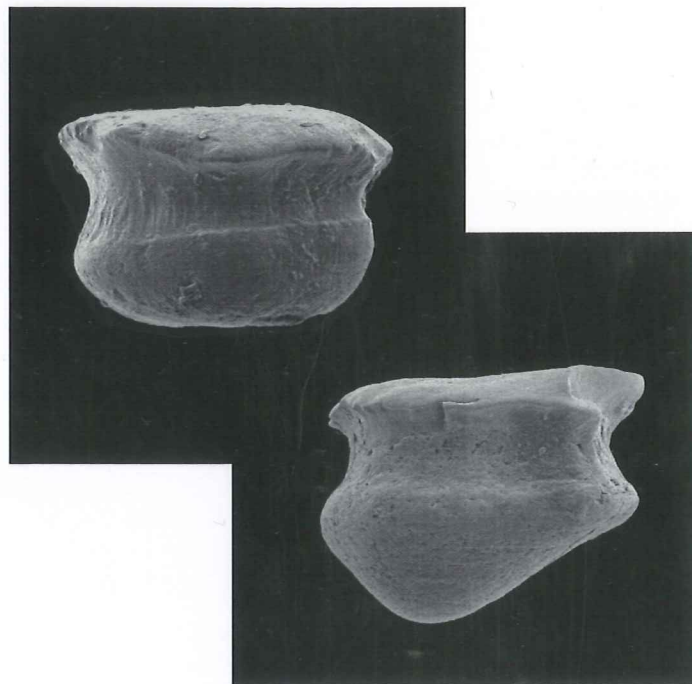


2005-05-30

# Extinctions and faunal turnovers of early vertebrates during the Late Silurian Lau Event, Gotland, Sweden

*Eva K. Nilsson*

Examensarbeten i Geologi vid  
Lunds universitet - Berggrundsgeologi, nr. 188



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**Cover picture:** vertebrate scales from the Ludfordian of Gotland. Left: the thelodont *Thelodus parvidens*, 0.50 mm in width. Right: the acanthodian *Gomphonchus sandelensis*, 0.55 mm in width.

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EVA K. NILSSON

Nilsson, E.K., 2005: Extinctions and faunal turnovers of early vertebrates during the Late Silurian Lau Event, Gotland, Sweden. Examensarbete i geologi vid Lunds universitet. 20 poäng. Nr. 188, 32 pp.

**Abstract:** The Late Silurian Lau Event is one of the three major events identified in the Gotland strata. It is associated with one of the largest stable carbon isotope excursions recorded in the Phanerozoic, as well as rapid lithology changes, and extinctions and faunal turnovers among various fossil groups. In this study, early vertebrates (fishes) were investigated over the Lau Event interval. The study was based on isolated scales, which are common in the Late Silurian Gotland bedrock. Twenty-six samples from the När Formation of the upper Hemse Group through the Hamra Formation yielded over 2500 vertebrate scales. They were studied in light microscope and identified in order to establish the vertical ranges of the taxa. Six different vertebrate groups occur in the Gotland strata; the agnathan thelodonts, anaspids, heterostracans, and osteostracans, and the gnathostome acanthodians and actinopterygians. There were pronounced faunal turnovers among the vertebrates during the event. The diverse and abundant pre-event fauna of the När Formation is dominated by acanthodians and includes *Archegonaspis lindstroemi*, *Andreolepis hedei*, *Gomphonchus sandelensis*, *Nostolepis striata*, *Phlebolepis elegans*, *Thelodus carinatus*, *Th. parvidens*, and *Paralogania martinssoni*. The succeeding event-fauna of the Botvide Member is marked by the extinctions of five (63 %) of these species; *Pa. martinssoni* disappears during the very beginning of the event, at the base of the Upper *Polygnathoides siluricus* conodont Subzone, the base of Botvide Member, whereas *Ar. lindstroemi*, *An. hedei*, *Ph. elegans*, and *Th. carinatus* disappear simultaneously in the Upper *P. siluricus* conodont Subzone slightly below the top of the Botvide Member. *Paralogania?* sp., *Pa. ludlowiensis*, *Thelodus* sp., Gen. indet. sp. A, *Lanarkia horrida*, Gen. indet. sp. B, and *Thelodonti* sp. A appear during the event and the latter five of these taxa occur exclusively in the event strata. The vertebrate fauna during the later phase of the event in the Icriodontid conodont Zone of the Eke Formation is low both in diversity and abundance. There is an evident decrease in scale frequency in the collections from the Botvide Member to the Upper Eke Formation event interval, also reflecting the severity of the event. Diversity and abundance increase considerably in the thelodont-dominated post-event fauna in the *Ozarkodina snajdri* conodont Zone of the Burgsvik and Hamra formations. It is characterised by the appearances of *Poracanthodes porosus*, *Th. sculptilis*, *Septentrionia mucronata*, *Tahulalepis elongituberculata*, *Osteostraci?* indet., type A, and *Osteostraci?* indet., type B. The changes in the vertebrate fauna can be noted also in other regions, indicating that the effects of the Lau Event on the vertebrates were restricted not only to Gotland and that vertebrates can be a useful tool for identifying the event elsewhere.

**Keywords:** Late Silurian, Lau Event, early vertebrates, scales, extinctions, Gotland.

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# Förändringar i den gotländska vertebratfaunan under den sensiluriska Laukastrofen

EVA K. NILSSON

Nilsson, E.K., 2005: Förändringar i den gotländska vertebratfaunan under den sensiluriska Laukastrofen. Examenarbete i geologi vid Lunds universitet. 20 poäng. Nr. 188, 32 sid.

**Sammanfattning:** En av de tre stora katastroferna som har identifierats i den gotländska lagerföljden är Laukastrofen. Denna inträffade under sensilurisk tid (sen Ludlow) och är förknippad med ett av de största positiva kolisotopvärdena som har uppmätts under de senaste 540 miljoner åren. Katastrofen är även associerad med snabba förändringar i litologi samt strukturella förändringar och utdöenden i olika fossila faunor. Syftet med denna studie är att undersöka hur de tidiga vertebraterna, i detta fallet representerat av fiskar, påverkades av Laukastrofen. Studien, som är baserad på fiskfjäll vilket är den vanligaste formen av vertebratrester som hittas i siluriska bergarter, har inneburit mikroskopering av 26 prover och identifiering av mer än 2500 vertebratfjäll. Proverna är insamlade från bergarter avsatta inom intervallet Närformationen (översta Hemsegruppen) till Hamraformationen. Sex olika vertebratgrupper har påträffats från detta intervall; de käklösa thelodonterna, anaspiderna, heterostrakerna och osteostrakerna, samt de käkförsedda acanthodierna och actinopterygierna. Laukastrofen innebar utdöenden och stora strukturella omvälvningar för vertebraterna. Den både rika och mångformiga acanthod-dominerade faunan som fanns före katastrofens början i Närformationen inkluderade *Archegonaspis lindstroemi*, *Andreolepis hedei*, *Gomphonchus sandelensis*, *Nostolepis striata*, *Phlebolepis elegans*, *Thelodus carinatus*, *Th. parvidens* samt *Paralogania martinssoni*. Den efterföljande faunan från katastrofens inledande skede, från Botvide Member, kännetecknas av utdöendet av fem (63 %) av de åtta ovan nämnda arterna, där *Pa. martinssoni* försvinner redan vid katastrofens början vid den undre gränsen för den Övre *Polygnathoides siluricus* conodontsubzonen, vid basen för Botvide Member, medan *Ar. lindstroemi*, *An. hedei*, *Ph. elegans*, och *Th. carinatus* försvinner något senare i den subzonen, strax under toppen av Botvide Member. Under katastrofen dyker sju nya arter upp, *Paralogania?* sp., *Pa. ludlowiensis*, *Thelodus* sp., Gen. indet. sp. A, *Lanarkia horrida*, Gen. indet. sp. B och *Thelodonti* sp. A, varav endast de två förstnämnda finns kvar efter katastrofen. Vertebratkollektionerna från den senare delen av katastrofen, Icriodontid conodontzonen i Ekeformationen, präglas av både få arter och få fjäll. Detta förändrades omedelbart efter katastrofen i *Ozarkodina snajdri* conodontzonen i Burgsvik- och Hamraformationerna där vertebratfaunan återigen är rik och mångformig, och där sex nya arter tillkommer; *Poracanthodes porosus*, *Th. sculptilis*, *Septentrionia mucronata*, *Tahulalepis elongituberculata*, *Osteostraci?* indet., typ A samt *Osteostraci?* indet., typ B. Till skillnad mot faunan som fanns före katastrofen där acanthodierna dominerade, är det thelodonterna som dominerar i lager avsatta efter katastrofen. Förutom dessa förändringar i faunasammansättningen minskar även antalet fjäll drastiskt i kollektionerna från Botvide Member till Övre Ekeformationen jämfört med kollektionerna före katastrofen. Liknande förändringar av vertebratsammansättningen har rapporterats även från regioner i andra länder vilket visar att Laukastrofen inte enbart påverkade Gotland och dess faunor. Detta indikerar även att vertebratfjäll kan vara till god hjälp för att identifiera katastrofen på andra platser.

**Nyckelord:** sensilur, Laukastrofen, vertebrater, fjäll, utdöenden, Gotland.

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## 1. Introduction

Gotland, the largest island of Sweden, is renowned for its excellent and numerous outcrops of Silurian sedimentary rocks. The island is also known for its extremely rich and well preserved fossil faunas. These aspects are very important since they provide deep insights to the long extinct ecosystems of the Silurian Period.

The Silurian was once believed to be a period characterised by stable environmental conditions (Boucot 1991), however, during later years research has revealed quite the opposite (e.g. Jeppsson 1990, 1998; Calner *et al.* 2004). The arguments that have led to the abandonment of the former view are reports of mass extinctions, rapid lithology changes, and large variations in stable isotopic values – characters now recognised as the result of events. Eight events have been identified in the Silurian of Gotland, three of which have now been recognised globally – the Llandovery-Wenlock Ireviken Event, the late Wenlock Mulde Event, and the late Ludlow Lau Event (e.g. Jeppsson 1998, 2005*a*, in press; Jeppsson & Aldridge 2000). The latter one is the subject of further investigation herein.

The aim of this thesis project is to document the vertebrate faunas during the Lau Event. It has previously been shown that various taxonomical groups, for example conodonts and brachiopods, were affected during the Lau

Event in ways that today can be seen in the rock record as extinctions, faunal turnovers, and “Lilliput faunas” (e.g. Jeppsson 1998 and references therein; L. Gustavsson pers. comm. 2005). It is now desirable to take a closer look at the vertebrates, first of all to see if they too were affected by this event, and if so, in what ways. The study is based on isolated scales with emphasis on occurrence data, and not on frequency.

The vertebrates of Gotland have been studied before; a thorough investigation was undertaken by Fredholm (1988*a, b*, 1989, 1990), however, her work was carried out before the Lau Event was discovered and dealt mostly with the vertebrates occurring in the strata older than those formed during the event. Also, the sampling sizes are considerably larger today compared to when Fredholm undertook her investigations (approximately 30 kg compared to about 2 kg), and the number of samples through the event interval is larger. Moreover, the methods for dissolving carbonate rocks have been improved (e.g., Jeppsson *et al.* 1999) since her work. The factors mentioned above should therefore, altogether, contribute to a more detailed study with a higher resolution of the vertebrate faunas through the event. Nonetheless, Fredholm’s (1988*a, b*, 1989, 1990) work when combined with the new samples investigated herein forms a very good basis for the present study.



Silurian Time Scale						
AGE (Ma)	Series/Stage	Baltic Regional Stages	Graptolites	Conodonts	Vertebrates	Bioevents
	<b>Devonian</b> 416.0±2.8		<i>Monograptus uniformis</i>	<i>Icriodus woschmidt/postwoschmidti</i>	<i>Nostolepis minima</i>	
	<b>Pridoli</b>	Ohesaare	<i>Monograptus transgrediens</i> <i>Monograptus bouceki-perneri</i>	<i>Oulodus elegans detortus</i>	<i>Katoporus timanicus-lithuanicus</i> <i>Poracanthodes punctatus</i> <i>Nostolepis gracilis</i>	← Klonk C ← <i>transgrediens</i> G
		Kaugetuma	<i>Monograptus lochkovenski</i> <i>Monograptus branikensis</i> <i>Monogr. parultimus-ultimus</i>	Interval Zone <i>Ozarkodina remscheidensis</i>		
		Kuressaare	<i>Monograptus formosus</i>	<i>Ozarkodina crispa</i> <i>Ozarkodina snajdri</i>	<i>Thelodus sculptilis</i>	← <i>spineus</i> G ← Klev C
420	<b>Ludlow</b>	Paadla	<i>Neocucullograptus kozlowskii</i> <i>B. comuatus-P. podoliensis</i>	Interval Zone	<i>Andreolepis hedei</i>	← <i>kozlowskii</i> G ← Lau C
			<i>Saetograptus leintwardinensis</i> <i>Saetograptus linearis</i>	<i>Polygnathoides siluncus</i> <i>Ancoradella ploeckensis</i>	<i>Phlebolepis elegans</i>	← <i>leintwardinensis</i> G ← Linde C
	<b>Gorstian</b>		<i>Lobograptus scanicus</i> <i>Neodiversograptus nilssoni</i>	not zoned <i>K. stauros</i>	<i>Phlebolepis ornata</i>	
	<b>Wenlock</b>	Rootsikula	<i>Colonograptus ludensis</i> <i>Colono. praedeubeli-deubeli</i> <i>Prstio. parvus-Gotho. nassa</i>	<i>Ozarkodina bohemia</i>	<i>Paralogana martinssoni</i>	← Mulde C ← <i>lundgreni</i> G
425		Jaagarahu	<i>Cyrtograptus lundgreni</i> <i>Cyrtograptus perneri</i> <i>Cyrtograptus rigidus</i>	<i>Ozarkodina sagitta sagitta</i>	<i>Loganellia grossi</i>	← Valleviken C ← Boge C
		Jaani	<i>Monogr. beloph.-anten.</i> <i>Monogr. riccartonensis</i> <i>Cyrtograptus purchisoni</i> <i>Cyrtograptus centrifugus</i> <i>Cyrtograptus insectus</i> <i>Cyrtograptus lapworthi</i>	<i>Ozarkodina sagitta rhenana</i> <i>Kockelella ranuliformis</i>	<i>Loganellia avonia</i>	← <i>murchinsoni</i> G ← Ireviken C ← lapworthi G
	<b>Llandovery</b>	Adavere	<i>Oktavites spiralis</i>	<i>Pterospathodus amorphognathoides</i>		
			<i>Monoclimacis crenulata</i> <i>Monoclimacis griestoniensis</i>	<i>Pterospathodus celloni</i>	<i>Loganellia scotica</i> <i>Loganellia sibirica</i>	
			<i>Monograptus crispus</i>			← <i>utilis</i> G C
435			<i>Spirograptus turriculatus</i> <i>Spirograptus guerichi</i>	<i>Pterospathodus tenuis</i> <i>Distomodus staurognathoides</i>		← Sandvika C ← <i>sedgwickii</i> G
	<b>Aeronian</b>	Raikkula	<i>Stimulograptus sedgwickii</i> <i>Lituigraptus convolutus</i> <i>Monograptus argenteus</i> <i>Demirastrites pectinatus</i> <i>Demirastrites triangulatus</i>			
440	<b>Rhuddanian</b>	Juuru	<i>Coronograptus cyphus</i>	<i>Distomodus kentuckyensis</i>	<i>Valyalaspis crista</i>	
			<i>Orthograptus vesiculosus</i> <i>Parakidograptus acuminatus</i>			← <i>acuminatus</i> G
			<i>Akidograptus ascensus</i>	<i>Rexroadus nathani</i>	not zoned	
	<b>Ordovician</b> 443.7±1.5					

Fig. 1. Silurian vertebrate biozones, based on the East Baltic vertebrate sequence, and correlation to the Baltic Regional Stages, graptolite and conodont zonations, and important bioevents recognised in graptolites (G) and conodonts (C). The lower boundaries of the vertebrate zones are defined by the first appearance datum (FAD) of the index-species. The index-species can extend into the succeeding zone, marked by a dashed line in the column. Shaded area marks the Lau Event interval. Modified from Gradstein et al. (2004).

## 2. Vertebrates

### 2.1. Early vertebrates

Fishes are the most diverse group of vertebrates living today (Long 1995), perhaps due to the fact that they have inhabited the seas, rivers, and lakes of our world for a very long time. The fossil record tells us that the early fishes, often referred to as the early vertebrates (excluding conodonts), have been around since the Early Ordovician, approximately 485 million years ago (Turner 1999). They might have existed even earlier as many scientists argue that the Furongian (late Cambrian) to the Early Ordovician *Anatolepis* was actually the oldest known fish (Smith *et al.* 1996). These oldest remains of vertebrates are no more than fragments, and the oldest articulated vertebrate specimen ever recorded is the 450 million year old arandaspid *Sacabambaspis* that was found in Bolivia in 1986 (Long 1995; Janvier 1996; Turner 1999). Although articulated specimens are rarely found in early to middle Palaeozoic sedimentary rocks, isolated vertebrate remains such as teeth, fin spines, and scales are abundant. Isolated scales, in particular, are very diverse and frequent in Silurian and Devonian sedimentary rocks. They are very useful for dating rocks (e.g., Long 1995; Märss *et al.* 1995; Valiukevicius 2003), and are used as a complement, or by themselves, to the graptolite and conodont biostratigraphy (Fig. 1). The study of fishes is called ichthyology and the study of fossil fishes is called palaeoichthyology.

Although the earliest fishes appeared in the Ordovician, or even Cambrian, Period, it was not until Silurian times that most groups originated (Janvier 1996; Benton 2000). They became abundant in the Devonian, which was a time of major radiation, and this period is therefore often referred to as "The Age of Fishes". The Devonian fishes gave rise to the modern sharks and bony fishes, and finally, the first terrestrial vertebrates (Benton 2000).

During the first millions of years of the vertebrate history, the jawless fishes – the agnathans, dominated the waters. Later on, the jawed fishes – the gnathostomes, took over (Turner 1999). Today, the latter group is well represented while the lampreys and hagfishes are the only living agnathans.

### 2.2. Silurian vertebrates

Nine groups of vertebrates inhabited the seas during the Silurian Period; they are represented by five agnathan groups termed thelodonts, heterostracans, anaspids, galeaspids, and osteostracans, and four gnathostome groups which are called placoderms, acanthodians, chondrichthyans, and actinopterygians (Long 1995). The thelodonts, heterostracans, anaspids, galeaspids, osteostracans, and placoderms became extinct during the Devonian. The acanthodians persisted until the Late Permian, whereas the large group of actinopterygians, which

comprises ray-finned fishes, are a very successful group of fishes that are still living today, as are the chondrichthyans (Fig. 2; Long 1995).

### 2.3. The Silurian vertebrates of Gotland

The only articulated vertebrate found on Gotland are two well preserved shields, *c.* 5 cm in length, of a cyathaspid (a heterostracan) collected at the locality Gannor and described by Lindström (1895). During later studies, Spjeldnaes (1950) found remains of acanthodians, "cephalaspids" (also known as osteostracans), and "coelolepids" (or thelodonts) on Gotland. Thelodonts, anaspids, and osteostracans have been reported by Martinsson (1966). So far, however, the most extensive study of the vertebrates of Gotland has been carried out by Fredholm (1988*a, b*, 1989, 1990). In her summary (Fredholm 1989), finds of heterostracans, thelodonts, anaspids, osteostracans, acanthodians, and actinopterygians are reported. The vertebrate remains include isolated scales and occasionally larger fragments. The six groups reported are briefly described below. For further information on Gotland vertebrates, see Fredholm (1988*a*, p. 157; 1990, p. 61-62) and Blom *et al.* (2002, p. 273).

#### *Heterostraci*

The characteristic features of the heterostracans (Fig. 3A) are their head shields and their single gill opening on each side of the body (Long 1995). Usually they have one dorsal and one ventral shield covering the head, and a single shield covering the gill opening, whereas the rest of the body is covered in smaller scales. Most heterostracans were small, about 10-15 cm in total length, but some could become as large as 1 m or more (Long 1995). The heterostracans are further subdivided into four groups; the cyathaspids, amphiaspids, pteraspids, and psammosteids (Benton 2000).

The cyathaspid "*Cyathaspis? Schmidtii*" described by Lindström (1895), later renamed *Archegonaspis lindstroemi* (see Fredholm 1988*a*, p. 160), is the only heterostracan species recorded on Gotland. It occurs in the När Formation of the Hemse Group (Fredholm 1988*a*; see the next section, "Geological setting", for a summary of the stratigraphical division of the Gotland strata). Heterostracans are known also from, for example, North America, Russia, Siberia, Ukraine, Britain, Germany, and Spitsbergen (Long 1995; Turner 1999).

#### *Thelodonti*

Thelodonts are common especially in Late Silurian strata (Benton 2000). Their bodies were flat, and they had either a caudal fin with an elongated lower lobe, called a hypocercal tail (Fig. 3B) or a forked caudal fin, then they are called "furcacaudiforms" (Fig. 3C; Long 1995). Some thelodonts could reach over 1 m in length, for example *Thelodus parvidens*, but most of them were less than 20 cm in length (Turner 1999). The thelodonts had



no head shields as the heterostracans, instead they were completely covered in minute and tooth-like scales that showed a variety of shapes depending on where on the body they were situated. The squamation – scale cover, of these vertebrates were very rich and Turner (1999) estimated that one 20 cm long individual had approximately 20,000 scales at any one time. Thelodont scales are among the most common microfossils in Palaeozoic rocks and many species are used in biostratigraphy.

Five thelodont genera are known from Gotland (Fredholm 1989); *Loganellia* (L. Visby-Hamra formations), *Paralogania* (Slite-Burgsvik formations), *Phlebolepis* (Hemse Group), *Thelodus* (L. Visby-Sundre formations), and *Lanarkia* (Burgsvik Formation). Thelodonts are a cosmopolitan fossil group that have been reported from, for example, Scotland, Canada, North America, Europe, Russia, Spitsbergen, Australia, Antarctica, China, South America, and Iran (Turner 1999).

### Anaspida

The small, rarely exceeding 15 cm in length, anaspids (Fig. 3D) are characterised by a strongly hypocercal tail and by gill openings, often between six and fifteen, that are arranged in a slanting row on both sides of the body (Blom *et al.* 2002). They had a fusiform head and a later-

ally compressed body (Long 1995). The anaspids did not possess any larger head shields, instead they were covered in scales and smaller head platelets. The name “anaspida” does, in fact, mean “shield-less” (Turner 1999).

Janvier (1996) discussed the relationship between the anaspids and the modern lampreys. The issue was brought up because both groups share the similar characteristics with a slender body shape and gill openings that are arranged in a slanting line, as well as the fact that both groups belong to the agnathans. Today the extinct anaspids are regarded as a sister group of the extant lampreys, as well as the closest relatives to the gnathostomes (Turner 1999).

For a long time the anaspids were poorly known with only a handful of species recognised, but this view dramatically changed with the thorough study undertaken by Blom *et al.* (2002), which added 15 new species to the former seven and greatly increased the knowledge of this group.

Anaspids found in Gotland strata belong to the order Birkeniida, and ten species are now known of which five were recently redescribed by Blom *et al.* (2002); *Rhyncholepis butriangula* (Halla Formation), *Septentrionia mucronata* (Burgsvik-Hamra formations), *Hoburgilepis papillata* (Burgsvik-Hamra formations), *Liivilepis cur-*

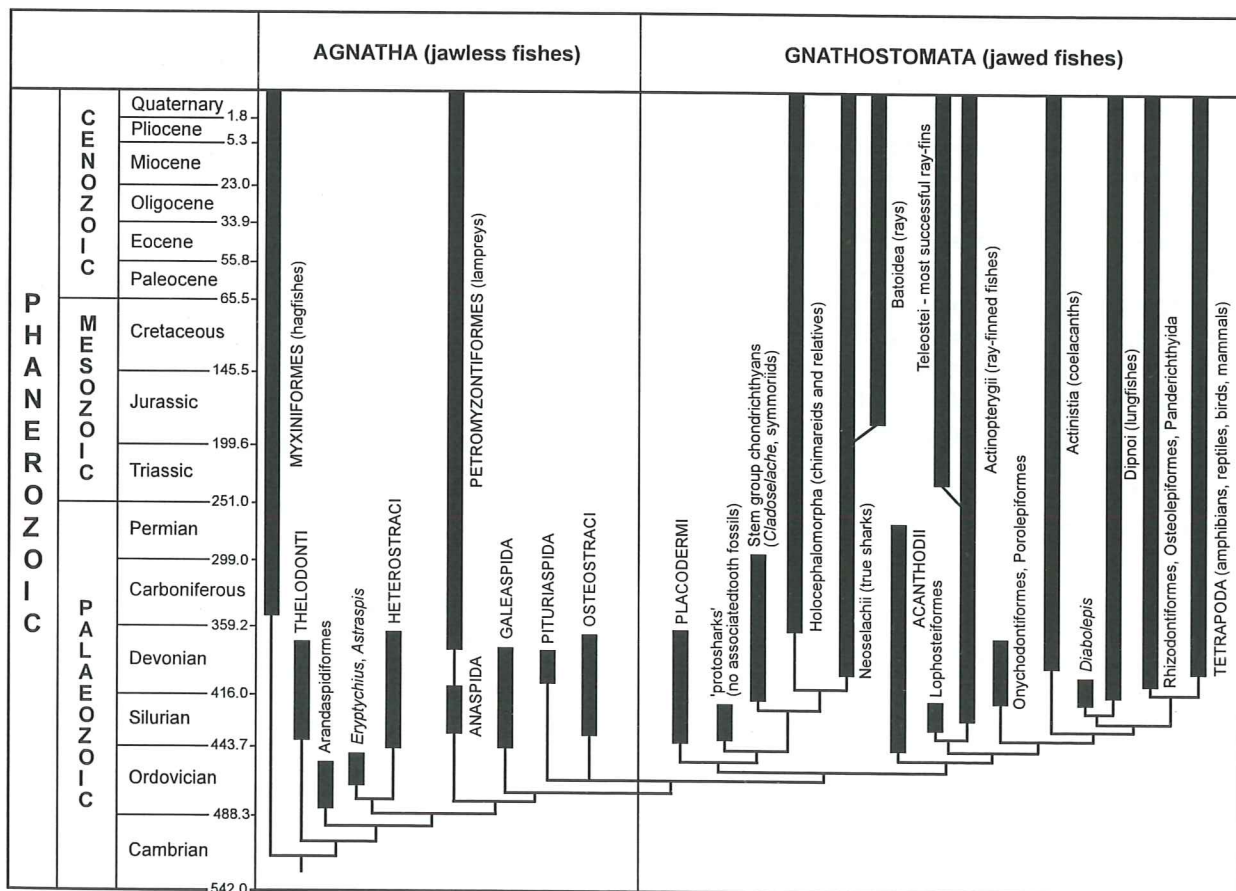


Fig. 2. Radiation of the major vertebrate groups through time. Modified from Long (2001), ages in million years from Gradstein *et al.* (2004).

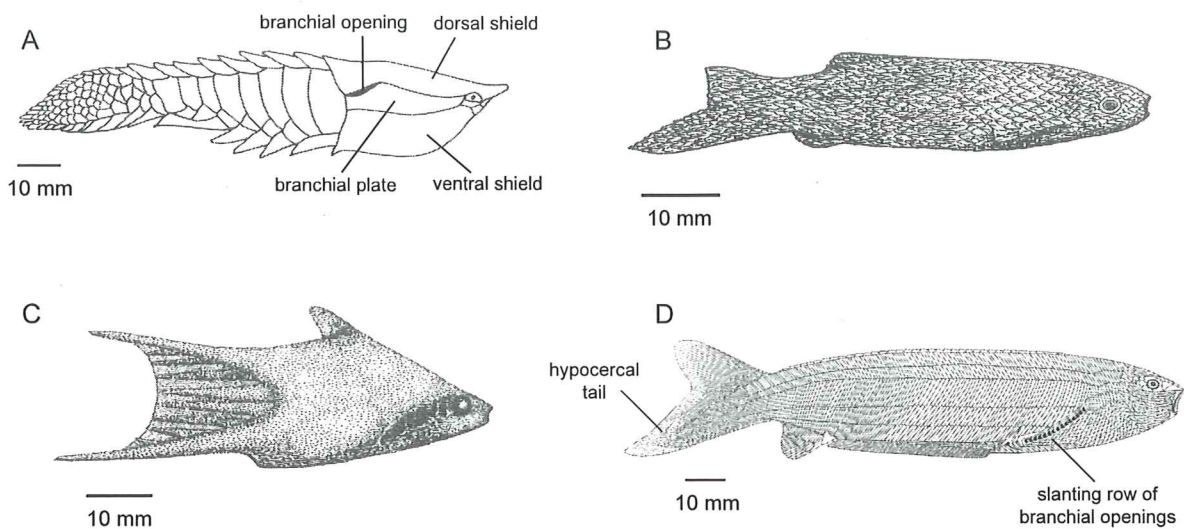


Fig. 3. **A.** The Devonian heterostracan *Anglaspis*, a cyathaspid. **B.** The Silurian thelodont *Phlebolepis* had a hypocercal tail. **C.** Reconstruction of the Devonian furcacaudiform *Furcacauda*. **D.** *Pharyngolepis*, a Silurian birkeniid anaspid. Figures A-C modified from Benton (2000), D modified from Blom *et al.* (2002).

*vata* (Hamra Formation), and *Tahulalepis elongituberculata* (Burgsvik Formation). The other, previously described species from Gotland are; *Rhyncholepis parvula* (Halla Formation), *Pterygolepis nitida* (Halla Formation), *Schidiosteus mustelensis* (Halla Formation), *Rytidolepis quenstedtii* (Halla Formation), and *Pharyngolepis?* sp. (Hemse Group). Anaspids are recorded from many different areas of the world, for example Norway, Scotland, Russia, Estonia, Latvia, and China (Blom *et al.* 2002).

#### Osteostraci

The osteostracans, about 20 cm in length, were heavily armoured in the head region, just like the heterostracans, and had small scales that covered their quite well developed pectoral fins (Benton 2000). During their evolution, the head shield have varied in shape (Benton 2000), some being horseshoe-shaped with two processes reaching out from the sides of their head, while some had a cornua protruding from the front part of their head (Fig. 4A).

From Gotland, Spjeldnaes (1950) reported finds of an osteostracan group called Cephalaspidida. Fredholm (1989) described fragments of the genera *Oeselaspis* (Slite Group), *Tremataspis* (Halla Formation-Hemse Group), *Procephalaspis* (Slite Group-Halla Formation), and *Dartmuthia* (Hemse Group). Osteostracans are known only from the present day Northern Hemisphere (Turner 1999), for example from North America, Russia, Ukraine, Britain, Estonia, and Spitsbergen.

#### Acanthodii

The acanthodians (Fig. 4B) are the earliest known gnathostomes (Benton 2000). They are also referred to as "spiny sharks" (Janvier 1996) since they had large spines

in front of all fins except the caudal fin, and they were previously believed to be relatives of sharks because they had a similar squamation to that of sharks. The name Acanthodii derives from the greek word *acanthos*, which means "spine" or "thorn" (Young 1999). The acanthodians were small, often less than 20 cm long, had a slender body covered in minute scales, and possessed a heterocercal tail (the upper lobe of the caudal fin being larger than the lower; Benton 2000). The acanthodians are one of the four major gnathostome groups; the other three being the extinct placoderms, the extant chondrichthyans (sharks, rays and rabbitfishes), and the extant osteichthyans (Young 1999; Benton 2000). Acanthodian scales are, just as thelodont scales, common fossils in Palaeozoic bedrock and they show great biostratigraphic potential as a tool for worldwide correlations (Valiukevicius 2003).

Fredholm (1989) reported three genera, *Gomphonchus* (Hemse Group-Sundre Formation), *Nostolepis* (Hemse Group-Sundre Formation) and *Poracanthodes* (Eke-Hamra formations), from the Silurian of Gotland. Acanthodian scales are found also, for example, in Germany, Scotland, Canada, Australia, Siberia, North America, China, Antarctica, Greenland, Russia, the Middle East, Africa, and South America (Young 1999), inferring a worldwide distribution.

#### Actinopterygii

The actinopterygians (Fig. 4C), or the ray-finned fishes, are included in the larger group called the osteichthyans, the true bony fishes, together with the sarcopterygians, the lobe-finned fishes. The actinopterygians, which appeared already in the Late Silurian (Gross 1968), are today represented by more than 23,000 living species,



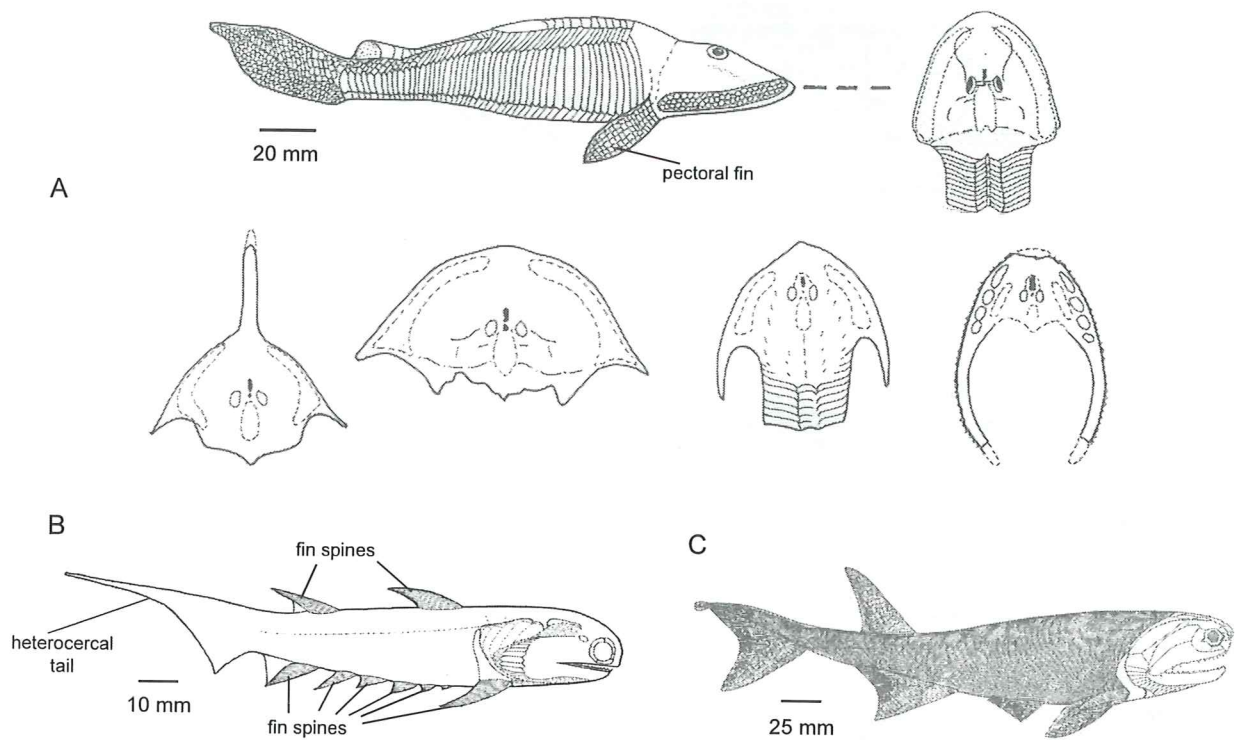


Fig. 4. A. The Silurian osteostracan *Hemicyclaspis*, and osteostracan head shield diversity (from left to right: *Boreaspis*, *Bennevispis*, *Thyestes*, and *Sclerodus*). B. The Devonian acanthodian *Climatius*. C. The Devonian actinopterygian *Cheirolepis*. Figures A and C modified from Benton (2000), B modified from Denison (1979).

whereas the sarcopterygians, which did not appear until the Devonian, are represented only by four extant genera (Benton 2000; Long 2001). During the Devonian Period the situation was the opposite; the sarcopterygians dominated over the actinopterygians with over 100 species compared to about 10 (Long 2001).

The earliest known remains of osteichthyans are the rhomboidal scales of the two actinopterygian genera *Andreolepis* and *Lophosteus* from the Late Silurian (Long 1995). Only one species, *Andreolepis hedei*, is known from Gotland. It is reported from the När Formation of the Hemse Group (Gross 1968; Fredholm 1988a). Other places where *Andreolepis* is found include Latvia, Great Britain, Russia, Siberia, and the Central Urals (Märss 2001).

### 3. Geological setting

#### 3.1. Silurian palaeogeography

The Silurian Period, comprising the Llandovery, Wenlock, Ludlow, and Přídolí epochs (Fig. 1), lasted for almost 28 million years (m.y.), from 443.7 to 416.0 Ma (Gradstein *et al.* 2004). At that time, most of the world's land masses were gathered in the southern hemisphere

(Fig. 5). The continental plate Baltica had previously collided with Avalonia in the Ordovician, and was now located in the equatorial belt on its way to collide with Laurentia (Torsvik *et al.* 1996). The collision between Baltica and Laurentia resulted in the closure of the Iapetus Ocean, the Scandian Orogeny and later, the formation of the Devonian Old Red Sandstone Continent (Benton 2000).

#### 3.2. The Silurian of Gotland

The strata of Gotland range from the uppermost Llandovery to the top of Ludlow (e.g., Laufeld 1974a; Calner *et al.* 2004), a time span of approximately 10 m.y. (Fig. 1). During this time, the climate of Baltica was tropical, and the environments favoured reef building organisms (corals, stromatoporoids and algae). Other taxa that thrived in these warm, shallow waters include molluscs, trilobites, brachiopods, ostracodes, echinoderms, graptolites, conodonts, polychaetes, and vertebrates amongst others.

The Silurian bedrock of Gotland was formed in a shallow sea, the Baltic Basin (Fig. 6). The strata are parts of a large carbonate platform complex that once covered an area of what is now known as the Baltic Sea, the East Baltic, and Ukraine (Calner *et al.* 2004). Three main lithologies are distinguished on Gotland: limestone, marlstone,

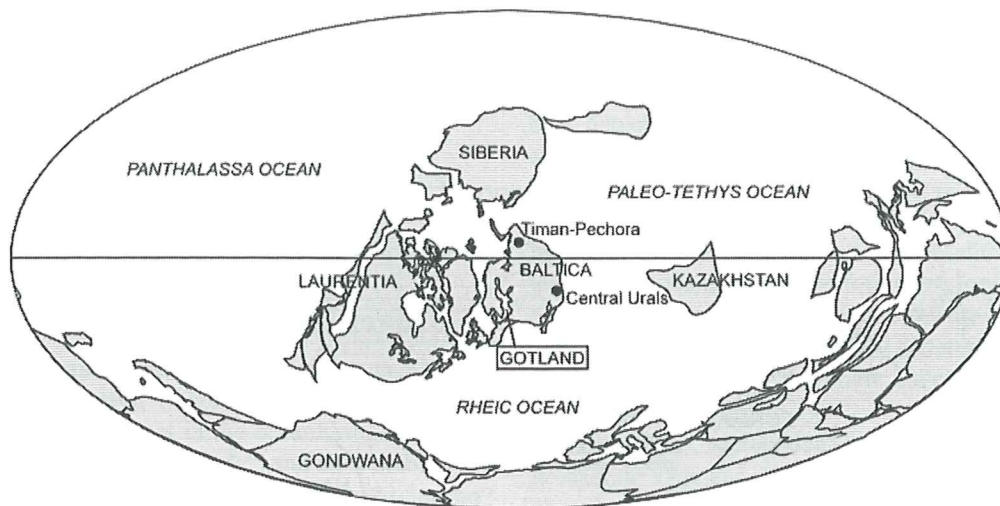


Fig. 5. The positions of the continents during the Silurian. Modified from Scotese & McKerrow (1990) and Scotese's PALEOMAP project, see <http://www.scotese.com>.

and sandstone (Fig. 7). Simplified, the north-western, central and south-eastern parts of the island constitute of limestone, whereas the areas in between are made up by marlstone. Sandstone is found mainly in the southern part of the island. In addition to these main large-scale divisions, Hede (1921, 1925, 1960) recognised 13 stratigraphical units, distinguished on the basis of faunal and lithological characteristics (e.g. Hede 1925, p. 9). The stratigraphy has subsequently been refined and revised (see e.g. Calner *et al.* 2004, pp. 118-122), however the main framework of Hede is still largely applicable. The units currently known and used are named as follows, from the oldest to the youngest: Lower Visby Formation, Upper Visby Formation, Högklint Formation, Tofta Formation, Slite Group, Fröjel Formation, Halla Formation, Klinteberg Formation, Hemse Group, Eke Formation, Burgsvik Formation, Hamra Formation, and Sundre Formation (Fig. 7). The oldest strata are found in the north-west part of the island and the youngest in the southeast. The thickness of the Gotland succession is 500-700 m, depending on where the measurements are done. There are just a few minor tectonic disturbances and no major diagenetic alterations (e.g., Laufeld 1974a; Calner *et al.* 2004).

The units dealt with herein are the the När Formation of the Hemse Group, the Eke, Burgsvik, and Hamra formations (Figs. 7 and 8). The following descriptions of lithologies are from Jeppsson (in press) unless stated otherwise.

#### The Hemse Group

The Hemse Group includes three distinct units; a lower marl unit that is termed the Hemse Marl, North-eastern Part, a limestone unit, and an upper marl unit, referred to as the När Formation (= the Hemse Marl, South-eastern Part in older literature). The main part of the När Formation consists of marls and argillaceous limestones. The

upper part of the När Formation is called the Botvide Member, the youngest unit of the Hemse Group. The Botvide Member (in older literature known as "the uppermost part" or "Top Part" of the Hemse Marl) corresponds to the Upper *Polygnathoides siluricus* conodont Subzone.

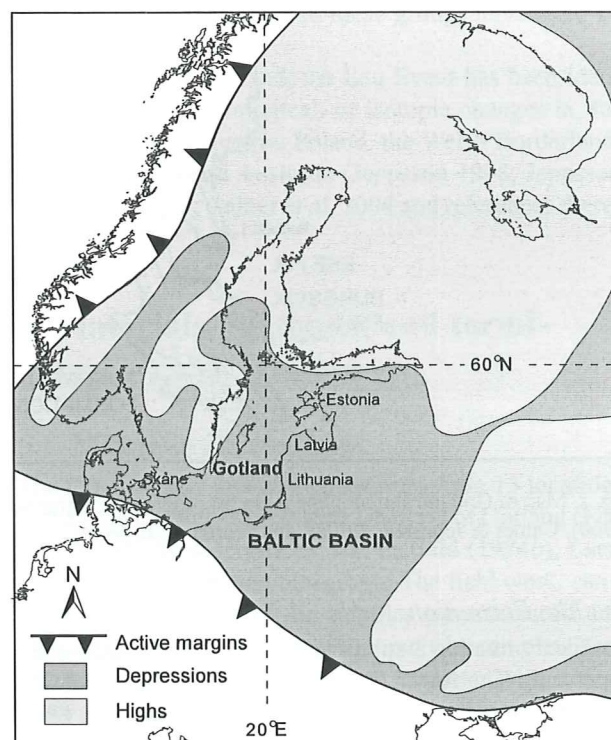


Fig. 6. Silurian palaeogeography of Baltica, showing the Baltic basin and the location of Gotland. Land areas are marked as highs, and seas as depressions. The active margins in the west and south mark the collisions with Laurentia and Avalonia, respectively. Modified from Baarli *et al.* (2003).



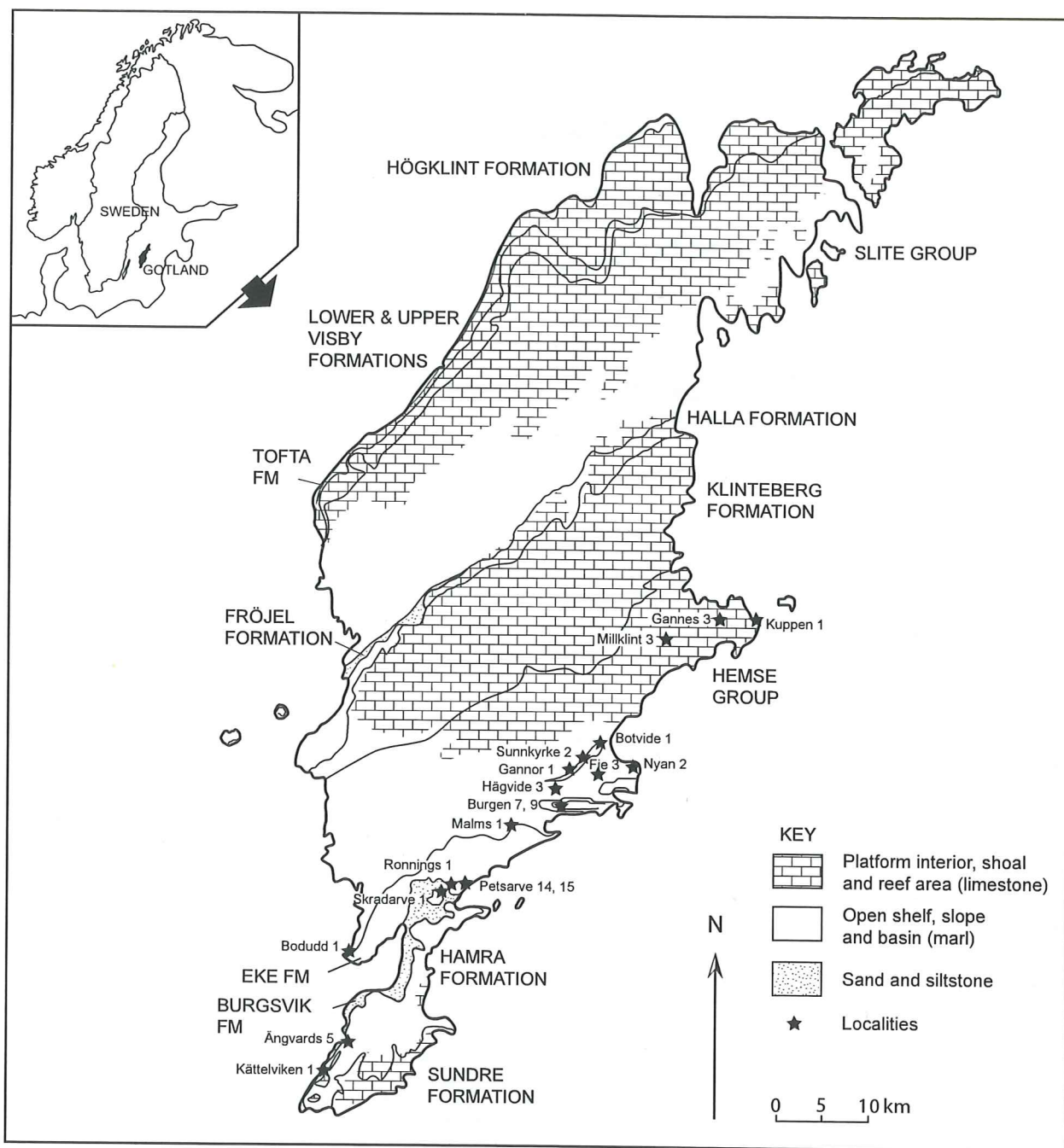


Fig. 7. Map of Gotland showing the main lithologies, stratigraphical units, and localities mentioned in the text. Modified from Hede (1960), Calner & Jeppsson (2003), and Jeppsson (in press).

### The Eke Formation

The Eke Formation is subdivided into a lower, middle and upper unit. The lower Eke is characterised by oncoidal crinoidal limestone and marl. The middle and upper Eke are also oncolitic and include argillaceous limestones and marls. The boundary between the Hemse Group and the Eke Formation is marked by a discontinuity surface (e.g. Spjeldnaes 1950; Cherns 1983). The lower, middle and upper Eke correspond to the Lower, Middle and Upper Icriodontid conodont Subzones, respectively.

### The Burgsvik Formation

The Burgsvik Formation comprises a lower shale unit, a middle siltstone unit, an upper sandstone unit called the Burgsvik Sandstone, and an overlying oolite unit called the Burgsvik Oolite. An erosive boundary is found between the Burgsvik Sandstone and the Burgsvik Oolite (Calner *et al.* 2004). The corresponding conodont zone is the lower part of the *Ozarkodina snajdri* Zone.

### *The Hamra Formation*

The Hamra Formation, also belonging in the *O. snajdri* conodont Zone, consists of oncolitic strata, marls, and limestones.

## 4. The oceanic model and the Lau Event

### 4.1. The oceanic model of Jeppsson (1990)

A model for oceanic cycles that predicts events has been developed by Jeppsson (1990, 1998). The model describes two different states in the oceanic regime; a stable state that is called an "episode", and an unstable state that is called an "event". An episode is termed "primo" if the conditions resemble the modern oceanic circulation pattern with upwelling and a stable primary planktic production, and "secundo" if the circumstances are characterised by reduced upwelling and a low planktic production. The events are the brief intervals that can develop between the two episodes, due to the changes in the oceanic regime. The effects of such intervals can be seen in the stratigraphic column as rapid sedimentological changes, oxygen and/or carbon isotope excursions, and turnovers and extinctions among various fossil groups. The oceanic model of Jeppsson (1990) has been of great help for finding minor Silurian events.

Eight events have hitherto been detected in the Silurian succession of Gotland (e.g. Jeppsson 1993, 1998, 2005a; Calner *et al.* 2004); they are the Ireviken, Ansarve, Boge, Valleviken, Mulde, Linde, Lau, and Klev events. The most severe ones are the Ireviken, Mulde, and Lau events, which now have been detected globally.

### 4.2. The Lau Event

The Lau Event was a primo-secundo event since it was preceded by the Havdhem Primo Episode and succeeded by the Hoburgen Secundo Episode. It is recorded from the base of the Botvide Member to the top of the Eke Formation on Gotland (Fig. 8). The event began just before the extinction of the conodont *Polygnathoides siluricus*, and its end coincided with the top of the Icriodontid conodont Zone (Jeppsson in press). The event comprises approximately 15 m of strata on Gotland. A rough but qualified guess is that this corresponds to 200,000-300,000 years (L. Jeppsson pers. comm. 2005). The event is associated with rapid changes in lithology (from marls and argillaceous limestones in the Botvide Member to oncolitic and crinoidal limestones and marls in the Eke Formation), which indicate a rapid relative regression, from below storm wave base in the upper Hemse Group to shallow water in the Eke Formation (Calner & Eriksson in press). Moreover, the event is associated with extinctions and faunal turnovers, and with one of the largest stable carbon isotope excursions recorded in the Phanerozoic (e.g.

Samtleben *et al.* 2000; Calner *et al.* 2004 and references therein).

Faunal changes in different taxonomical groups have been detected through the event interval on Gotland. For example, approximately 50 % of the conodont taxa disappeared in the Upper *P. siluricus* Subzone during stepwise extinctions (Jeppsson in press). A fauna solely comprising small specimens, called a "Lilliput fauna" is found in the topmost Hemse, and the following Icriodontid Zone of the Eke Formation is characterised by low diversity. The post-event fauna is markedly different from the pre-event fauna, including both new lineages and surviving taxa (Jeppsson in press).

Among the scolecodont-bearing polychaetes, nine taxonomic lineages identified before the event disappeared completely (Eriksson *et al.* 2004). In addition, six lineages disappeared during the event, but reappeared afterwards, showing Lazarus patterns. By contrast to the disappearing lineages, three new ones appeared during the event. Hence there was a prominent change in the faunal composition, approximately 50 % of the polychaete species disappeared, of which 30 % seem to have gone extinct (Eriksson *et al.* 2004).

Other taxa affected include graptolites, chitinozoans, brachiopods, ostracodes, tentaculitids, trilobites, acritarchs, and corals (Jeppsson 1998; Jeppsson & Aldridge 2000; Calner *et al.* 2004 and references therein). However, the precise response of these groups remains to be analysed.

In addition to Gotland, the Lau Event has been identified by faunal, lithological, or isotopic changes in, for example, Latvia, Austria, Poland, the Welsh Borderland, North America, and Australia (Jeppsson 1998; Jeppsson & Aldridge 2000; Calner *et al.* 2004 and references therein).

## 5. Materials, methods, and terminology

### 5.1. Materials and methods

The present study includes 26 samples from 13 localities in the Late Ludlow (Ludfordian) interval of Gotland (Fig. 7). For locality descriptions, see Laufeld (1974b), Larsson (1979) and the next paragraph. The field work, sampling and processing of the samples were financed and organised by Lennart Jeppsson, Lund (the samples were primarily collected for conodont studies), who generously put the phosphatic residues at my disposal for this project. In addition, one sample was collected by Claes Bergman, Kristianstad. The sample sizes are, on average, 30 kg. The method used for extracting phosphatic microfossils from carbonates by dissolving the rocks in acetic acid, is the pH-measured, buffered technique of Jeppsson *et al.* (1999), see also Jeppsson (2005b) for other details



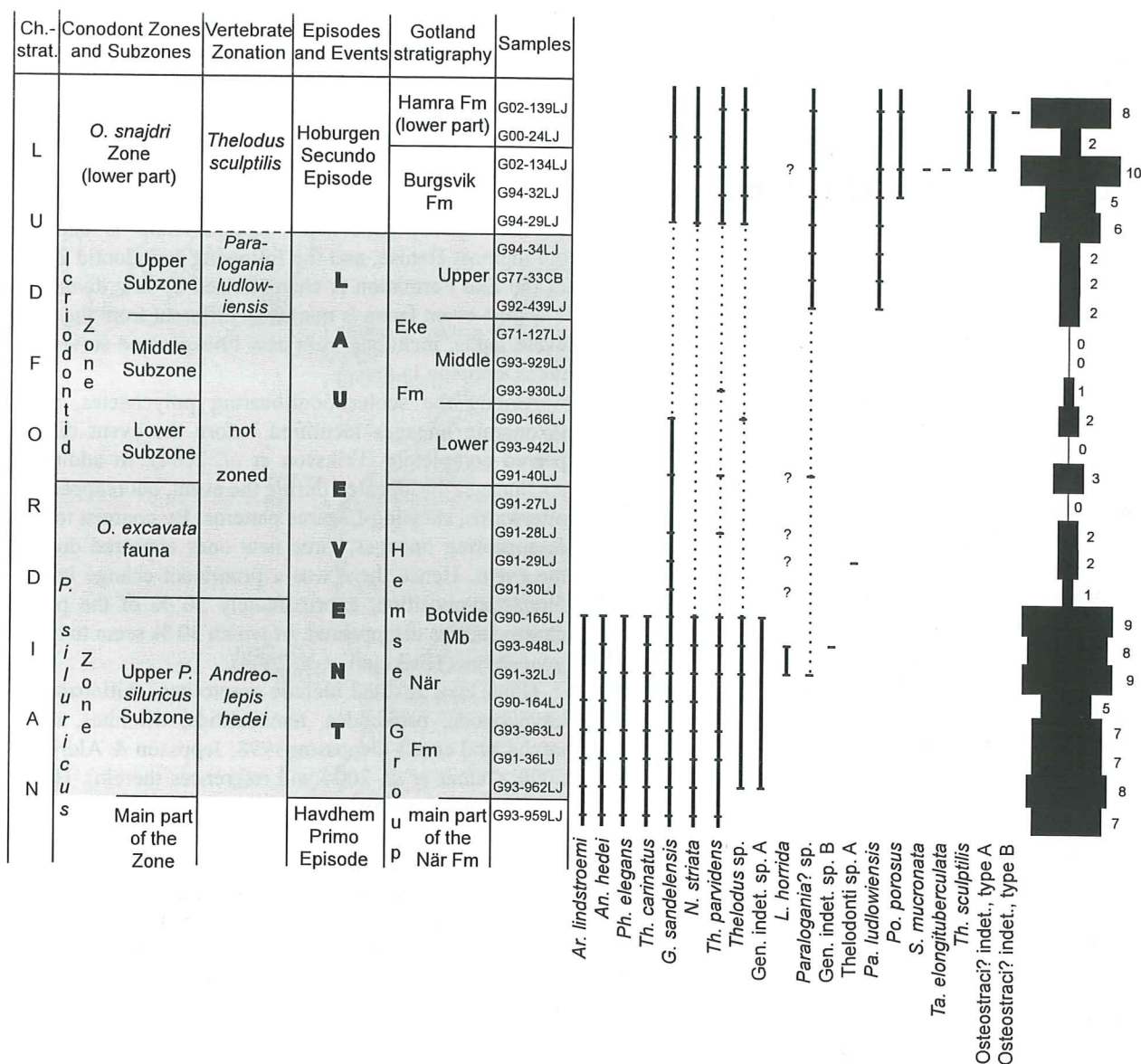


Fig. 8. The distribution of vertebrates during the Lau Event of Gotland, the chronostratigraphy, conodont zonation, suggested vertebrate zonation herein (cf. the standard vertebrate zonation in Fig. 1; the lower boundaries of the zones are defined by the first appearance of the species, dashed lines indicate that the species may range into the succeeding zone), episodes and events, Gotland stratigraphy, and investigated samples (partly modified from Jeppsson in press). The presence of a taxon in a sample is marked by a horizontal dash on the range-line. Uncertain identifications are represented by a question mark. A vertical range-line that continues upwards/downwards means that the taxon is recorded in succeeding/preceding strata, where a dotted range-line indicates Lazarus patterns. The right-hand diagram shows changes in diversity through the studied interval where only the presence of taxa in the samples is counted, thus excluding uncertain identifications. Observe that the vertical scale is not equal to thickness or time units, only to the number of studied samples.

about the extraction work and references. The residues further underwent magnetic separation and density separation, whereafter the phosphatic residue was split into different size fractions by sieving. The sample residues used in this investigation include all fractions larger than 0.063 mm.

New locality: ÄNGVARDS 5, 631977 164570, 2.2 km WNW Vamlingbo church. Top. map 56A Hoburgen (5I Hoburgen SO & 5J Hemse Sv). Geol. map A 152 Burgsvik.

Exposure in the ford on the eastern side of the creek, at the intersection between the north-going road along the beach. Hamra Fm.

The purpose of this study is to document the vertebrate fauna before, during and after the Lau Event and it was my ambition to study samples at even intervals. During the course of time, however, samples have been added where needed (e.g., at critical intervals or in search for rare taxa). Since Fredholm (1988a, b) studied the ver-

tebrate fauna of the pre-event Hemse Group in detail, her results from that interval were used.

The vertebrate scales were picked from the residues, either by Doris Fredholm, by employees under the surveillance of Lennart Jeppsson, or by myself. In those cases where the scales were picked by someone other than me, I have checked the remaining residues and, if needed, done some complementary picking in order to get a representative distribution of vertebrate scales. Approximately 25-100 % of the residues were picked for scales, which means that the total number of scales in most samples are unknown. The numbers of picked scales, however, give a fairly good understanding of the abundance of the different taxa recorded in the samples. The number of picked scales from each sample varies from a few specimens (in poorly yielding samples) up to c. 500. After the scales were picked, they were sorted into micropalaeontological slides and studied in a light microscope. Identification was based on morphological criteria, where the appearance of the crown, neck, base, and pulp cavity are important taxonomical characters (see the following section). The literature used for identification was mainly that of Denison (1979), Märss (1986), Fredholm (1988a), Karatajūtė-Talimaa (1997), Märss & Ritchie (1998), Blom (1999), Blom *et al.* (2002), Karatajūtė-Talimaa & Märss (2002), Vergoossen (2002), and Märss & Miller (2004). Selected representative scales were mounted on stubs, coated in gold, and photographed in a scanning electron microscope (SEM). See Fig. 10 for further information about the samples and species found.

## 5.2. Scale morphology and terminology

On average, Silurian vertebrate scales are 0.5-1.0 mm in length. Their morphology is variable and include, e.g., rhomboidal, circular, elongated, and triangular shapes. Most scales share characters such as a crown, a neck and a base (e.g. Long 1995). The crown is the upper part of the scale (Fig. 9). It can be smooth or ornamented in many different ways. The intermediate part of a scale is called the neck. It can be very distinct and outlined, as in many *Theلودus* scales, or, simply absent, as in the acanthodian *Nostolepis* scales. The base is the lower part of the scale. In the base there is a hole – the pulp cavity, which often is visible. The pulp cavity is where the living cells that sustained the scale were housed. Narrow channels, called dentine tubules, pass from the pulp cavity to the scale surface (e.g. Benton 2000).

Vertebrate scales consist of three different hard tissues; bone, dentine, and enamel (Janvier 1996). Even though the scale composition varies between the different vertebrate groups, the main component is often dentine. Dentine is a hard tissue, closely similar to the material from which bone is made up of, and constitutes of apatite (calcium phosphate). Bone, dentine, and enamel are tissues that also are present in vertebrates living today (Benton 2000).

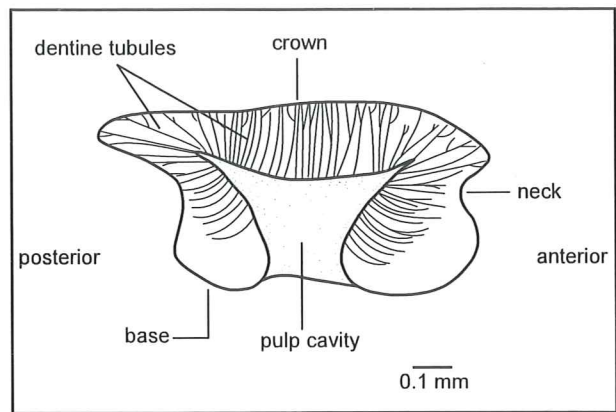


Fig. 9. Line drawing of thin section of a thelodont scale, *Theلودus parvidens*, showing general morphology and terminology. Modified from Gross (1967) and Moy-Thomas & Miles (1971).

The “front” part of the scale, which was directed towards the head of the animal, is called the anterior end, whereas the “rear” part, often seen as where the crown exceeds the base, is called the posterior end (Fig. 9).

The function of the scales is to support and protect the vertebrate body and carry sensory organs such as eyes, nostrils, and the lateral line system with which the vertebrate can detect chemical changes, electric fields, and changes in water direction (Long 1995).

## 6. Results

The samples investigated yielded more than 2,500 vertebrates scales, deriving from six vertebrate groups (Fig. 10, see also Fig. 8), namely acanthodians, actinopterygians, anaspids, heterostracans, osteostracans, and thelodonts.

### Acanthodii

- Gomphonchus sandelensis*
- Nostolepis striata*
- Poracanthodes porosus*
- Acanthodian tesserae plates
- Acanthodian dental elements
- Unidentifiable acanthodian scales, too worn down

### Actinopterygii

- Andreolepis hedei*

### Anaspida

- Septentrionia mucronata*
- Tahulalepis elongituberculata*

### Heterostraci

- Archegonaspis lindstroemi*

### Osteostraci

- Osteostraci? indet., type A
- Osteostraci? indet., type B

### Thelodonti

- Lanarkia horrida*



Gotland stratigraphy		Localities	Samples	Level (m)	Sample weight (kg)	Number of picked scales/sample	<i>Ar. lindstroemi</i>	<i>An. hedei</i>	<i>Ph. elegans</i>	<i>Th. carinatus</i>	<i>G. sandelensis</i>	<i>N. striata</i>	
HAMRA FM		Skradarve 1	G02-139LJ	ditch outcrop	28.40	209							
		Ängvards 5	G00-24LJ	surface outcrop	42.57	25					8	17	
BURGSVIK FM		Kätteleviken 1	G02-134LJ	coastal cliff section	96.00	151						14	
		Burgen 9	G94-32LJ	c. +2.75	58.30	c. 260							
		Burgen 7	G94-29LJ	-0.50 – -0.40	76.30	26					7	1	
E K K  F M	U	Ronnings 1	G94-34LJ	topmost bed	47.90	28							
		Petsarve 15	G77-33CB	ditch outcrop	?	44							
		Petsarve 14	G92-439LJ	ditch outcrop	50.20	168							
	M	Sunnkyrke 2	G71-127LJ	ditch outcrop	0.50	-							
		Bodudd 1	G93-929LJ	+1.16 – +1.20	57.20	-							
		Bodudd 1	G93-930LJ	+0.65 – +0.70	26.40	2							
	L	Botvide 1	G90-166LJ	c. +7.75	28.70	3						1	
		Malms 1	G93-942LJ	+0.10 – +0.13	29.30	-							
		Botvide 1	G91-40LJ	+0.95 – +1.10	19.10	13						5	
H E M S E  G R O U P	N Ä R  F M	B o t v i d e	Nyan 2	G91-27LJ	-0.09 – -0.06	10.20	-						
			Nyan 2	G91-28LJ	-0.10 – -0.09	6.70	7						5
			Nyan 2	G91-29LJ	-0.14 – -0.11	8.63	4						1
			Nyan 2	G91-30LJ	-0.21 – -0.16	20.50	2						1
			Botvide 1	G90-165LJ	-0.15 – -0.10	21.90	138	1	13	10	1	77	27
			Nyan 2	G93-948LJ	-0.29 – -0.24	39.30	190		14		33	54	
		M b  Main part	Nyan 2	G91-32LJ	-0.34 – -0.30	30.70	c. 500		32	8	20	170	52
			Botvide 1	G90-164LJ	-0.51 – -0.45	10.61	49	1	12		5	24	6
			Botvide 1	G93-963LJ	-1.26 – -1.18	25.40	79	3	14	6	3	30	15
			Nyan 2	G91-36LJ	-1.47 – -1.43	27.60	130	5	5	6	8	91	6
			Botvide 1	G93-962LJ	-1.70 – -1.63	32.70	91	3	26	5	8	20	14
			Botvide 1	G93-959LJ	-2.25 – -2.23	37.80	c. 410	13	18	1	6	350	20

Fig. 10. Distribution of vertebrate taxa in the studied samples, including Gotland stratigraphy, localities, sample level (where possible, given in metres from a reference level; Jeppsson in press, pers. comm. 2005), sample size, and number of picked scales per sample. Uncertain identifications are marked by a question mark. A c. in front of the number of picked scales indicates that the number is estimated, as sorting is incomplete. The samples are in stratigraphically descending order.

*Paralogania ludlowiensis*

*Paralogania?* sp.

*Phlebolepis elegans*

*Thelodus carinatus*

*Thelodus parvidens*

*Thelodus sculptilis*

*Thelodus* sp.

Thelodonti sp. A

Unidentifiable *Thelodus* scales, too worn down

Gen. indet.

Gen. indet. sp. A

Gen. indet. sp. B

### 6.1. The pre-event fauna

Only one sample has been studied by me from the interval prior to the onset of the Lau Event, from the strata of the När Fm, Hemse Group (sample G93-959LJ from Botvide 1, see Fig. 10). This sample is rich in scales, more

<i>Th. parvidens</i>	<i>Thelodus</i> sp.	Gen. indet. sp. A	<i>L. horrida</i>	<i>Paralogania?</i> sp.	Gen. indet. sp. B	<i>Thelodonti</i> sp. A	<i>Pa. ludlowiensis</i>	<i>Po. porosus</i>	<i>S. mucronata</i>	<i>Ta. elongituberculata</i>	<i>Th. sculptilis</i>	Osteostraci? indet., type A	Osteostraci? indet., type B	Acanthodian tesseræ plates	Unidentifiable <i>Thelodus</i> scales, too worn	Unidentifiable acanthodian scales, too worn	Acanthodian dental elements
1	13			120			30	16			1	17	10	1			
27	10		3?	24			2	32	13	2	2	2		2		18	
120	20			110			10	2									
4	1			9			4										
				22			6										
				16			28										
				100			43							2		23	
2																	
	2																
1			1?	1												3	
1			1?														
			1?			2											
			1?														
1	1	3												4			
43	9		24		11									2			
24	4		200	12										16			
														1			
2														6			
2														7			
	3	4												3			5
5														3			

Fig. 10. cont.

than 400, and yielded a diverse fauna that includes seven identified species: the heterostracan *Archegonaspis lindstroemi* (Figs. 11C-E), the actinopterygian *Andreolepis hedei* (Figs. 11A-B), the two acanthodians *Gomphonchus sandelensis* (Figs. 14A-F) and *Nostolepis striata* (Figs. 14G-I), and the three thelodonts *Phlebolepis elegans* (Figs. 12G-I), *Thelodus carinatus* (Figs. 12A-C), and *Thelodus parvidens* (Figs. D-F). In this sample acanthodian tesseræ plates were also recorded (Fig. 14L). These are star-like scales that covered parts of the head region in certain acanthodians (Denison 1979).

Although half the number of species in this fauna is represented by thelodonts, it is the acanthodian scales that greatly outnumber other vertebrate scales; *G. sandelensis* is the most abundant acanthodian represented by 350 scales, and together with *N. striata* and acanthodian tesseræ plates, they represent more than 90 % of the total scale number.

The vertebrate distribution in the main part of the När Formation investigated by Fredholm (1988b, fig. 2; selected sample data from her study is shown in Table 1 herein) is similar to that of the present study. Only one

additional taxon was recorded, namely the thelodont *Paralogania martinssoni*. This species is rare in her samples, represented only by a few specimens, which may explain the absence in my sample. As seen in Fredholm's samples (Table 1), the acanthodian scales dominate the scale number here as well, by approximately 90 %.

In total, eight species have been found in the pre-event interval of the När Formation, whereof half the number of species in the fauna is represented by thelodonts, and 90 % of the scales derive from acanthodians.

## 6.2. The early event faunas

The event faunas of the Botvide Member, topmost Hemse Group, were analysed in eleven samples (Fig. 10). The samples are fairly rich in scales, between 49 and 500 scales per sample, although these numbers abruptly decrease in the *Ozarkodina excavata* conodont fauna of the Upper *P. siluricus* conodont Subzone, slightly below the top of the Botvide Member (see Figs. 8 and 10). The four samples from this interval (from Nyan 2) yielded only 13 scales in total. The acanthodians still are the dominating group in the Botvide Member, based on scale counts.

Seven of the eight species recorded in the pre-event strata of the main part of the När Formation range into the event-strata of the Botvide Member (Fig. 8; *Ar. lindstroemi*, *An. hedei*, *G. sandelensis*, *N. striata*, *Ph. elegans*, *Th. carinatus*, and *Th. parvidens*) whereas *Pa. martinssoni* disappear during the very beginning of the event at the base of the Botvide Member (Fredholm 1988b).

The thelodont *Thelodus* sp. (Figs. 13A-B), and one vertebrate species of unknown affinity assigned to Gen. indet. sp. A (Fig. 16E) appear near the base of the Botvide Member. The thelodonts *Lanarkia horrida* (Figs. 13D-F), *Paralogania?* sp. (Figs. 13G-K), and *Thelodonti* sp. A (Fig. 13C), and yet one more species of unknown affinity referred to as Gen. indet. sp. B (Fig. 16F) appear slightly later in these strata. The latter three of these taxa

are recorded only in one sample each. In addition to the identified taxa mentioned above, acanthodian tesseræ plates and acanthodian dental elements (Figs. 15E-F) are also recorded in the Botvide Member, and altogether this unit holds thirteen species. However, of these, *Ar. lindstroemi*, *An. hedei*, *Ph. elegans*, *Th. carinatus*, *N. striata*, *Thelodus* sp., and Gen. indet. sp. A disappear at the lower boundary of the *O. excavata* conodont fauna in the Upper *P. siluricus* conodont Subzone, slightly below the top of the Botvide Member (Fig. 8).

## 6.3. The late event faunas

The nine samples investigated from the Eke Formation yielded poorly in vertebrates scales (Fig. 10). Three of the lower and middle Eke samples were barren, whereas three contained very few specimens ( $\leq 13$  scales per sample). In the upper Eke the scale yield increases and sample G92-439LJ from Petsarve 14 contains more than 160 scales.

The fauna of the lower and middle Eke includes *G. sandelensis*, *Th. parvidens*, *Thelodus* sp. (the latter species makes a brief reappearance here), *Paralogania?* sp., and a questionable find of *L. horrida* (identification is rather uncertain; only one scale is recorded, compared to the 200 scales recorded in the preceding unit, see Fig. 10). *G. sandelensis*, *Th. parvidens*, and *Thelodus* sp. disappear at the boundary between the lower and middle Eke (Fig. 8). In the upper Eke a new species appear, the thelodont *Paralogania ludlowiensis* (Figs. 13L-O). Other vertebrate remains recorded in the Eke Formation are acanthodian tesseræ plates and *Thelodus* and acanthodian scales that are too worn for proper identification. The fauna of the Eke Formation holds five species (not counting *L. horrida*), four of which are thelodonts and one acanthodian.

Although acanthodians occur in the event fauna of the Eke Formation, represented by *G. sandelensis* and uni-

Table 1. Selected samples showing the vertebrate distribution in the pre-event strata of the main part of the När formation, Hemse Group (data from Fredholm 1988b, Fig. 2). Samples are not in any particular order. *Thelodus* spp. include scales of both *Thelodus carinatus* and *Th. parvidens*. Considering the low bulk weight, the samples are quite rich in vertebrate scales. Note also the dominance of acanthodian scales.

Localities	Samples	Sample weight (kg)	Number of scales/sample	<i>G. sandelensis</i>	<i>N. striata</i>	<i>An. hedei</i>	<i>Ar. lindstroemi</i>	<i>Pa. martinssoni</i>	<i>Ph. elegans</i>	<i>Thelodus</i> spp.
Botvide 1	G69-18LJ	0.49	101	13	79	3	3			3
Fie 3	G71-128LJ	2.50	562	108	396	22	3		8	25
Gannor 1	G82-311DF	1.45	191	119	42	16	1	3	1	9
Kuppen 1	G81-45LJ	1.40	1250	>770	>410	33			2	36
Kuppen 1	G81-44LJ	0.65	347	140	156	18			1	12
Millklint 3	G69-31LJ	0.50	46	39	5	2				
Millklint 3	G69-36LJ	0.50	242	163	46					17



identifiable acanthodian scales, they no longer dominate the scale numbers. The thelodonts *Paralogania?* sp. and *Pa. ludlowiensis* are the dominating taxa in the upper part of the Eke, representing up to 100 % of the scale numbers here.

#### 6.4. The post-event faunas

The transition from the event faunas of the Eke Formation to the post-event faunas of the Burgsvik and Hamra formations is quite striking, showing a conspicuous change from a low diversity and low abundance fauna to a high diversity and high abundance fauna. *G. sandelensis*, *N. striata*, *Th. parvidens*, and *Thelodus* sp. reappear after the event, showing Lazarus patterns (Fig. 8), *Paralogania?* sp. and *Pa. ludlowiensis* continue to exist, and as many as five new taxa appear in the Burgsvik Formation: the acanthodian *Poracanthodes porosus* (Figs. 14J-K), the anaspids *Septentrionia mucronata* (Figs. 15A-B) and *Tahulalepis elongituberculata* (Figs. 15C-D), the thelodont *Thelodus sculptilis* (Figs. 13P-R), and the osteostracan *Osteostraci?* indet., type A (Figs. 16A-B). Additionally, one species appear in the Hamra Formation, the osteostracan *Osteostraci?* indet., type B (Figs. 16C-D).

Other vertebrate remains found in the five samples from the Burgsvik and Hamra formations are acanthodian tesserae plates and unidentifiable acanthodian scales. In total, the post-event faunas include twelve species, where the acanthodians are represented by three species, the thelodonts by five, and the anaspids and osteostracans by two species, respectively. The thelodonts clearly are the dominating vertebrate group, both in terms of number of species and scale numbers.

Fredholm (1989) concluded that *Po. porosus* and *Th. sculptilis* appeared already in the lower Eke Formation, but I did not record any scales of those species in that interval. Fredholm (1989) studied ten samples from the Eke Formation. Nine of these show the same characteristics in faunal composition and abundance as those from the Eke Formation of the present study, i.e., a low abundance and low diversity. The tenth sample (G82-321DF from Hågvide 3, referred to the lower Eke Formation; see Fredholm 1989, p. 12), and the only one in which *Po. porosus* and *Th. sculptilis* were recorded, shows quite the opposite characteristics. Here the two species co-occurred with *G. sandelensis*, *Paralogania?* sp., *Pa. ludlowiensis*, *N. striata*, and *Th. parvidens*. This is a species composition that, in this study, characterises the post-event fauna of the Burgsvik Formation, not the lower Eke Formation. When looking at the conodonts in the sample, they as well exclude a lower Eke derivation (L. Jeppsson pers. comm. 2005). It seems most likely that a sampling or labeling mistake have occurred, since all evidence indicate that sample G82-321DF derives from the very basal Burgsvik Formation rather than from the basal Eke Formation.

#### 6.5. Calculations for a "Lilliput fauna"

The percentages of small and large scales of the acanthodian *G. sandelensis* have been calculated in order to determine a possible size reduction (Table 2). Samples from Fredholm (1988b) have been incorporated with those investigated herein. See discussion below for comments.

### 7. Discussion

The results show that there were pronounced faunal turnovers of the vertebrates during the Lau Event. The acanthodians dominate the scale numbers in the pre-event faunas, whereas the thelodonts dominate the post-event faunas. The event faunas are characterised by low diversity and low abundance compared to those of both the pre- and post-event faunas. Five of the eight pre-event species disappeared during the early phase of the event, that is, 63 % of the taxa that existed before the event did not prevail. By contrast, the post-Lau Event was marked by speciation among the vertebrates, where seven of the twelve species (58 %) in the post-event faunas were newcomers (one species appeared in the strata of the upper Eke Formation, five in the Burgsvik Formation, and additionally one in the Hamra Formation). Some species disappeared during the event but reappeared afterwards, indicating Lazarus patterns.

Many questions arise from the results of this investigation; for example, are the low numbers recorded in the event-faunas true, or are they merely a consequence of bad luck when selecting samples for this study? Can a "Lilliput fauna" be distinguished? Is a similar trend seen in other parts of the world where the Lau Event has been identified?

#### 7.1. Scale abundance during the event

The number of vertebrate scales per sample in the lower and middle Eke formations is much lower than in the preceding and succeeding strata. To find out if these low figures are representative for that interval, one may consider the sample sizes – if these were very small it could have explained the low scale numbers in the residues from these units. One may also look at how other taxonomic groups are represented in the same samples – if they too show a low frequency, it would support the idea that the low number of vertebrate scales is real, and thus is an "event-effect". Regarding the sample sizes, I believe that they are adequately large, being approximately 30 kg each on average (Fig. 10). Although being this large, three samples were barren of vertebrate scales and three additional ones yielded 13 or less scales per sample. By comparison, the samples from the Botvide Member and the main part of the När Formation, of approximately the same weight, yielded as many as up to 500 scales per sample (Fig. 10). It can thus be concluded that the



Table 2. Size differences in *Gomphonchus sandelensis*. Scales of *G. sandelensis* have been measured and divided into two size groups, the numbers shown are percentage of the total number of *G. sandelensis*-scales in investigated samples. Samples of Fredholm (1988b) are included to show the percentage of sizes in the pre-event strata of the När Formation, these are not in any particular order. The other samples are in stratigraphically descending order. Sample levels are included where possible (Fredholm 1988b; Jeppsson in press), number of scales of *G. sandelensis* for each sample is also included.

Localities	Samples	Level (m)	Number of scales of <i>G. sandelensis</i>	% <5 mm	% ≥5mm
Ängvards 5	G00-24LJ	-	8	67	33
Burgen 7	G94-29LJ	-0.50 – -0.40	7	43	57
Botvide 1	G90-166LJ	c. +7.75	1	100	0
Botvide 1	G91-40LJ	+0.95 – +1.10	5	71	29
Nyan 2	G91-28LJ	-0.10 – -0.09	5	100	0
Nyan 2	G91-29LJ	-0.14 – -0.11	1	100	0
Nyan 2	G91-30LJ	-0.21 – -0.16	1	100	0
Botvide 1	G90-165LJ	-0.15 – -0.10	77	84	16
Nyan 2	G93-948LJ	-0.29 – -0.24	54	100	0
Nyan 2	G91-32LJ	-0.34 – -0.30	170	85	15
Botvide 1	G90-164LJ	-0.51 – -0.45	24	46	54
Botvide 1	G93-963LJ	-1.26 – -1.18	30	67	33
Nyan 2	G91-36LJ	-1.47 – -1.43	91	69	31
Botvide 1	G93-962LJ	-1.70 – -1.63	20	20	80
Botvide 1	G93-959LJ	-2.25 – -2.23	350	91	9
*Gannes 3	G84-2LJ	-	>680	79	21
*Kuppen 1	G81-45LJ	±0.0 – +0.11	>770	32	68
*Kuppen 1	G81-44LJ	+0.11 – +0.14	140	29	71
*Millklint 3	G69-31LJ	c. +2.0	163	100	0
*Millklint 3	G69-36LJ	c. -0.5	39	97	3

\* = Samples from Fredholm (1988b), all from the pre-event strata of the När Formation.

lowered scale yield of the lower and middle Eke formations is not an artificial effect caused by smaller samples. When comparing the frequencies of other taxonomical groups with that of vertebrate scales, conodonts are an excellent candidate since they have been thoroughly studied through the Lau Event interval. Both the abundance and diversity of conodonts are low in these same samples investigated from the lower and middle Eke formations (L. Jeppsson pers. comm. 2005), which suggest that the low abundance of vertebrate scales in this interval is an "event-effect".

When looking at the scale frequencies as a whole, from the När Formation of the Hemse Group to the Hamra Formation, a negative trend in scale frequency through the event is detected. The scale yield in the samples of the pre-event strata (data analysed from Fredholm (1988b), see Table 1 herein) is very high; for example, sample G71-128LJ from Fie 3 yielded 562 scales per 2.5 kg rock, whereas sample G81-45LJ from Kuppen 1 yielded as many as 1250 scales from only 1.4 kg rock (Table 1). These numbers are very high when compared to the yields of the Botvide Member samples investigated herein (of which I have observed and estimated, thus taken into account that not all scales have been picked; Fig.

10) and particularly the lower and middle Eke formation samples (most of which have been completely picked). The sample sizes from both the Botvide Member and the lower and middle Eke formations are considerably larger, 30 kg on average (Fig. 10), and if the scale yields were as high here as in the two samples mentioned above from the pre-event strata (Table 1), they would yield approximately 7,000-26,000 scales per 30 kg rock (calculated on the numbers above). Instead, only about 10-500 scales per 30 kg rock were calculated. The negative trend takes a turn in the upper Eke Formation and particularly in the post-event strata, where the scale yields return to higher numbers, although still lower than in the samples from the pre-event strata. To conclude, it seems evident that there is a pronounced decrease in scale frequency per kg rock through the Lau Event.

## 7.2. Facies differences – preferences among vertebrates

Janvier (1985 and references therein) studied the distribution of vertebrates in various facies and concluded that some vertebrates are found only in certain environments; thelodonts, anaspids, and osteostracans seem to have occurred only in low energy environments such as, for ex-

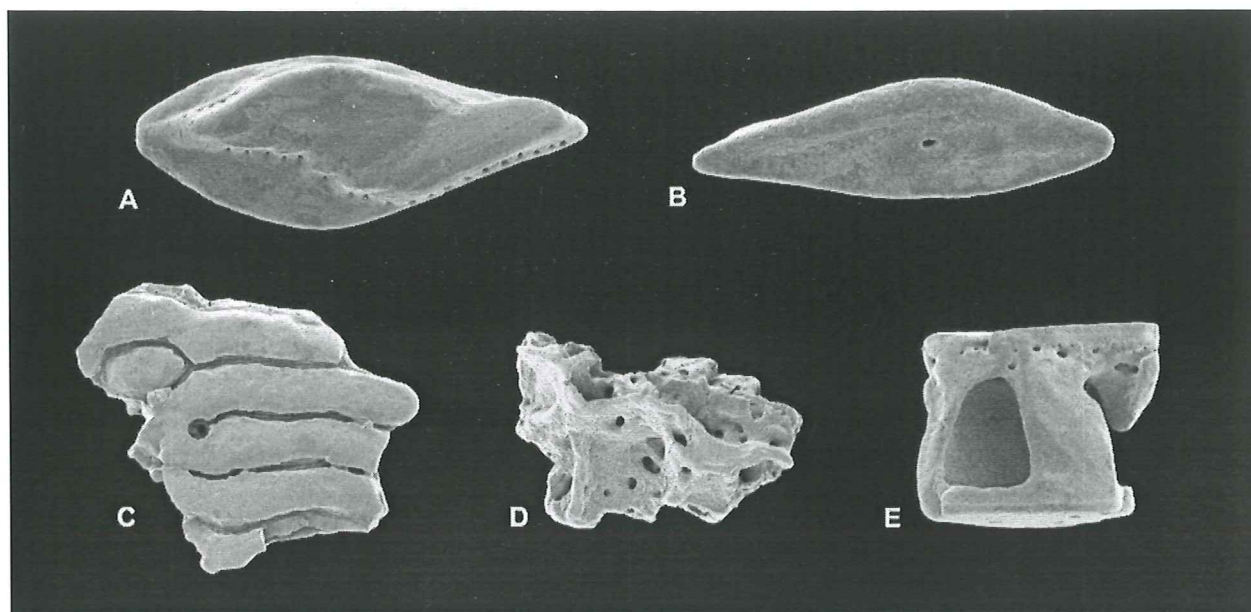


Fig. 11. Actinopterygii (A-B) and Heterostraci (C-E) from the Ludfordian of Gotland. A-B. *Andreolepis hedei*. A. Crown view, x41. B. Base view, x40. A-B from sample G93-959LJ from Botvide 1, main part of the När Fm, Hemse Group. C-E. *Archegonaspis lindstroemi*. C. Crown view, x32. D. Base view, x42. E. Lateral view, x40. C-D from sample G91-56LJ from Nyan 2, Botvide Mb, Hemse Group, E from sample G93-959LJ from Botvide 1, main part of the När Fm, Hemse Group.

ample, lagoons, whereas the heterostracans, acanthodians, and actinopterygians seem to have preferred deeper, more open marine environments. Fredholm (1989, p. 27) suggested that “thelodonts preferred a muddy habitat, or at least more quiet waters”. Märss (1997) came to similar conclusions – in the shallow shelf strata both agnathans and gnathostomes were found, but in the deep shelf sediments gnathostomes, and particularly acanthodians, predominated. Thus such habitat preferences may explain why some samples investigated herein are barren of scales, as the samples are from different localities and of different facies. Moreover, if the Lau Event strata were deposited, more or less, during a regression, this naturally leads to a change in the environments and the disappearance of niches, also explaining the low scale numbers in the event samples. Based on the above, I think that facies preferences are an issue to take into account. The results from this study indicate that acanthodians, heterostracans, and actinopterygians preferred a deeper water environment because they dominate in the pre-event and early phase of the event, while in the more shallow water facies of the Eke Formation, and particularly in the upper Eke, the thelodonts dominate. However, if facies preferences were the only reason for some samples being barren of scales, then all the disappearing species would be expected to return as soon as a suitable facies returns. Hence, the fact that not all species return supports the idea that the barren and low abundance samples in the Lau Event interval of Gotland is an “event-effect”. This also leads me to conclude that even though facies differences are an important issue to consider, they are not the only reason for the barren samples.

### 7.3. Disappearances or extinctions?

Sixty-three percent of the species that occurred in the pre-event fauna disappeared during the early phase of the event (*Ar. lindstroemi*, *An. hedei*, *Ph. elegans*, *Th. carinatus*, and *Pa. martinssoni*). The question is if these taxa went extinct, or if they disappeared, i.e., found refugia somewhere else. This can easily be answered by the fact that they are not reported in any younger strata on Gotland, nor in other places of the world (see discussion in the next section), hence it can be concluded that they became extinct. Other species, on the other hand, disappeared and reappeared in younger strata (*G. sandelensis*, *N. striata*, *Th. parvidens*, *Thelodus* sp., and *Paralogania?* sp.), obviously finding refugia somewhere else. These are called Lazarus taxa.

The next question to consider is if the extinctions are associated with the event, or if they are merely normal background extinctions. The fact that this many vertebrates disappeared more or less simultaneously during such a short time in Gotland strata indicates that this is not a normal background extinction. A similar trend is seen among the conodonts, which disappear stepwise and several of them at the same time, and during the same time span as the vertebrates (e.g. Jeppsson 1998). This also reinforces the theory that the disappearances are more than just normal background extinction. It seems that the disappearances are associated with the event, as concluded also in previous sections, and that a large number of species really did go extinct.



#### 7.4. Extinctions outside Gotland

Another argument that supports the idea that the disappearances are associated with the event and not merely background extinction-related, is that extinctions among vertebrates are recorded in other coeval areas of the Baltic region as well. Märss (1992) discusses and compares the middle to Late Ludlow vertebrate faunas of Estonia, Latvia, Lithuania, British Isles, Central Urals in Russia, Timan-Pechora in Siberia, and Gotland (based on Fredholm 1988b, 1989; Figs.5 and 6) and concluded that a complete faunal turnover took place in these areas. This faunal turnover among the vertebrates was referred to as the “*A. hedei*-event”, and was characterised by an innovation event at the start and an extinction event at the end. It begun already during the middle Ludlow and ended in the Late Ludlow, hence, the Lau Event corresponds to the latter part of the “*A. hedei*-event”. The vertebrate faunas recorded during the “*A. hedei*-event” were conspicuously different from the post-event faunas, just like the Late Ludlow faunas of Gotland. Märss (1992) also concluded that these changes were not simply environment-triggered appearances and disappearances, but rather extinction, innovation, and radiation events in the evolution of vertebrates.

The disappearing and appearing species discussed by Märss (1992) are partly the same as those recorded on Gotland, and their ranges agree well. For example, the thoroughly studied Estonian Uduvere Beds of the Paadla “regional stage” (corresponding to pre-Lau Event strata; Fig. 1) includes *Ph. elegans*, *An. hedei*, *Archegonaspis* sp., *Th. carinatus*, *Th. parvidens*, *Pa. martinsoni*, *N. striata*, *G. sandelensis*, *Thelodus* sp., and *Th. laevis*. Of these ten species, at least the first eight are found in the main part of the När Formation on Gotland. The succeeding Tahula Beds of the Kuressaare “regional stage” (corresponding to post-Lau Event strata; Fig. 1) are represented by *Th. traquairi*, *Th. admirabilis*, *Loganellia cuneata*, *Katoporodus tricavus*, the osteostracan *Zenaspis?* sp., *Th. sculptilis*, *Pa. ludlowiensis*, the anaspid Birkeniida sp. A (= *Ta. elongituberculata*; Blom *et al.* 2002), and *Po. porosus*. At least the latter four species are recorded in the Gotland strata of the Burgsvik and Hamra formations. In Lithuania one additional species, *Th. parvidens*, is recorded in the latter fauna as well, where it co-occurs with *Pa. ludlowiensis* and *Th. sculptilis* in the top part of the Pagegiai Formation, Late Ludlow (Märss 1992), as is the case in this study where these species co-occur in the post-event strata of the Burgsvik and Hamra formations.

The most striking characteristics in common for the Late Ludlow vertebrate faunas in the areas discussed by Märss (1992) is that *Ph. elegans* and *An. hedei* seem to occur only in the older strata, before the onset of the Lau Event, and *Th. sculptilis* only in the younger, post-Lau Event strata. However, two exceptions have been published: scales of *An. hedei* are reported together with the

younger fauna in the Tabuska Beds in the Central Urals (Märss 1992), and in one sample from the Öved Sandstone Formation of Helvetesgraven, Skåne, the southernmost province of Sweden (Vergoossen 1999). The specimens from the Central Urals have later been re-assigned to a new species (Märss 2001). The scales of this new species, *Andreolepis petri*, are superficially similar to those of *An. hedei*, but they are larger – between 1-4.5 mm in length compared to about 1-2 mm in *An. hedei*, and have a greater number of ridges on the crown surface – nine as a maximum compared to four, at the most, in *An. hedei*. It is here suggested that this could be the case also with the few specimens (one complete and a few broken scales) from Skåne, i.e., that they too belong to *An. petri* instead of *An. hedei*. Another possibility is that the presence of *An. hedei* in the latter region could be a result of reworking. Nevertheless, it seems most likely that *An. hedei* occurs exclusively in the older fauna.

Based on the above, it is concluded that two distinct vertebrate faunas occur in the Late Ludlow, and that extinctions among the vertebrates were not only restricted to Gotland.

#### 7.5. The “Lilliput effect”

The “Lilliput effect” was named by Urbaneck (1993) during a study of Silurian graptolites. It is the phenomenon where extinction events are associated with taxa of reduced size, which is a fairly common feature in the Phanerozoic. The size reduction is a response to stress and unfavourable conditions such as, for example, habitat loss, drastical changes in temperature and salinity, and/or oceanic stratification and stagnation. The latter condition often result in insufficient food supply, as nutrient recycling from the deep ocean is limited (Urbaneck 1993; Twitchett 2001).

A size reduction has been noted in some taxa during the Lau Event on Gotland; Jeppsson (in press) stated that the conodonts showed a decrease in size, as was seen in scolecodonts (Eriksson *et al.* 2004) and in some brachiopod taxa (L. Gustavsson pers. comm. 2005). After having examined all vertebrate scales in light microscope, I noted that the only species in which size variations seem to occur are those of the acanthodian *G. sandelensis*. Therefore, they were chosen to test the “Lilliput effect”. The scales of this species range in size between 0.2 mm and 1.0 mm, and seem to display two very distinct size-groups. Both the smaller and the larger scales co-occur in the samples. In order to statistically test if these scales may show evidence of size reduction, they were counted and divided into two groups – small scales (< 0.5 mm in width) and large scales ( $\geq$  0.5 mm in width), whereafter the percentage was calculated (Table 2). The result shows that the percentages through the studied interval are unequal and variable, and no trend can be detected. Instead, the differences in scale size are interpreted as ontoge-



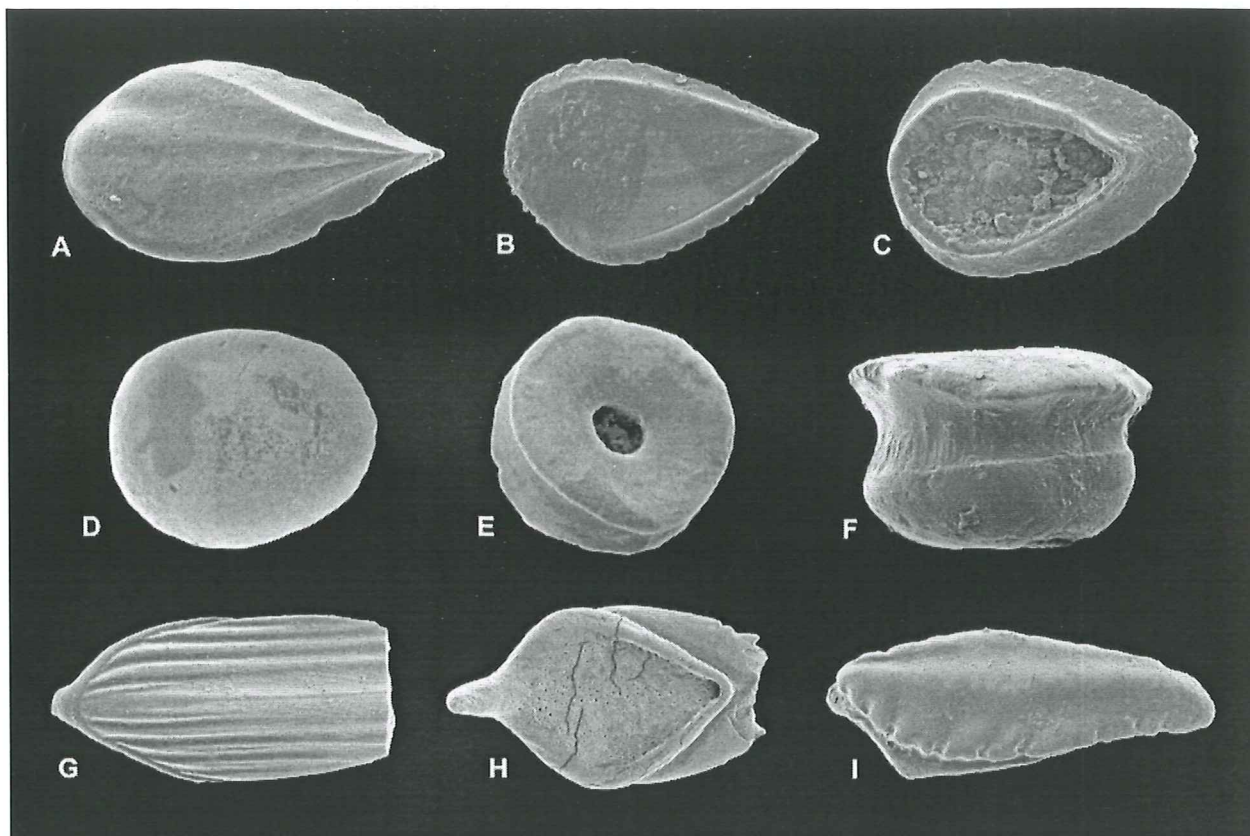


Fig. 12. Thelodonti from the Ludfordian of Gotland. **A-C.** *Thelodus carinatus*. A. Crown view, x69. B. Crown view, x50. C. Base view, x53. A from sample G91-36LJ from Nyan 2, Botvide Mb, Hemse Group, B-C from sample G93-963LJ from Botvide 1, Botvide Mb, Hemse Group. **D-F.** *Th. parvidens*. D. Crown view, x53. E. Base view, x 48. F. Lateral view, x73. D-E from sample G93-959LJ from Botvide 1, main part of the När Fm, Hemse Group, F from sample G94-32LJ from Burgen 9, Burgsvik Fm. **G-I.** *Phlebolepis elegans*. G. Crown view, x 41. H. Base view, x56. I. Crown view, x57. G-H from sample G91-36LJ from Nyan 2, Botvide Mb, Hemse Group, I from sample G93-963LJ from Botvide 1, Botvide Mb, Hemse Group.

netic rather than a "Lilliput effect". Moreover, because the scales of thelodonts differ in morphology depending on their position on the body, this could perhaps also be the case with acanthodians. However, one must take into consideration that not all scales have been picked in the samples analysed by me, and during picking the tendency is often that the larger scales are easier seen and thus picked first. Further analyses, based on larger collections and also on other vertebrate taxa, are needed before the "Lilliput effect" can be discarded.

#### 7.6. The Gotland vertebrate faunal succession

Four different vertebrate faunas can be distinguished in the studied sequence. The oldest is the *G. sandelensis*-fauna that is found in the pre-event and early phase of the event. The acanthodian *G. sandelensis* dominate, but actinopterygians (the index-species *An. hedei*) and heterostracans are also present. Thelodonts are found, but are less frequent than other vertebrates.

The second fauna, the *L. horrida*-fauna, can be distinguished slightly later during the event in the Botvide Member. The dominating species are the thelodont *L. horrida* and the acanthodian *G. sandelensis*. In contrast

to the previous fauna, other thelodont species generally are more abundantly represented here, otherwise it is very alike to the preceding *G. sandelensis*-fauna.

Fredholm (1988b, p. 245) also distinguished two faunas, one *G. sandelensis*-fauna that continued from older strata up into the Botvide Member, and one "*Logania*" *cuneata*?-fauna that appeared slightly below the Hemse-Eke boundary. This latter fauna is here termed the *L. horrida*-fauna. Another fauna, the *N. striata*-fauna was distinguished prior to (or co-eval to?) the *G. sandelensis*-fauna in the När Formation (Fredholm 1988b, p. 244), but this fauna has not been detected in this study.

The third fauna detected in this study is the paraloganiid-fauna that appears during the late phase of the event, in the upper Eke Formation. It consists almost exclusively of the two thelodonts *Paralogania?* sp. and *Pa. ludlowiensis*.

The fourth and youngest fauna appears after the Lau Event and is characterised by new taxonomic groups such as anaspids and osteostracans. Although acanthodians are present in this fauna, the thelodonts predominate. In contrast to the previous paraloganiid-fauna, this one is very diverse.



### 7.7. Silurian vertebrate biozones

In this study three index-species for the Silurian vertebrate biozonation (Fig. 1) have been recorded: *Ph. elegans*, *An. hedei*, and *Th. sculptilis*. From this it is suggested that the Lau Event started within the latter part of the *An. hedei* vertebrate Zone, and that its end coincided with the lower boundary of the *Th. sculptilis* vertebrate Zone (Fig. 8).

The Silurian vertebrate biozonation is based on the East Baltic vertebrate sequence (Fig. 1; Märss *et al.* 1995). I believe that this zonation could be further refined with the help of some species recorded in the Gotland succession. In the East Baltic region the *An. hedei* Zone ranges to the top of the Paadla "regional stage" (Fig. 1), whereas the succeeding *Th. sculptilis* Zone begins at the base of the Kuressaare "regional stage". However, the East Baltic strata are marked by a hiatus in the upper part of the Paadla "regional stage" (Jeppsson *et al.* 1994), that corresponds to the Botvide Member of the Hemse Group, the Eke, Burgsvik, and lower part of the Hamra formations of Gotland. Thus, the current vertebrate zonation is partly applicable in the Gotland strata, but it leaves a gap where no index-species are recorded; *An. hedei* disappeared in the Botvide Member, whereas *Th. sculptilis* appeared late in the Burgsvik Formation (Fig. 8), leaving the strata of the Eke Formation unzoned in terms of vertebrates. Therefore, it would be convenient to have a higher resolution zonation that is applicable for the Gotland strata.

Based on this study, *Pa. ludlowiensis* is a plausible index-species candidate. This species appears in the upper Eke Formation and ranges to the Hamra Formation (Fig. 8) and is, except for *Paralogania?* sp., the only species recorded in the upper Eke interval. Hence the first appearance datum (FAD) of *Pa. ludlowiensis* could be used to define a vertebrate zone in the upper Eke, which narrows the gap in the Eke Formation.

Perhaps *L. horrida* could be used as well. Its range begins slightly below the last appearance datum (LAD) of *An. hedei* in the Botvide Member (Fig. 8), and succeeds into the lower Eke Formation. However, since the already established index-species *An. hedei* co-occurs in most of the latter species range, this suggestion is rather vague. Therefore, I suggest that the LAD of the latter species is used to define the upper boundary of the *An.*

*hedei* Zone in the top part of the Botvide Member, rather than using the FAD of *L. horrida*. Nonetheless, *L. horrida* and *An. hedei* might indicate, if recorded together, a correspondence to the top part of the Botvide Member, whereas *L. horrida* recorded solely, may indicate the correspondence to the topmost part of the Botvide Member or the lower Eke Formation.

Hence, a suggested tentative vertebrate zonation applicable for the Lau Event interval of Gotland is as follows: *An. hedei*, *Pa. ludlowiensis*, and *Th. sculptilis* vertebrates zones (see suggestion in Fig. 8).

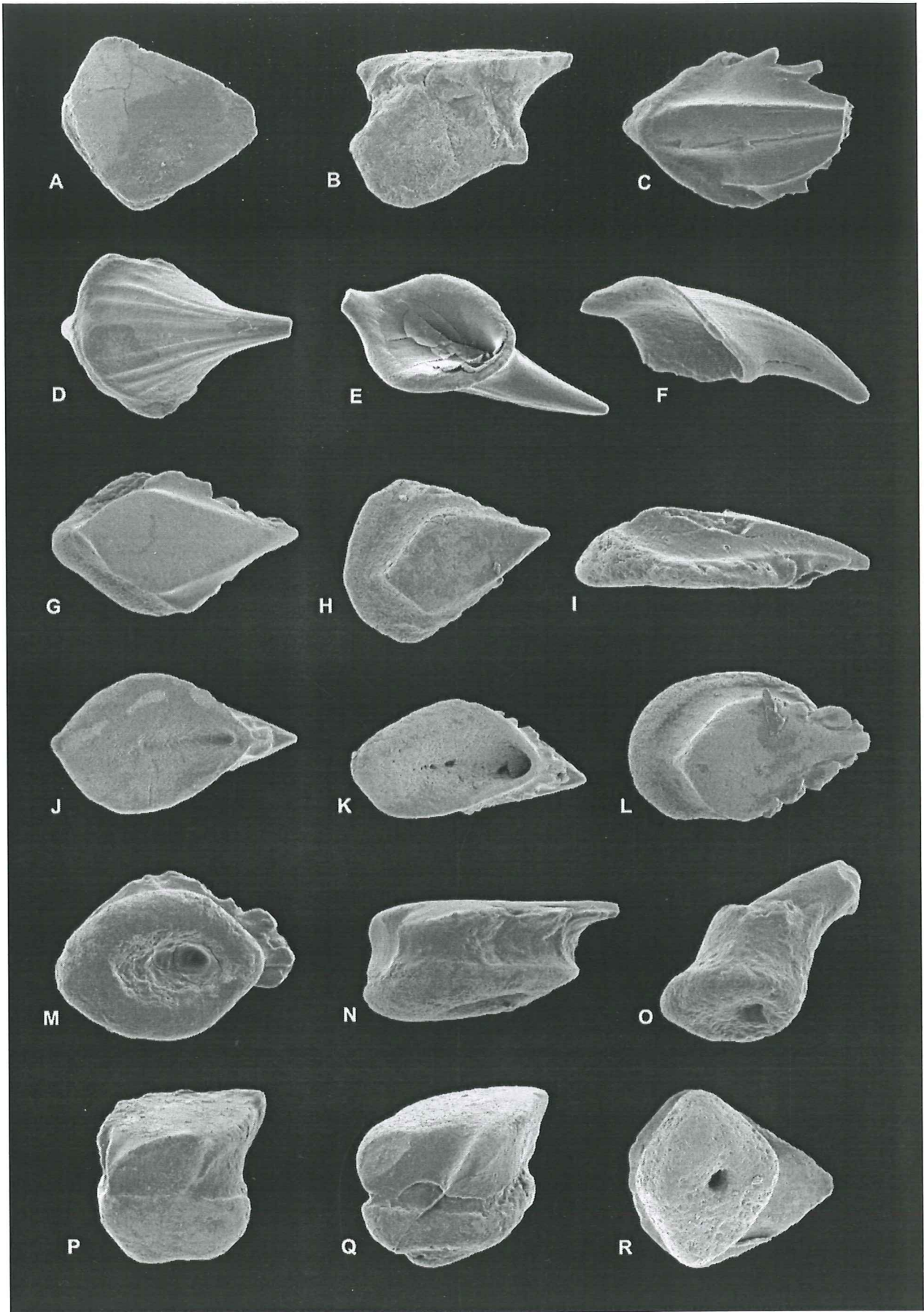
### 7.8. Revisions of previously documented species ranges and comments on other taxa

In this study, three species have new ranges compared to previous studies. *Th. sculptilis* was by Fredholm (1989) reported from the basal Eke to the Sundre formations. As concluded in section 6.4., sample G82-321DF from Hågvide 3 derives from Burgsvik Formation instead of the basal Eke. Thus, the range for *Th. sculptilis* started at the base of the Burgsvik Formation. The same cause as described above is valid also for *Po. porosus*, instead of ranging from the basal Eke it ranges from the basal Burgsvik to the Hamra formations. *Pa. ludlowiensis* has been reported from the basal Eke to the Burgsvik Formation (Fredholm 1989). The occurrence in basal Eke (based on sample G82-321DF from Hågvide 3) is now excluded (cf. above), and its range begins in the upper Eke. Moreover, this study has extended its known range upwards into the Hamra Formation.

Four anaspid species have been reported in the post-event interval of Gotland (see section 2.3.). Two of these have been recorded herein as well; *Ta. elongituberculata* and *S. mucronata*. The latter species have been reported from both the Burgsvik and Hamra formations (Blom *et al.* 2002), but herein it was only found in the Burgsvik Formation. This is probably due to the fact that only two samples represent this unit in this study (Fig. 10). The two additional anaspid species, *H. papillata* and *L. curvata*, have been reported from the Burgsvik-Hamra formations and Hamra Formation, respectively (Blom *et al.* 2002). Neither of these have been found in this study, probably also due to few samples investigated herein, but also because these species are rare (Blom *et al.* 2002).

Fig. 13. Thelodonti from the Ludfordian of Gotland. A-B. *Thelodus* sp. A. Crown view, x81. B. Lateral view, x95. A-B from sample G02-139LJ from Skradarve 1, Hamra Fm. C. Crown view of Thelodonti sp. A, x160, sample G91-29LJ from Nyan 2, Botvide Mb, Hemse Group. D-F. *Lanarkia horrida*. D. Crown view, x51. E. Base view, x64. F. Lateral view, x69. A-C from sample G91-32LJ from Nyan 2, Botvide Mb, Hemse Group. G-K. *Paralogania?* sp. G. Crown view, x66. H. Crown view, x84. I. Lateral view, x94. J. Base view, x63. K. Base view, x63. G, J-K from sample G92-439LJ from Petsarve 14, Upper Eke Fm, H-I from sample G02-139LJ from Skradarve 1, Hamra Fm. L-O. *Paralogania ludlowiensis*. L. Crown view, x70. M. Base view, x98. N. Lateral view, x101. O. Lateral view, x97. L-O from sample G92-439LJ from Petsarve 14, Upper Eke Fm. P-R. *Thelodus sculptilis*. P. Oblique crown view, x68. Q. Oblique crown view, x66. R. Base view, x99. P from sample G02-134LJ from Kättelviken 1, Burgsvik Fm, Q-R from sample G02-139LJ from Skradarve 1, Hamra Fm.







## 8. Conclusions

1. The vertebrates were strongly affected during the Late Silurian Lau Event, both by extinctions, new appearances, Lazarus patterns, and frequency changes. Sixty-three percent of the taxa that occurred before the event went extinct during the event, whereas the post-event faunas were marked by speciation where 58 % of the species were newcomers. By contrast to the pre-event faunas in which acanthodians dominated, thelodonts were more common in the post-event faunas. The scale frequency decreases considerably from the Botvide Member to the upper Eke Formation event interval, reflecting the severe environmental conditions caused by the event.

2. The presence of the index-species *Ph. elegans*, *An. hedei*, and *Th. sculptilis* enables a correlation of the Lau Event to the vertebrate biozonation – the onset of the Lau Event took place during the *An. hedei* vertebrate Chron, and its end coincided with the lower boundary of the *Th. sculptilis* vertebrate Zone. A more detailed biozonation that is applicable for the Eke Formation is also suggested herein, with the index-species *Pa. ludlowiensis*.

3. Patterns similar to those found on Gotland are noted in the vertebrate faunas also in other regions, inferring that the pronounced effects on the vertebrate faunas were not exclusive to Gotland and that vertebrates will be a useful tool in identifying this event elsewhere.

## 9. Suggestions for further studies

Further high resolution studies through the Gotland succession with focus on the vertebrates are desirable. This would help in establishing the FADs and LADs of each species, as well as providing statistical support for whether the disappearances are event-related or simply related to normal background extinction. Moreover, it would be interesting to study the distribution of vertebrates in various environments, in order to identify the degree of facies dependence.

During this study I have come to realize that vertebrate studies of this nature (i.e., a high resolution study with dense collecting of large samples), have been restricted mostly to the Baltic area. It would therefore be most desirable to make comparable analyses in other areas as well, as for example Australia and Canada. The Lau Event has been identified in the latter regions by conodonts and stable carbon isotopes, however, a systematic and detailed study of the vertebrates has not yet been made (e.g. Märss *et al.* 1998; Burrow & Turner 2000).

## 10. Selected systematic palaeontology

Most of the vertebrate taxa recorded in the studied interval are well known from the work by e.g., Fredholm

(1988a, b, 1989). However, some taxa have been re-assigned since then, and these are briefly discussed below. Moreover, also included in this selected systematic palaeontology are all taxa of uncertain affinity. The vertebrate descriptive terminology follows that of Gross (1967) and Karatajūtė-Talimaa (1997), see also Fig. 9. All figured specimens and collections studied are housed at the Department of Geology, GeoBiosphere Science Centre, Lund University, Sweden.

PHYLUM CHORDATA

SUBPHYLUM VERTEBRATA

CLASS AGNATHA COPE, 1889

SUBCLASS THELODONTI KIAER, 1932

*Thelodonti* sp. A

Fig. 13C

*Remarks.* – Small, thin and pointed scales, *c.* 0.02 mm long, which have wide and open pulp cavities. Two spurs on either lateral side are present. One of the two scales recorded possesses a spur anteriorly. The general morphology indicates that these scales belong to a thelodont. Pending further material, the specimens at hand are assigned to *Thelodonti* sp. A.

*Material.* – 2 scales.

*Occurrence.* – Gotland: *Botvide Mb*: Nyan 2.

ORDER KATOPORIDA KARATAJŪTĖ-TALIMAA, 1978

FAMILY LOGANIIDAE KARATAJŪTĖ-TALIMAA, 1978

Genus *Paralogania* Karatajūtė-Talimaa, 1997

*Paralogania?* sp.

Figs. 13G-K

*Remarks.* – The specimens at hand are *c.* 0.8 mm long, and rhomboidal or diamond-shaped. The crown is flat and smooth. The pulp cavity is well developed and displaced towards the posterior end, where it narrows into a canal. Some scales have *c.* 4-10 spurs posteriorly, located right below the tip of the crown. Furthermore, there are scales that have a row of thornlets (small spines) developed on their lateral sides, and others that seem to lack this feature. A spur-like process is developed on the anterior part in some specimens.

The scales belong either to *Loganellia* or *Paralogania*. Identification is difficult due to the morphological similarities between these two genera. According to Karatajūtė-Talimaa (1997), *Loganellia* scales are somewhat more compact, and do not possess thornlets on their



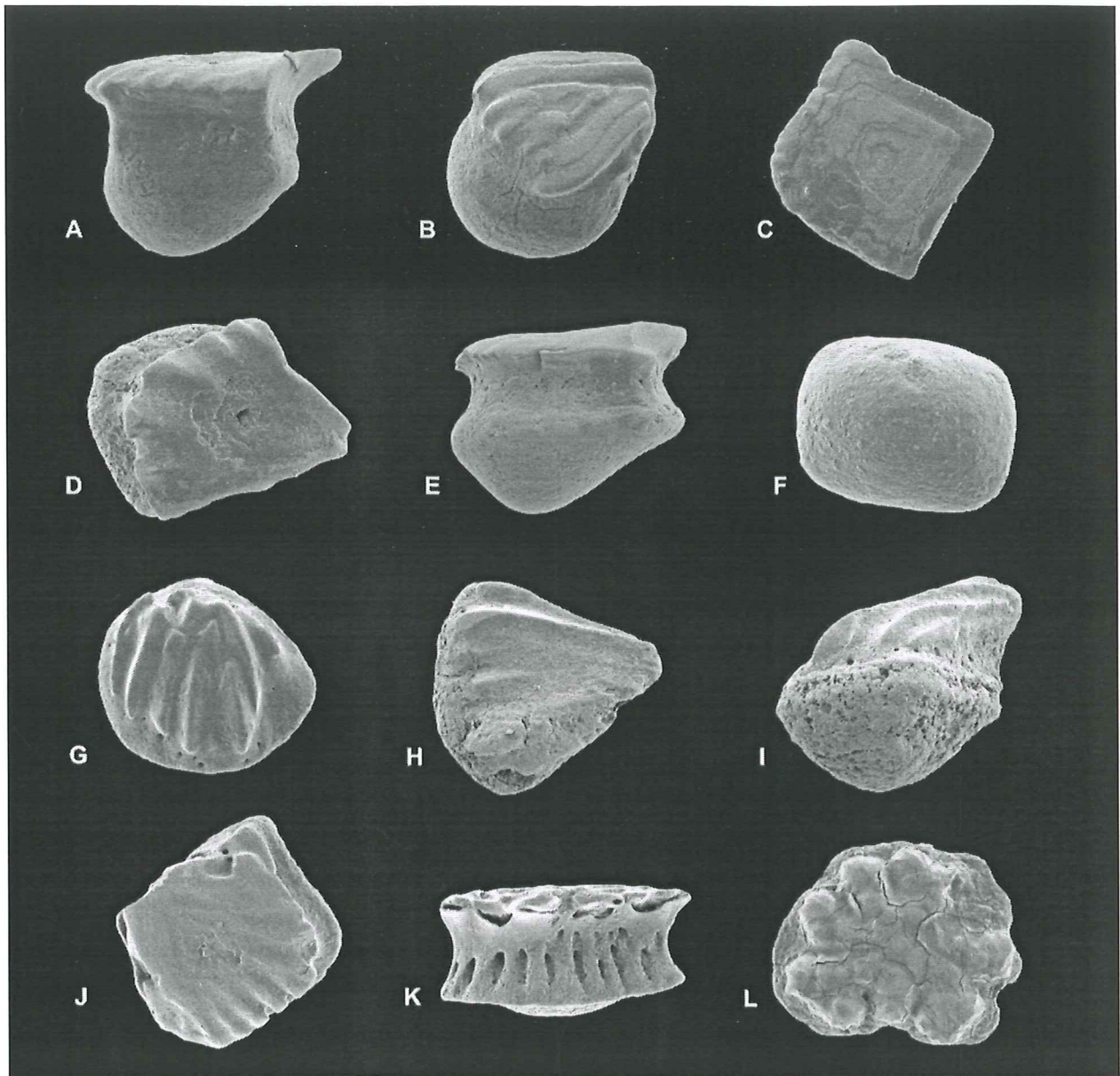


Fig. 14. Acanthodii from the Ludfordian of Gotland. A-F. *Gomphonchus sandelensis*. A. Lateral view, x82. B. Oblique crown view, x53. C. Crown view, x43. D. Crown view, x89. E. Lateral view, x61. F. Base view, x50. A-C from sample G93-959LJ from Botvide 1, main part of the När Fm, Hemse Group, D from sample G00-24LJ from Ängvards 5, Hamra Fm, E from sample G02-134LJ from Kätteleviken 1, Burgsvik Fm, F from sample G91-32LJ from Nyan 2, Botvide Mb, Hemse Group. G-I. *Nostolepis striata*. G. Crown view, x52. H. Crown view, x41. I. Lateral view, x49. G from sample G91-32LJ from Nyan 2, Botvide Mb, Hemse Group, E-F from sample G00-24LJ from Ängvards 5, Hamra Fm. J-K. *Poracanthodes porosus*. J. Crown view, x39. K. Lateral view, x45. J-K from sample G02-134LJ from Kätteleviken 1, Burgsvik Fm. L. Acanthodian tesserae plate, crown view, x41, sample G93-962LJ from Botvide 1, Botvide Mb, Hemse Group.

lateral sides. *Paralogania* scales, on the other hand, possess a row of thornlets on their lateral sides. Otherwise their morphology is more or less identical. When studied in light microscope, some of the scales lack this row of thornlets. However, when studied in SEM, they do show tendencies to possess this characteristic feature. A possible explanation is that the thornlets are missing due to erosion. Both kinds of scales co-occur in the samples and they have similar ranges. It is possible that there are more than one species in the samples at hand, howev-

er, because of the difficulty in separating them, and the fact that they co-occur, I prefer to assemble them under one single name, pending further studies. Because most scales possess a row of thornlets, the specimens are assigned to *Paralogania?* sp. Fredholm (1989) assigned this species to *Loganellia cuneata*. These kinds of scales were reported from the upper Eke and Burgsvik formations. Additional scales that she assigned to "*Logania*" *cuneata*, reported from the Botvide Member, have herein been referred to *Lanarkia horrida* (cf. *Lanarkia* below).



*Material.* – Approximately 280 scales.

*Occurrence.* – Gotland: *Botvide Mb*: Nyan 2. *Lower Eke Fm*: Botvide 1. *Upper Eke Fm*: Petsarve 14 (herein), Petsarve 15, Ronnings 1 (Fredholm 1989 and herein), Kullunde 2 (Fredholm 1989). *Burgsvik Fm*: Burgen 7, Burgen 9, Kättelviken 1 (herein), Glasskär 1, Hägvide 3, Hoburgen 2, Kapelludden 1, Kroken 1, Närshamn 1 (Fredholm 1989). *Hamra Fm*: Skradarve 1.

ORDER THELODONTIDA GROSS, 1967 SENSU MÄRSS & RITCHIE (1998)

FAMILY LANARKIIDAE OBRUCHEV, 1949

Genus *Lanarkia* Traquair, 1898

*Lanarkia horrida* Traquair, 1898  
Figs, 13D-F

*Remarks.* – Erect and pointed, cone-like scales, c. 0.5 mm long. The scales are thin and have wide, open pulp cavities. Some of them possess a spur anteriorly. The crown has at least three ridges that converge at the posterior tip. Such scales were described as "*Logania*" *cuneata* by Fredholm (1988a, fig. 4G, H). That taxon has been revised by Märss & Ritchie (1998, p. 173) and referred to as *Lanarkia horrida*, hence, the this name is used herein.

*Material.* – Approximately 200 scales.

*Occurrence.* – Gotland: *Botvide Mb*: Nyan 2 (Fredholm 1988a and herein), Bodudd 1, Burgen 1, Hallsarve 1, Hörte 1, När 2 (Fredholm 1988a). *Eke Fm*: Lau Backar 1 (Spjeldnaes 1950). *Burgsvik Fm*: Kättelviken 1. *Southern Scotland*: lower Wenlock, Waterhead Group, Glensbuck Group, Henshaw Formation (Märss & Ritchie 1998). *Canada*: Wenlock of Avalanche Lake sections (Märss & Ritchie 1998 and references therein).

ORDER THELODONTIFORMES KIAER, 1932 SENSU MÄRSS & MILLER, 2004

FAMILY COELOLEPIDIDAE PANDER, 1856 SENSU MÄRSS & MILLER, 2004

Genus *Thelodus* Agassiz, 1838

*Thelodus* sp.  
Figs. 13A-B

*Remarks.* – Medium-sized scales (0.5-0.7 mm in length). Crown surface is smooth, with a posteriorly pointed part and a slightly rounded anterior part, almost triangular in

shape; the posterior part of the crown exceeds the base. Neck is distinct. The centred pulp cavity is deep and narrow. These specimens resemble *Th. sculptilis*, however, the crowns of the latter have furrows that become deeper and steeper towards the anterior end (Märss 1986, p. 87). This character is missing in the specimens at hand – they lack ornamentation on the crown surface. They also resemble *Th. parvidens*, see Vergoossen (2002, p. 139), in having a deep and centered pulp cavity, and a smooth crown surface, however, the general shape of the two taxa differs – the latter one has a circular crown while the specimens at hand are triangular. Hence the species level affinity of the Gotland specimens remains uncertain.

*Material.* – 50 scales.

*Occurrence.* – Gotland: *Botvide Mb*: Nyan 2. *Lower Eke Fm*: Botvide 1. *Burgsvik Fm*: Burgen 7, Burgen 9, Kättelviken 1. *Hamra Fm*: Skradarve 1.

SUBCLASS ANASPIDA TRAQUAIR, 1899

ORDER BIRKENIIDA BERG, 1937

FAMILY SEPTENTRIONIIDA BLOM, MÄRSS & MILLER, 2002

Genus *Septentrionia* Blom, Märss & Miller, 2002

*Septentrionia mucronata* Blom, Märss & Miller, 2002  
Figs. 15A-B

*Remarks.* – 1-2 mm long fragments, made up of an elongated rib that is covered by small and pointed spines. The specimens at hand agree well with the description of *Septentrionia mucronata* by Blom *et al.* (2002, p. 309).

*Material.* – 13 fragments.

*Occurrence.* – Gotland: *Burgsvik Fm*: Kättelviken 1 (herein), Uddvide (Blom *et al.* 2002). *Hamra Fm*: Hoburgen 2 (Blom *et al.* 2002), Hoburgen 3 (Blom *et al.* 2002).

FAMILY TAHULALEPIDIDAE BLOM, MÄRSS & MILLER, 2002

Genus *Tahulalepis* Blom, Märss & Miller, 2002

*Tahulalepis elongituberculata* Blom, Märss & Miller, 2002  
Figs. 15C-D

*Remarks.* – The specimens at hand agree with the description of *Tahulalepis elongituberculata* by Blom *et al.*

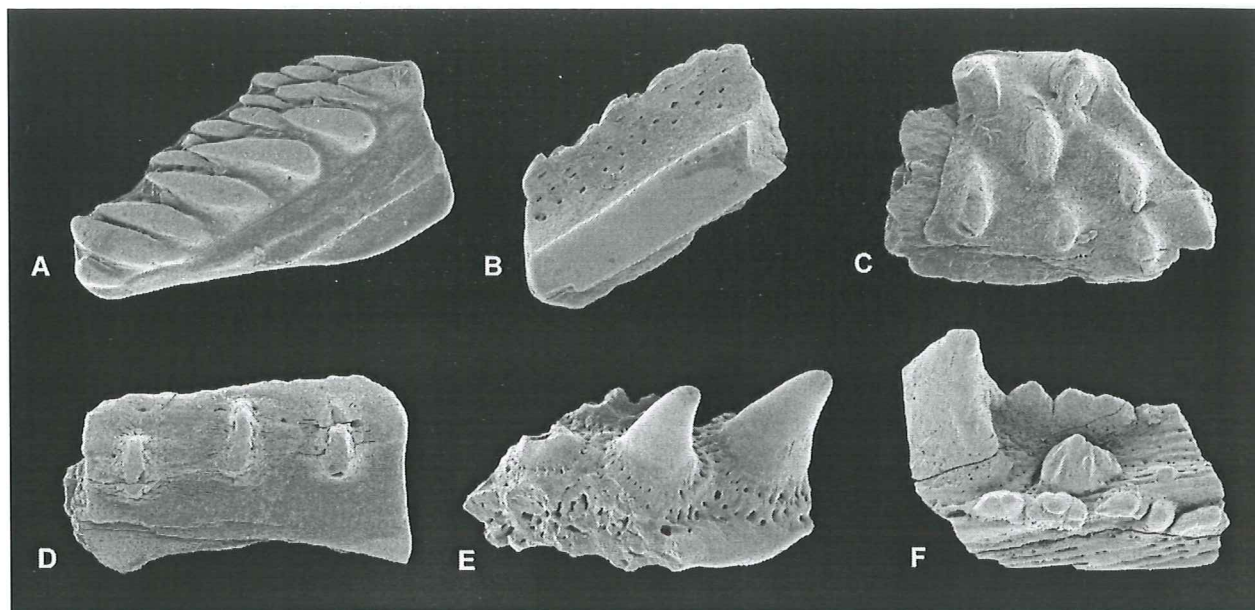


Fig. 15. Anaspida (A-D) and acanthodian dental elements (E-F) from the Ludfordian of Gotland. **A-B.** *Septentrionia mucronata*. A. Crown view, x28. B. Base view, x27. A-B from sample G02-134LJ from Kättelviken 1, Burgsvik Fm. **C-D.** *Tahulalepis elongituberculata*. C. Crown view, x33. D. Crown view, x32. C-D from sample G02-134LJ from Kättelviken 1, Burgsvik Fm. **E-F.** Oblique view of acanthodian dental elements, x20 (E) and x10 (F), sample G93-962LJ from Botvide 1, Botvide Mb, Hemse Group.

(2002, pp. 305-307, fig. 40). The fragments are 1.0-1.5 mm in length and characteristically covered by well-spaced tubercles on an otherwise smooth surface. The species is the same as *Birkeniida* sp. A that Fredholm (1989, p. 13) recorded in the Burgsvik Oolite from the Burgsvik Fm.

*Material.* – 2 fragments.

*Occurrence.* – Gotland: *Burgsvik Fm*: Kättelviken 1 (herein), Hoburgen 1 (Fredholm 1989). *Skåne*: Ramsåsa, late Ludlow (Blom *et al.* 2002). *Estonia*: Saaremaa, Kuressaare “regional stage”, late Ludlow (Blom *et al.* 2002).

#### SUBCLASS OSTEOSTRACI

##### Osteostraci? indet., type A Figs. 16A-B

*Remarks.* – Elongated (0.5-1.0 mm in length) and elliptical fragments with a convex surface lacking ornamentation. The visceral side is perforated by holes and canals. Due to the smooth upper surface the specimens at hand are suggested to derive from the outer ornamentation, or scale cover, of the vertebrate.

*Material.* – 19 fragments.

*Occurrence.* – Gotland: *Burgsvik Fm*: Kättelviken 1. *Hamra Fm*: Skradarve 1.

##### Osteostraci? indet., type B Figs. C-D

*Remarks.* – Small and large perforated fragments, 0.5-1.5 mm long. The visceral side is similar to the upper side, indicating an internal position of this fragment rather than belonging to the scale cover.

*Material.* – 10 fragments.

*Occurrence.* – Gotland: *Hamra Fm*: Skradarve 1.

#### CLASS INDETERMINED

##### Gen. indet. sp. A Fig. 16E

*Remarks.* – Articulated scale cover plates, 1-2 mm in length. Plate surface covered with small scales (*c.* 0.3 mm in length and width) that are oriented in rows, all facing the same direction. Visceral side of plate is flat, striated, and perforated with small and well-spaced holes.

*Material.* – 7 plates.

*Occurrence.* – Gotland: *Botvide Mb*: Botvide 1.



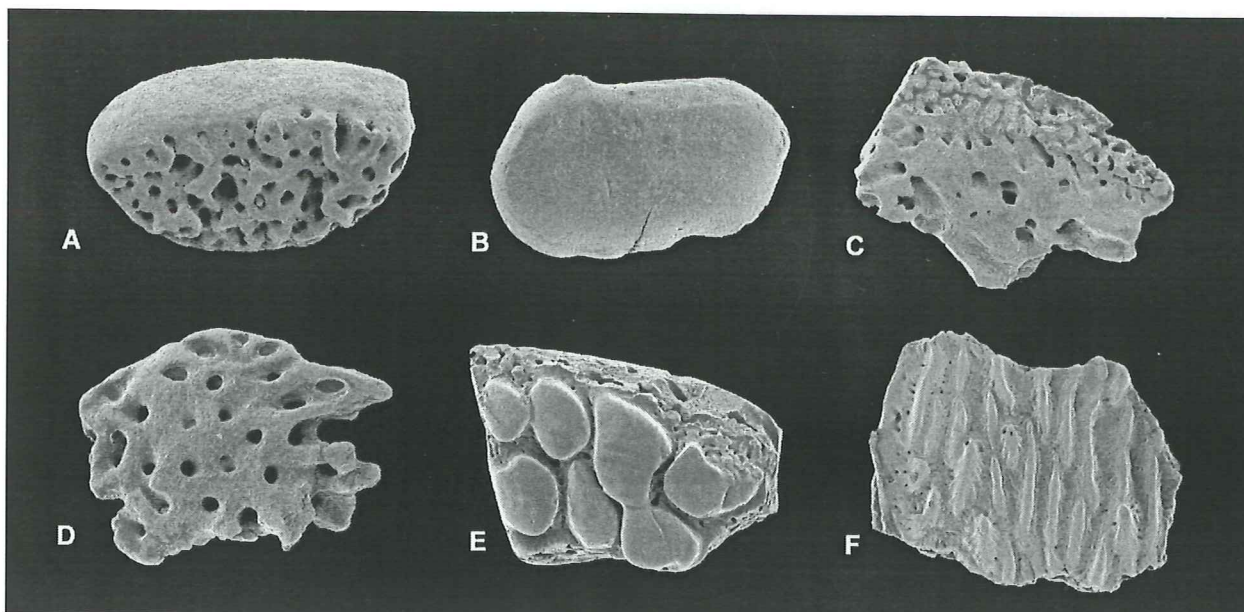


Fig. 16. Osteostraci? (A-D) and Gen. indet. (E-F) from the Ludfordian of Gotland. **A-B.** Osteostraci? indet., type A. A. Oblique crown view, x53. B. Crown view, x43. A-B from sample G02-139LJ from Skradarve 1, Hamra Fm. **C-D.** Osteostraci? indet., type B. C. Fragment in upper view, x30. D. Fragment in visceral view, x46. C-D from sample G02-139LJ from Skradarve 1, Hamra Fm. **E.** Crown view of Gen. indet. sp. A, x29, sample G93-962LJ from Botvide 1, Botvide Mb, Hemse Group. **F.** Crown view of Gen. indet. sp. B, x12, sample G93-948LJ from Nyan 2, Botvide Mb, Hemse Group.

#### Gen. indet. sp. B

Fig. 16F

*Remarks.* – C. 5 mm long scale cover plates. Plate surface is covered with oblong scales, c. 1 mm in length and 0.2 mm in width, that are oriented in rows, all facing the same direction. Visceral side is flat and smooth, and occasionally perforated with well-spaced holes.

*Material.* – 11 plates.

*Occurrence.* – Gotland: *Botvide Mb*: Nyan 2.

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