The event faunas

The beyrichiid faunas of the Eke Fm. include 18 species distributed among eight localities, from Lau Backar 1 of the Lower Icriodontid Subzone, to Petsarve 1 of the Upper Icriodontid Subzone. An additional taxon, *H. tenerrima*, has a Lazarus gap throughout the formation. A characterizing attribute for the Eke Fm. faunas is that the lineages of several species have gaps through large parts of the formation. All species, except *H. tenerrima*, with gaps in Eke Fm. strata are however recorded at Lau Backar 1, before temporarily disappearing. Another aspect of the Eke Fm. faunas is that a small number of dominating species occur at each Eke Fm. locality or at several Eke Fm. localities. The great majority of species are only occurring very scarcely in the Eke Fm. strata.

The greatest diversity of the Eke Fm. is decisively recorded at Lau Backar 1. Martinsson (1962) recorded 15 beyrichiid species from Lau Backar 1 (Fig. 8) and I recorded 10 beyrichiid species in the Lau Backar 1 sample (G03-004LG) (Fig. 5). The beyrichiid diversity of Lau Backar 1 is also higher as compared to the När Fm. localities treated herein. The Lau Backar 1 sample yielded 132 beyrichiid specimens. Also, 109 specimens derive from other families than Beyrichiidae and will remain taxonomically unassigned herein. A considerable amount of specimens in the sample are thus deriving from other affinities, as compared to the Mattsarve 1 sample.

Among the beyrichiid specimens in the Lau Backar 1 sample, 21 derive from the 0.5-1.0 mm fraction and 111 derive from the 1.0-2.0 mm fraction. Among the taxonomically unassigned ostracodes the ratio is different, as 85 specimens derive from the 0.5-1.0 mm fraction, and 24 specimens derive from the 1.0-2.0 mm fraction.

Martinsson (1962) reports occurrences of *B.* (*S.*) globifera at Lau Backar 1. The gap of *B.* (*S.*) globifera in the När Fm. is thus interrupted in Eke Fm. strata. Similarly, I recorded 76 *B.* (*S.*) globifera specimens in the Lau Backar 1 sample and the taxon is thus



Fig. 9. SEM photograph of incertae sedis taxa, Olsvenne 3, x75. The specimens lack straight hingelines and clear ornamentation.

the most abundant of the Lau Backar 1 sample. H. pirulifera, K. cf. grandis and N. (Ne.) ctenophora of which lineages have gaps through the upper När Fm., likewise reappear at Lau Backar 1. I recorded 26 N. (Ne.) ctenophora specimens in the Lau Backar 1 sample. N. (Ne.) ctenophora occurs frequently throughout the Eke Fm. as it is recorded at each treated Eke Fm. locality. I recorded one specimen of H. pirulifera in the Lau Backar 1 sample and Martinsson (1962) also recorded H. pirulifera at Lau Backar 1. Also, Martinsson (1962) reported a LAD of K. cf. grandis at Lau Backar 1. I recorded no appearances of the taxon in the Lau Backar 1 sample. N. (No.) scissa and N. (Ne.) lauensis are represented also in the Lau Backar 1 sample, as eight and nine specimens respectively. Further, S. equestris occurs at all localities of the Lower- to the Upper Icriodontid Subzone. Still, Martinsson (1962) only reports one specimen of S. equestris in a vast quantity of Lau Backar 1 material. I did not find S. equestris in the Lau Backar 1 sample.

Martinsson (1962) recorded a fairly high number of species with FAD at Lau Backar 1. Among these are Aitilia calcarulata (Fig. 4), Plicibeyrichia ornatissima, Calcaribeyrichia bicalcarata (Fig. 4), Hemsiella loensis (Fig. 3), Hemsiella anterovelata, Clintiella cf. hyrsiniana, Retisacculus commatatus, Beyrichia (Simplicibeyrichia) duplicicalcarata and Gannibeyrichia biplicata (Fig. 4). Likewise, I have recorded two specimens of A. calcarulata at Lau Backar 1, two specimens of C. cf. hyrsiniana, six specimens of R. commatatus and one specimen of G. biplicata. The lineages of C. bicalcarata, H. tenerrima, P. ornatissima, and H. anterovelata have extensive gaps through the Eke Fm., and reappear in strata deposited after the Lau Event (post-event strata). A. calcarulata, B. (S.) duplicicalcarata and G. biplicata occur only at Lau Backar 1, thus Lau Backar 1 marks both the FAD and the LAD of each species.

As mentioned earlier, a large fraction of the recorded beyrichiid specimens of the Lau Backar 1 sample derive from the 1.0-2.0 mm fraction. I e.g. recorded 69 specimens of *B.* (*S.*) globifera from the 1.0-2.0 mm fraction, compared to seven recorded specimens from the 0.5-1.0 mm fraction. I recorded 24 specimens of *N.* (*Ne.*) ctenophora from the 1.0-2.0 mm fraction and two specimens from the 0.5-1.0 mm fraction. I recorded all *N.* (*Ne.*) lauensis specimens from the 1.0-2.0 mm fraction. I also recorded five specimens of *R. commatatus* from the 1.0-2.0 mm fraction,





as compared to one specimen from the 0.5-1.0 mm fraction. However, species yielding noticeably low number of specimens, such as *H. loensis, H. pirulifera, G. biplicata* and *C.* cf. *hyrsiniana* are exclusively picked in the 0.5-1.0 mm fraction. I further recorded one *A. calcarulata* specimen from each fraction, and five *N. (No.) scissa* specimens from the 0.5-1.0 mm fraction compared to three specimens from the 1.0-2.0 mm fraction.

The Olsvenne 3 sample (G03-017LG) (Fig. 5) of the Middle Icriodontid Subzone yields 201 beyrichiid specimens spread among nine species. S. equestris is the most abundant species, yielding 98 specimens. S. equestris has thus increased noticeably in abundance in comparison to Lau Backar 1. Similarly, H. loensis have increased appreciably in abundance. I recorded 86 specimens of the taxon in the sample, compared to one specimen in the Lau Backar 1 sample. Conversely, B. (S.) globifera has decreased noticeably in abundance in the Olsvenne 3 sample compared to the Lau Backar 1 sample as I recorded merely one B. (S.) globifera specimen in the Olsvenne 3 sample. Martinsson (1962) reports no find of B. (S.) globifera above Lau Backar 1, and Olsvenne 3 hence marks the LAD of the taxon.

I have recorded nine specimens of *Neobeyrichia* in the Olsvenne 3 sample. Three specimens derive from N (*No.*) *scissa*, and six specimens derive from *N*. (*Ne.*) *ctenophora*. *N*. (*Ne.*) *ctenophora* has hence decreased somewhat in relative abundance in the sample, compared to the Lau Backar 1 sample. I further recorded three specimens of *C*. cf. *hyrsiniana* and two specimens of *R*. *commatatus*. Similar to the Lau Backar 1 sample, the taxa display low abundances in the Olsvenne 3 sample. Lastly, I have recorded one specimen and a FAD of *Retisacculus semicolonatus* (Fig. 4) in the Olsvenne 3 sample.

Among the recorded beyrichiid specimens in the Olsvenne 3 sample, the majority are collected from the 0.5-1.0 mm fraction. E.g. all recorded specimens of *H. loensis* derive from the 0.5-1.0 mm fraction, as are all recorded specimens of *N. (No.) scissa, N. (Ne.) ctenophora, R. commatatus* and *R. semicolonatus.* I also recorded 76 specimens of *S. equestris* from the 0.5-1.0 mm fraction compared to 22 specimens from the 1.0-2.0 mm fraction.

A substantial amount of specimens in the Olsvenne 3 sample derive from families other than Beyrichiidae and these remain taxonomically unassigned herein. The sample yields 468 ostracode specimens of other affinities (Fig. 9). 346 specimens derive from the 0.5-1.0 mm fraction, and 122 specimens from the 1.0-2.0 mm fraction. The relative abundance of incertae sedis specimens in the sample is noticeably higher than in the Mattsarve 1 sample and the Lau Backar 1 sample.

Summarised; The Lau Backar 1- and Olsvenne 3 samples yield an abundant amount of specimens relative to the Mattsarve 1- and Botvide 1 samples. Also, Lau Backar 1 and Olsvenne 3 yield diverse faunas, while the other localities of När Fm. recorded by Martinsson (1962) yield faunas of low diversities in comparison. The most frequently occurring species of the Eke Fm. fauna are *N. (Ne.) ctenophora* and *S. equestris,* which are recorded at each locality. *H. loensis* are also rather frequent as it occurs at five localities. Conversely, the lineages of *H. anterovelata, C. bicalcarata, H. tenerrima* and *P. ornatissima* have extensive gaps through the Eke Fm.

The most abundant taxa in the Lau Backar 1 sample are *B. (S.) globifera* and *N. (Ne.) ctenophora*. In the Olsvenne 3 sample the most abundant taxa are *S. equestris* and *H. loensis*. A common feature of both samples is that a few taxa have high relative abundances relative to the majority of taxa which have noticeably lower relative abundances.

6.4 The post-event faunas

The post-event faunas are represented by 16 species recorded from Husryggen 2 of the Burgsvik Fm. to Hoburgen 3 of the lower Hamra Fm. The Beyrichiidae diversity is high compared to that in the Eke Fm., except for the exceptionally diverse faunas of Lau Backar 1 and Olsvenne 3. Further, the diversities of the localities in the Hamra Fm. are generally higher than the diversity of Husryggen 2 of the Burgsvik Fm. At Husryggen 2 of the Burgsvik Fm., three species are recorded by Martinsson (1962). Among these are Cryptolopholobus semilaqueatus which has a FAD at the locality, and N. (Ne.) ctenophora. Also, the gap in the lineage of *H. tenerrima* is interrupted at Husryggen 2, where the taxon reappears and ranges into the Hamra Fm. Conversely, the lineages of S. equestris and H. loensis have gaps throughout the Burgsvik Fm. The lineages of C. bicalcarata, C. cf. hyrsiniana, P. ornatissima, H. anterovelata and R. semicolonatus similarly have gaps through the formation.

The diversities of Lunde 1 and Uddvide 1 of the lowermost Hamra Fm. are considerably high. Seven taxa are recorded by Martinsson (1962) from Lunde 1, including reappearances of R. semicolonatus, C. bicalcarata, H. loensis, P. ornatissima and S. equestris. N. (Ne.) ctenophora and H. tenerrima are also recorded. The Uddvide 1 fauna also amounts to seven species, including R. semicolonatus (R. semicolonatus has its LAD at the locality), C. bicalcarata, C. semilaqueatus, S. equestris, H. loensis, P. ornatissima and a reappearance of H. anterovelata. The diversity decreases further up in the Hamra Fm. Merely two species are recorded by Martinsson (1962) at Gisle 1, namely; C. bicalcarata and a FAD of Beyrichia (Simplicibeyrichia) barbulimentata. Likewise, two species are recorded by Martinsson (1962) at Norrgårde 1; C. bicalcarata and a FAD and LAD of Navibeyrichia balticivaga.

The Bankvät 1 sample (G03-374LJ) (Fig. 5) yields 388 ostracode specimens. 259 specimens derive from family Beyrichiidae and 129 specimens derive from other affinities and will remain taxonomically unassigned herein. Among the incertae sedis taxa, 65

specimens are deriving from the 0.5-1.0 mm fraction and 64 specimens are deriving from the 1.0-2.0 mm fraction. The beyrichiid specimens are split among eight genera and nine species. Similar to the Mattsarve 1 sample and the Botvide 1 sample, the most abundant genus is Neobeyrichia. I recorded 155 specimens of Neobeyrichia in the sampled material. 133 specimens derive from *Neobevrichia* (Nodibevrichia) regnans (Fig. 3) and 22 specimens from N. (Ne.) ctenophora. H. loensis is also abundant in the Bankvät 1 sample, as I recorded 67 specimens. I also recorded 18 specimens of S. equestris. Moreover, I recorded, one specimen of C. bicalcarata, two specimens of C. cf. hyrsiniana, six specimens of C. semilaqueatus, seven specimens of B. (S.) barbulimentata, and three specimens and a FAD of Juviella juvensis. The bulk of the Bankvät 1 sample yields Beyrichiidae specimens of the 1.0-2.0 mm fraction. 193 specimens derive from the 1.0-2.0 mm fraction and 66 specimens from the 0.5-1.0 mm fraction. N. (No.) regnans occurs as five specimens in the 0.5-1.0 mm fraction and 128 specimens in the 1.0-2.0 mm fraction. S. equestris occurs as five specimens in the 0.5-1.0 mm fraction and 13 specimens in the 1.0-2.0 mm fraction. N. (Ne.) ctenophora yields 10 specimens in the 0.5-1.0 fraction and 12 specimens in the 1.0-2.0 mm fraction. B. (S.) barbulimentata, C. bicalcarata, C. cf. hyrsiniana and J. juvensis are recorded from the 1.0-2.0 mm fraction only. Conversely, H. loensis yields 40 specimens in the 0.5-1.0 mm fraction and 27 specimens in the 1.0-2.0 mm fraction. C. semilaqueatus are only recorded from the 0.5-1.0 mm fraction.

At Hoburgen 2, Hoburgen 4 and Hoburgen 3, Martinsson (1962) recorded eight, nine and eight species respectively. A FAD of Lophoctenella angustilaqueata and Retisacculus cf. commatatus are recorded from Hoburgen 2. Martinsson (1962) also recorded N. (Ne.) ctenophora, S. equestris, H. loensis, H. tenerrima, J. juvensis and N. (No.) regnans from Hoburgen 2. Martinsson (1962) recorded L. angustilaqueata, R. cf. commatatus, N. (No.) regnans, N. (Ne.) ctenophora, J. juvensis, H. tenerrima, S. equestris, H. loensis and B. (S.) barbulimentata from Hoburgen 4. At Hoburgen 3 Martinsson (1962) recorded LAD:s of C. semilaqueatus and L. angustilaqueata. Martinsson (1962) also reports appearances of S. equestris, H. loensis, H. tenerrima, N. (No.) regnans, B. (S.) barbulimentata and R. cf. commatatus at the locality.

Which taxa that dominate the post-event fauna are not entirely apparent since as many as 11 out of the 16 species occur at three localities or more in the Hamra Fm. The occurrences of beyrichiid specimens from the Hamra Fm. altogether reflect a fauna that is more diverse and with less interrupted lineages than the faunas of pre-event and event strata. Considering abundance in the Bankvät 1 sample, species such as *N. (No.) regnans* and *H. loensis* are dominating the fauna.

7 Discussion

Data obtained from the studied localities herein signal

differences in frequencies among beyrichiid taxa and differences in beyrichiid diversity which can be correlated with transitions between pre-event strata, event strata and post-event strata. Also, during comparison of the studied samples herein, changes in relative abundances among specific taxa are evident. These changes could be interpreted as to signal a response the Lau Event.

I recorded only a minute amount of specimens from the Mattsarve 1 sample and the Botvide 1 sample. The particularly low number of specimens hampers comparison between the studied samples. The Lau Backar 1 sample and the Olsvenne 3 sample yielded faunas that are particularly diverse in relation to the fauns of the other Lau Event localities studied by Martinsson 1962. Similarly, Martinson (1962) reports an especially diverse fauna at Lau Backar 1. The faunas of the other localities of the Eke Fm. are of noticeably lower diversities.

The average number of species per locality in the pre-event strata from Mattsarve 1 and above is 3,5 The average number of species per locality in the Botvide 1 Mbr. is 3,5. The average number of species per locality in the Eke Fm. is 5,5. If excluding the anomalously diverse faunas of Lau Backar 1 and the Olsvenne 3, the average number of species per locality of the Eke Fm. is three. At Hoburgen 2 of the Burgsvik Fm. three species are reported. The average number of species per locality in the Hamra Fm. is 6,5. Conclusively, the beyrichiid diversity prevails in post-event fauna, which suggests that the Lau Event had an temporarily negative effect on the beyrichiid diversity. Also, the post-event strata reflects a noticeable speciation.

Eight FAD:s are recorded from Lau Backar 1. Martinsson (1962) reports gaps in the lineages among three species with FAD:s at the Lau Backar 1. One taxon, (*C*. cf. *hyrsiniana*), also has a gap through the Eke Fm., which is interrupted at Olsvenne 3 before continuing into post-event strata. The gaps in the lineages of the remaining species extend through the entire Eke Fm. above Lau Backar 1, and must be defined as Lazarus taxa. Lau Backar 1 and Olsvenne 3, could possibly be interpreted as windows in the stratigraphy, e.g., putting less abundant species on display. The high number of FAD:s at Lau Backar 1 could signal a speciation during the event, which among the three species with gaps above Lau Backar 1, were immediately followed by gaps and Lazarus faunas (?).

A common feature of the Lau Backar 1 sample and the Olsvenne 3 sample is that they yield a small number of species which occur in particularly high abundances, compared to the other recorded species. In the Lau Backar 1 sample, *B. (S.) globifera* is particularly abundant and is dominating the beyrichiid fauna. In the Olsvenne 3 sample, *H. loensis* and *S. equestris*, and to some extent *N. (Ne.) ctenophora*, are very abundant relative to the other recorded species. These species could perhaps be opportunistic taxa which were benefitting on the event, such as niches that were offered as other taxa disappeared temporarily or permanently (e.g. *H. anterovelata*, *H. tenerrima*, *C. bicalcarata* and *P. ornatissima* that occurred as Lazarus faunas).

11 LAD:s are recorded from Lau Event strata, which are anomalous to the recorded number of LAD:s in pre-event strata and post-event strata. 4 LAD:s are recorded in pre-event strata from Mattsarve 1 and above, and seven LAD:s are recorded in postevent strata. As 11 FAD:s are also recorded in the Lau Event strata, a faunal re-organisation could be associated with the event.

The lineages of seven out of ten taxa ranging through the Burgsvik Fm. are absent in Burgsvik Fm. strata. These taxa include *S. equestris* and *H. loensis* which occur very frequently in the Eke Fm. Taxa of the Burgsvik Fm. were perhaps negatively affected by the prograding delta of the Burgsvik Sandstone Mbr.

H. anterovelata, C. bicalcarata, H. tenerrima and *P. ornatissima* which lineages show Lazarus patterns in the Eke Fm. return in the Burgsvik Fm. or in the Hamra Fm. *H. tenerrima* reappears in the Burgsvik Fm. before occurring rather regularly in the Hamra Fm. *H. anterovelata* reappears with a LAD in the Hamra Fm. Also *C. bicalcarata* and *P. ornatissima* reappear in the Hamra Fm. Other taxa, such as *S. equestris* and *H. loensis* which have Lazarus gaps in the Burgsvik Fm. reappear in the Hamra Fm. The postevent strata so likely signal recoveries from Lazarus faunas.

The Bankvät 1 sample yielded the highest amount of beyrichiid specimens of the five studied samples. The high abundance of specimens is noteworthy since the volume of sampled material is considerably smaller, compared to the Botvide 1 sample, the Lau Backar 1 sample and the Olsvenne 3 sample. Considering the smaller sample residue of Bankvät 1 (see Table 2), the recorded species in the sample are fairly abundant compared to the species recorded in the Botvide 1 sample, the Lau Backar 1 sample, and the Olsvenne 3 sample. The Bankvät 1 fauna are overall seemingly more stable.

7.1 Podocopinas of uncertain affinities

Martinsson (1962) notes that the beyrichiid population is often mixed with other palaeocope ostracodes. This is in accordance with the sampled data herein, as I recorded ostracodes of other affinities than Beyrichiidae from Mattsarve1, Lau Backar 1, Olsvenne 3 and Bankvät 1. As apparent in table 2, specimens in the Mattsarve 1 sample which could not confidently be assigned to family Beyrichiidae are markedly few. However, in the Lau Backar 1 sample, recorded specimens of uncertain taxa amount to a fairly large quote (109 specimens). C. 45 % of the total bulk of ostracodes in the Lau Backar 1 sample derives from taxa of uncertain affinities. The specimens are high in proportion to length, and have rounded venters and straight hinge lines. The specimens have small punctuated pits distributed evenly over the carapace. Straight hinge lines are characteristic for beyrichiids; however I could not successfully identify the specimens to family Beyrichiidae. The Olsvenne 3 sample yields 468 ostracodes specimens of taxa which undoubtedly belong to other families than Beyrichiidae. The number of unclassified specimens in the Olsvenne 3 sample thus amount to over twice the number of Bevrichiidae specimens. The specimens are entirely smooth, and are long in proportion to height. Concerning the recorded incertae sedis specimens of the Bankvät 1 sample, the abundance is lower than compared to the recorded beyrichiid specimens. I recorded 129 incertae sedis specimens, which amounts to c. 35 % of the total bulk of recorded specimens in the sample. The incertae sedis specimens in the Bankvät 1 sample are entirely smooth and very elongate in proportion to length. As compared to the Lau Backar 1 and the Olsvenne 3 sample, ostracodes of uncertain affinities constitute a less significant part of the Bankvät 1 fauna. Overall, the Bankvät 1 sample, seemingly reflects an ostracode fauna of which the incertae sedis taxa are not dominating the fauna to the extent seen in the Olsvenne 3 sample.

Taxa of other affinities were seemingly flourishing during the later part of the event, as reflected by high abundances in the Olsvenne 3 sample. Possibly, ostracodes of other affinities were occupying niches during the Lau Event, that in the Hoburgen Secundo Episode were instead occupied by beyrichiids. If so, ostracodes of other affinities recorded herein, were seemingly positively affected by the Lau Event.

7.2 Lilliput patterns among beyrichiids

After comparison of taxa recorded in more than one sample herein, I have concluded that size variations among taxa recorded in different samples are evident. I have recorded substantial differences in shell sizes of particular taxa when comparing the Lau Backar 1 fauna, the Olsvenne 3 fauna and the Bankvät 1 fauna. In the Lau Backar 1 sample I e.g. recorded two N. (Ne.) ctenophora specimens from the 0.5-1.0 mm fraction, and 24 specimens from the 1.0-2.0 mm fraction. In the Olsvenne 3 sample I conversely, recorded all six specimens of N. (Ne.) ctenophora exclusively from the 0.5-1.0 mm fraction. In the Bankvät 1 sample, it is noticeable that the ratio is more even, as I recorded 10 N. (Ne.) ctenophora specimens from the 0.5-1.0 mm fraction and 12 specimens from the 1.0-2.0 mm fraction

Hinge-lengths and sulcal heights of three heteromorph *N. (Ne.) ctenophora* specimens collected from Lau Backar 1 on Gotland are presented by Martinsson (1962). The hinge-lengths are varying between 2630 μ m and 2695 μ m and the sulcal heights are varying between 1459 μ m and 1615 μ m. If comparing to the sizes presented above with the recorded specimens in the Olsvenne 3 samples, it is noticeable that the recorded specimens are quite small in comparison. Further, the *N. (Ne.) lauensis* specimens recorded from the Lau Backar 1 sample are recorded from the 1.0-2.0 mm fraction only. No specimens of the taxon were however recorded in the Olsvenne 3 sample, as the lineage of the taxon has a Lazarus gap at the locality. Hinge lengths and sulcal heights of three heteromorph N. (Ne.) lauensis specimens are presented by Martinsson (1962). One specimen recorded from Hulte 1 is 4050 um long and 2650 um high. Two heteromorphs are recorded from Botvide 1. One specimen is 3860 µm long and 2595 µm high, whereas the other specimen is 4025 µm long and 2695 µm high. The sizes presented above are quite large in comparison with the majority of the recorded specimens from the Lau Backar 1 sample. However, since the recorded specimens in the Lau Backar 1 sample are tecnomorphs, the small sizes might reflect juvenile specimens. S. equestris occurs predominantly in the 0.5-1.0 mm fraction of the Olsvenne 3 sample, as 76 specimens are picked from the 0.5-1.0 mm fraction, and 22 specimens are picked from the 1.0-2.0 mm fraction. In the Bankvät 1 sample however, the ratio is reversed as 5 specimens are recorded from the 0.5-1.0 mm fraction and 13 specimens are recorded from the 1.0-2.0 mm fraction. S. equestris so prevails in the 1.0-2.0 mm fraction of the Bankvät 1 sample, contrary to the Olsvenne 3 sample. Martinsson (1962) presents measurements of five heteromorph S. equestris specimens picked in material collected from Uddvide 1 of the Hamra Fm. The length of the specimens ranges between 880 µm and 960 µm and the height ranges between 1350 µm and 1565 µm. Compared to the size of the majority of recorded specimens in the Olsvenne 3 sample, the sizes presented from Uddvide 1 are particularly large. The perhaps most apparent size variation is noticeable among H. loensis. In the Olsvenne 3 sample H. loensis exclusively occurs in the 0.5-1.0 mm fraction, while the ratio is more even in the Bankvät 1 sample where 40 specimens are part of the 0.5-1.0 mm fraction and 27 specimens are part of the 1.0-2.0 mm fraction. Hinge lengths and sulcal heights of five heteromorph H. loensis specimens from Lau Backar 1 are reported by Martinsson (1962). The lengths are varying between 965 µm to 1100 µm. The corresponding sulcal heights are varying between 700 µm to 765 µm. Also, Martinsson (1962) presents measurements of five heteromorph specimens from Sles, Hamra Fm. The hinge lengths are varying between 765 µm to 900 µm and sulcal heights are varying between 960 µm to 1220 µm. Size differences among e.g. R. commatatus, N. (No.) scissa, C. cf. hyrsiniana and H. pirulifera, are also evident when comparing the Lau Backar 1 sample with the Olsvenne 3 sample. However, I recorded particularly low numbers of the species in both samples, and the size differences might be coincidental.

Summarised, in the Lau Backar 1 sample the 1.0-2.0 mm fraction of beyrichiids indeed dominates. Lilliput patterns are apparent in the Olsvenne 3 sample which yields a dominantly small sized beyrichiid fauna. The ratios of *N. (Ne.) ctenophora* and *H. loensis* are more even in the Bankvät 1 sample, in relation to

the Lau Backar 1 sample and the Olsvenne 3 sample. Also, the ratio of *S. equestris* is more even in the Botvide 1 sample than compared to the Olsvenne 3 sample.

7.3 Lau Event and other clades on Gotland

Stricanne et al. (2006) summarise changes among acritarch palynomorphs in Lau Event strata. Acritarch palynomorphs are primary producing phytoplanktons which are inhabiting the photic zone. As they are on the bottom level of the food chain, Stricanne et al. (2006), suggest the possibility that they could have an effect on other clades during an event. Stricanne et al. (2006) conclude that initial changes within palynomorph lineages are seen further up in the stratigraphical column than initial changes within e.g. lineages of conodonts and graptolites. They suggest that the Lau Event first affected deep water settings and then affected the photic zone. Moreover, they summarise that clades living in the hemipelagic zone were more severely affected by the event than clades living in shallow water settings. Previous studies on Silurian polychaete jaws (scolecodonts) are thoroughly summarised by Eriksson et al. (2004). Scolecodonts are abundant in the Gotland succession and similar to ostracodes, both long ranging taxa, and more facies dependent short ranging taxa, are identified in the Gotland succession. Eriksson et al. (2004) (referring also to Jeppsson & Aldridge (2000) and Bergman (1989)), note that the polychaetes were affected by the Lau Event, as reflected by LAD:s and gaps in polychaete lineages. Nine out of 30 polychaete taxa went extinct during the event, and six ranges have gaps in event deposited strata. Also, three taxa have FAD:s during the event. Lilliput patterns are also recorded. In the Burgsvik Fm., the polychaete fauna differs from the pre-event fauna, as new lineages appear and as there are reappearances of Lazarus taxa or recoveries of taxa which only occurrences scarcely in the Eke Fm. (Eriksson et al. 2004).

Conodont response to the Lau Event is summarised by Jeppsson & Aldridge (2000) and Jeppsson (2006). Although the När Fm. yields more than 20 conodont taxa, it is characterised by four conodont species: Ozarkodina confluens confluens, P. siluricus, Coryssognathus dubius, and in the lower När Fm., also Silurognathus maximus (Jeppsson 2006). As mentioned earlier, the lower Botvide Mbr. corresponds to the Upper P. siluricus Subzone, in which c. 50 % of the conodont taxa disappear in rapid but stepwise extinctions. The initiation of the event is represented by the disappearance of *P. siluricus*, followed by disappearances of seven other species further up in the Botvide Mbr. 13 out of 18 species of which are present in the very early stage of the event, have disappeared by the end of the event (Jeppsson & Aldridge 2000). The Icriodontid Zone and its three subzones; the Lower-Middle- and Upper Icriodontid Subzones, are named after icriodontids of different type, varying locally in the zone. The conodont fauna of the Lower Icriodontid Subzone is reflected by a low diversity, and is characterised by e.g. O. confluens, Ozarkodina excavata, Panderodus unicostatus, Pseudooneotodus beckmanni and Decoriconus sp. The Middle Icriodontid Subzone is characterised by Panderodus equicostatus which reappears after a wide gap extending from early Ludlow strata. O. confluens, O. excavata, Panderodus serratus, P. beckmanni, Decoriconus sp. and rare Belodella sp., are also recorded. The Upper Icriodontid Subzone is dominated by taxa that are previously rare, e.g. P. equicostatus, and taxa such as Ps. beckmanni and Decoriconus (Jeppsson 2006). Other specific icriodontids presented by Jeppsson & Aldridge (2000) are present also. The Burgsvik Fm. is characterised by an abrupt faunal change and a relatively balanced fauna with species reappearing after the Lau Event. Ozarkodina wimani, Ozarkodina snajdri, O. confluens, Oulodus novoexcavatus, and Pa. equicostatus are all well represented in the fauna of the lower Burgsvik Fm. Ps. beckmanni and Decoriconus sp. are less frequent. O. excavata and other species of Panderodus are notably absent even in larger collections. O. excavata returns later and occurs in the upper Burgsvik Fm. Except taxa present also in the Burgsvik Fm., collections from the Hamra Fm. include other taxa such as Pa. unicostatus which survives the event. New lineages also appear higher up in the Hamra Fm. (Jeppsson 2006; Jeppsson et al. 2007).

7.3.1. Ostracodes and other clades

The ostracodes studied herein show patterns in the Botvide Mbr., and the Eke Fm. similar to e.g. the disappearances and Lazarus patterns of polychaetes, and the disappearances and disaster faunas of conodonts during the Lau Event. I would therefore like to conclude that the beyrichiid species herein were similarly affected by the event. My conclusions are based on the following observations; first of all, six of the nine lineages of pre-event taxa that continue into event strata, have LAD:s in the event strata. I would like to compare these taxa to the 13 conodont taxa which are present in the very early stage of the Lau Event, but which disappear by the end of the event (Jeppsson & Aldridge 2000). Moreover, at least four species in Lau Event-strata have Lazarus gaps in the Eke Fm. Polychaete taxa with similar gaps in the Eke Fm. have been recorded by Eriksson et al. (2004). N. (Ne.) ctenophora, S. equestris and H. loensis are the most frequently occurring taxa of the Eke Fm. Regarding abundance, B. (S.) globifera dominates the Lau Backar 1 fauna, and S. equestris and H. loensis dominate the Olsvenne 3 fauna. This noticeable faunal turnover can be compared to e.g. conodont taxa such as P. equicostatus, Ps. beckmanni and Decoriconus which are rare in the lower Eke Fm. but which dominates the upper Eke Fm. (Jeppsson 2006).

Similar to polychaetes in the Eke Fm. recorded

by Eriksson *et al.* (2004), Lilliput faunas are present in event strata, recorded from the sampled material of Olsvenne 3. Further, the Burgsvik Fm. yields a more stable fauna, which is more diverse, and in which Lazarus taxa reappear. Also, new taxa appear in the Hamra Fm., similar to conodont taxa presented by Jeppsson (2006) and polychaete taxa presented by Eriksson *et al.* (2004).

The excursion in frequency of the brachiopod Davia navicula (see Munthe 1910; Hede 1921; Spjeldnaes 1950) in the Botvide Mbr., can possibly be compared with specific changes regarding beyrichiid taxa of the Botvide 1 sample relative to the Mattsarve 1 sample. The relative abundance of Neobevrichia is higher in the Botvide 1 sample compared to the Mattsarve 1 sample. E.g., the relative abundance of N. (No.) scissa is higher in the Botvide 1 sample than in the Mattsarve 1 sample. The percentage of N. (No.) scissa specimens amounts to c. 20 % of the Mattsarve 1 fauna, but c. 50 % of the Botvide 1 fauna. Martinsson (1962) reports a slight gap in the lineage of N. (Ne.) lauensis at the stratigraphic interval of Mattsarve 1. In the Botvide 1 sample, N. (Ne.) lauensis amounts to c. 45 % of the beyrichiid fauna. Conclusively, there is an excursion in the abundance of Neobeyrichia specimens in the Botvide 1 sample. Neobevrichia comprises c. 45 % of the Mattsarve 1 beyrichiid fauna, and indeed dominates the faunal assemble. However, the domination is more apparent in the Botvide 1 sample, where the genus comprises c. 95 % of the beyrichiid fauna. Although, N. (Ne.) lauensis and N. (No.) scissa are abundant in the Lau Backar 1 sample the taxa are less dominating as the sample yields a more diverse fauna.

7.4 Ostracode morphology and depositional environment

Martinsson (1962) concurs that beyrichiids were most likely benthic organisms, and confirms that they occur in a wide range of sedimentary rocks. He further notes that beyrichiids to a large extent lived among algal vegetation. Martinsson (1962) also mentions that strata in which ostracodes other than beyrichiids are abundant and in which one or two beyrichiid taxa dominate, are often associated with the algae Sphaerocodium gotlandicum. These coupled occurrences are deposited within reef pockets. S. equestris is commonly associated with S. gotlandicum. S. gotlandicum is recorded in the oncolites of the Eke and Hamra Formations (Rothpletz 1913, see Stel & de Coo 1977). As proposed by Wood (1948) and quoted in Stel & de Coo (1977) Sphaerocodium were composed of three algae which lived in symbiosis. One of these algae is Rothpletzella which encrusts the Sphaerocodium intergrowths. Rothpletzella is part of the anachronistic facies present in the Eke Fm. and the Hamra Fm., described e.g. by Calner (2005). This is analogous with my sampled data from Olsvenne 3, in which ostracodes of other affinities are very abundant and where

S. equestris dominates the beyrichiid fauna. Benson (1961) mentions that the ostracodes which are living in environments with coarse or calcareous sediments, often are spinose and reticulate, which is demonstrated as ribs which protect the carapace against impacts from sand grains. For example, C. bicalcarata specimens which first appear in the Burgsvik Fm. have robust carapaces (Fig. 4) which were possibly adapted to the prograding delta sands of the formation, despite many other taxa having concurrent gaps in the formation. The sampled material from the Bankvät 1 fauna agree with the ostracode morphologies found in calcareous sediments, as demonstrated e.g. by C. bicalcarata, N. (No.) regnans, N. (Ne.) ctenophora, and B. (S.) barbulimentata, which all have spinose and ornamented carapaces.

8 Conclusions

The aim of this paper was to identify if and how the Late Silurian Lau Event affected the ostracode faunas on Gotland. To answer this matter, the following conclusions were drawn according to the results obtained from the literature studies and the sampled material:

- 1. The beyrichiid faunas on Gotland were reorganised during Late Silurian Lau Event.
- The re-organisation is recognised as various signals in Lau Event strata. Among these are: 10 FAD:s, 11 LAD:s, four Lazarus faunas in the Eke Fm., and three, or perhaps more, Lilliput faunas.
- 3. The Lau Backar 1 fauna and the Olsvenne 3 fauna are far more diverse as compared to the other Eke Fm. localities studied.
- 4. *N. (Ne.) lauensis* and *N. (No.) scissa* which are abundant and frequent in the När Fm. only have scare occurrences above Lau Backar 1 of the Eke Fm. Both species have their LAD in the Upper Eke Fm.
- 5. The Eke Fm. above Lau Backar 1 displays a generally low diversity beyrichiid succession. The interval is characterised by *N. (Ne.) ctenophora, S. equestris* and *H. loensis* which are dominating the succession with high abundances and frequent occurrences.
- 6. Out of 10 lineages recorded in the Burgsvik Fm., seven lineages have gaps with reappearances in the Hamra Fm. The scarce beyrichiid diversity of the Burgsvik Fm., could be related to lithology changes caused by sand accumulations.
- A reappearance of Lazarus taxa is recorded in the Burgsvik Fm. Four reappearances are recorded in the Hamra Fm. The Hamra Fm. is characterised by a speciation and a diverse and established beyrichiids association.
- 8. Ostracodes of uncertain taxa in the sampled mate-

rial show a positive response to the Lau Event. An increased abundance is recorded from the Lau Backar 1 sample as compared to the Mattsarve 1 and Botvide 1 samples. The high abundance is significantly prominent in the Olsvenne 3 sample. A moderate abundance is recorded from Bankvät 1.

- 9. Correlation to other studied clades on Gotland concludes that beyrichiids experienced a similar response to the Lau Event, as recorded among conodonts and polychaetes.
- 10. Sampling of a large scale collection from Gotland is suggested for detailed recognition of Lau Event induced patterns.

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Appendix 1. List of taxa

List of Beyrichiidae ostracodes included in this thesis, based on Martinsson (1962). Craspedobolbininae Martinsson 1962 Craspedobolbina Kummerow 1924 Craspedobolbina (Mitrobeyrichia) Henningsmoen 1954 Craspedobolbina (Mitrobeyrichia) robusta Martinsson 1962 Aitilia Martinsson 1962 Aitilia calcarulata Martinsson 1962 Hamulinavis Martinsson 1962 Hamulinavis pirulifera Martinsson 1962 Clintiella Martinsson 1962 Clintiella cf. hyrsiniana Martinsson 1962 Treposellinae Henningsmoen 1954 Retisacculus Martinsson 1962 Retisacculus commatatus Retisacculus cf. commatatus Retisacculus semicolonatus Amphitoxotidinae Martinsson 1962 Sliea Martinsson 1962 Sleia equestris Martinsson 1962 Hemsiella Martinsson 1962 Hemsiella hemsiensis Martinsson 1962 Hemsiella loensis Martinsson 1962 Hemsiella anterovelata Martinsson 1962 Hammariella Martinsson 1962 Hammariella pulchrivelata Martinsson 1962 Hoburgiella Martinsson 1962 Hoburgiella tenerrima Martinsson 1962 Juviella Martinsson 1962 Juviella juvensis Martinsson 1962 Lophoctenella Martinsson 1962 Lophoctenella angustilaqueata Martinsson 1962 Lophoctenella cf. scanensis Martinsson 1962 Cryptolopholobus Martinsson 1962 Cryptolopholobus semilaqueatus Martinsson 1962 Lauella Martinsson 1962 Lauella uncinata Martinsson 1962 Vinculoveliger Martinsson 1962 Vinculoveliger catenulatus Martinsson 1962 Atterdagia Martinsson 1962 Atterdagia paucilobata Martinsson 1962 Beyrichiinae Matthew 1886 Beyrichia M'Coy 1846 Beyrichia (Simplicibeyrichia) Martinsson 1962 Beyrichia (Simplicibeyrichia) globifera Martinsson 1962 Beyrichia (Simplicibeyrichia) duplicicalcarata Martinsson 1962 Beyrichia (Simplicibeyrichia) barbulimentata Martinsson 1962 Neobeyrichia Henningsmoen 1954 Neobeyrichia (Neobeyrichia) Henningsmoen 1954 Neobeyrichia (Neobeyrichia) ctenophora Martinsson 1962 Neobeyrichia (Neobeyrichia) lauensis Kiesow 1888 Neobeyrichia (Neobeyrichia) nutans Kiesow 1888 Neobeyrichia (Nodibeyrichia) Henningsmoen 1954 Neobeyrichia (Nodibeyrichia) scissa Martinsson 1962 Neobeyrichia (Nodibeyrichia) regnans Martinsson 1962 Calcaribeyrichia Martinsson 1962 Calcaribeyrichia bicalcarata Martinsson 1962 Calcaribeyrichia calcarata Martinsson 1962

Plicibeyrichia Martinsson 1962 Plicibeyrichia ornatissima Martinsson 1962 Gannibeyrichia Martinsson 1962 Gannibeyrichia biplicata Martinsson 1962 Navibeyrichia Martinsson 1962 Navibeyrichia hanseatica Martinsson 1962 Navibeyrichia balticivaga Martinsson 1962 Hexophthalmoidinae Martinsson 1962 Hexophthalmoides craterilobatus Martinsson 1962 Beyrichia incertae sedis Kolmodinia cf. grandis Martinsson 1962

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