Conodont-based revisions of the Late Ludfordian on Gotland, Sweden

LENNART JEPPSSON¹

Jeppsson, L., 2005: Conodont-based revisions of the Late Ludfordian on Gotland, Sweden. *GFF*, Vol. 127 (Pt. 4, December), pp. 273–282. Stockholm. ISSN 1103-5897.

Abstract: The Late Ludlow topmost Hemse–Burgsvik succession includes more substantial and more rapid facies changes than most older and younger intervals on Gotland. A revised conodont zonation for this interval includes three zones, the *Polygnathoides siluricus*, the Icriodontid, and the *Ozarkodina snajdri* zones and four subzones, the Upper *P. siluricus*, the Lower, the Middle and the Upper Icriodontid subzones. The three zones are approximately coeval with the *Neocucullograptus kozlowskii* graptolite fauna, the succeeding impoverished graptolite fauna and the *Monograptus balticus/Pseudomonoclimacis latilobus* Zone (= the lower *M. formosus* Zone), respectively. The new zonation permits the first high-resolution correlations across Gotland, despite very large differences in facies from SW to NE. Another result is a more detailed stratigraphic subdivision and revised boundaries of most of the units. The Mill-klint, the main and the Botvide members of the När Fm. (new, the upper part of the Hemse Group), the lower, middle, and upper Eke Fm., and the Burgsvik Fm. are distinguished. Well known names are kept, as far as possible, but the lateral extent of their boundaries is revised, resulting in a considerable increase in precision and very different thickness data, e.g. the Ludlow is calculated to be somewhere between 337 and 425 m instead of the 215 m given hitherto. Faults or disturbances with similar effects are identified for the first time on Gotland. *Silurognathus maximus* is named.

Keywords: Silurian, Ludlow, conodont zonation, correlations, Gotland, lithostratigraphy.

¹Department of Geology, Sölvegatan 12, SE-223 62 Lund, Sweden; lennart.jeppsson@geol.lu.se Manuscript received 25 November 2004. Revised manuscript accepted 21 November 2005.

Introduction

Late Ludlow sediments in Sweden are limited to Gotland and Skåne. The stratigraphy of Skåne has been revised recently (Jeppsson & Laufeld 1987), but that on Gotland has not been improved since it was introduced by Hede (1921, 1925, 1927, 1929, summarised in English in 1960). The focus herein is on the interval that spans the upper Hemse to the Burgsvik formations.

The strata on Gotland are not affected by metamorphism or strong folding (the strongest local folding is displayed at Botvide 1 (Fig. 1). They have also been considered unaffected by appreciable faulting. However, the distribution of the strata as now known on southern Gotland seems to indicate abrupt lateral displacements of the regular trend of the stratal boundaries (Fig. 1). Closely spaced parallel jointing in a similar direction to these displacements in the westernmost parts of Bodudd 1 may be related to the most southerly one of these disturbances. This fault turned out to coincide with the Precambrian Loftahammar-Linköping Shear Zone as extended below Gotland by Sundblad et al. (1998; reference from Karin Högdahl, Lund). Outcrops of coeval sediments form very narrow belts striking NE-SW and mostly dipping 0-4° to the SE. The original depth contours were closer to E-W. The acute angle between the depth contours and present day outcrop belts amplifies all displacements of facies belts. Along the outcrop, the facies changes from shallow water limestone with reefs in the NE to distal marls, often with sparse graptolites in the SW. The sedimentation pattern and rate were strongly influenced by oceanic changes (regarding this interval see Jeppsson 1990, 1993; Jeppsson & Aldridge 2000). Reef growth essentially ceased during primo episodes, and argillaceous limestone expanded across the marginal reef area. During secundo episodes a reef belt formed, and the platform expanded seawards shifting the facies boundaries tens of kilometres along strike. The strong Lau Event caused distinctive sediments and faunas (Jeppsson 1990, 1998; Jeppsson & Aldridge 2000; Eriksson et al. 2004). Further, global effects in stable isotope ratios have been predicted (Jeppsson 1990) and found (Talent et al. 1993). Correlations of such effects have, however, been hampered by low stratigraphic resolution, and erroneous correlations have confused the temporal order of discovered effects leading to erroneous conclusions regarding the cause and the effects. Hence, a more detailed stratigraphy of these strata is of special interest, providing a framework for future studies of these changes. Only within such an improved local framework will it be possible for different authors to correlate their identification of various effects and to trace them globally.

Knowledge of the succession is based mostly on minor exposures (mainly in ditches), though up to 3 m around the Hemse/ Eke boundary is exposed in several sections, and so is also the interval with the Burgsvik/Hamra boundary. Most localities were described in the catalogue produced by Laufeld (1974b); an updated version (Jeppsson & Jerre: Catalogue of formally

Hamra and Sundre formations

0

1650

almundsudd

1660

Vamlingbo church

Grump

But

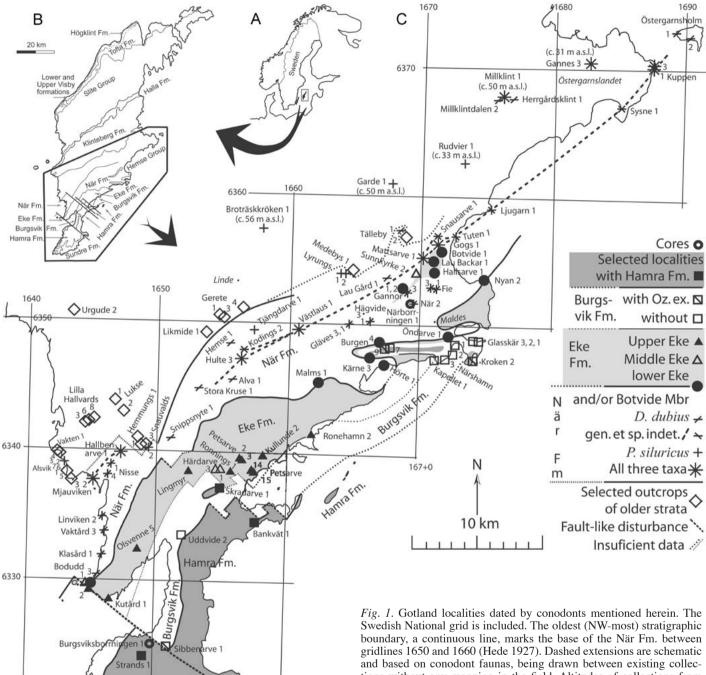
X

Hoburgen 2

Kättelviken 1

6320

1640



boundary, a continuous line, marks the base of the När Fm. between gridlines 1650 and 1660 (Hede 1927). Dashed extensions are schematic and based on conodont faunas, being drawn between existing collections without any mapping in the field. Altitudes of collections from previously unmapped outliers NW of the lower boundary of the När Fm. are approximated from the isometric lines on the topographical map. Localities yielding *Silurognathus maximus* are connected with a dashed line, except those in outliers. Other boundaries are based on the outcrops as mapped on the geological map sheets Burgsvik, Hemse, Ronehamn, and Katthammarsvik. The continuous parts of the Burgsvik/Hamra boundary are drawn using the numerous exposures with oolite marked on the geological maps. Disturbances in the regular SW–NE trend of this and other boundaries are drawn as NW–SE dashed lines. Identifying the number, exact position and direction of such disturbances will require detailed mapping. For clarity, boundaries on Burgen and around outliers N thereof are omitted. Botvide Mbr, the lower Eke and a part of the middle Eke are exposed at Bodudd 1. Fig. A and B modified from Jeppsson & Calner 2003; original by Calner.

described localities in the Silurian of Gotland, 600 pp.) is available at Allekvia Geological Field Station on Gotland. Metric data refer to below (–) and above (+) the reference level as defined in these catalogues. The interval of a single sample is given as, e.g., -1.75/-1.70 m; i.e. the lower boundary first. Localities are listed from SW to NE unless stated.

Conodont collections

Sampling strategy, sample size, processing technique, yield/kg, vield/hour, and average number of conodonts/collection have improved enormously since collecting began in 1969, in some of these variables more than hundredfold. As a result later collections mostly contain at least a few 1000s of elements each. Collections before 1983 were mostly from 0.5 to a few kg processed using an unbuffered technique. After 1983 the adequate sample size was based on known or estimated yields/kg and the assumed optimal collection size. Thus, usually 10 to >100 kg, in average c. 30-40 kg/sample, were processed, from 1985 with the pH-measured buffered technique of Jeppsson et al. (1999). That technique resulted in an increase in the yield/kg varying from moderate, to more than 10 times. A gentle under-water-screenwashing-technique (using a 63 μ m screen) and other methods that limit damage to the brittle elements have resulted in a considerable further increase (Jeppsson 2005). During the last 13 years dolomite has been removed with buffered formic acid (technique by Jeppsson & Anehus 1995) and other non-phosphatic minerals with magnetic separation and density separation at 2.84 and 3.04 kg/l (Jeppsson & Anehus 1999). Afterwards, each residue (±pure phosphate) was split into size fractions. Picking started with the coarsest one; usually only a small part of the finest fraction $(63-125 \ \mu m)$ was picked, due to funding constraints; similarly parts of the coarser fractions had often to be left unpicked. However, this method produces the most complete species list for a sample, since large forms usually are more rare than the very small ones; further, taxa hitherto used in stratigraphy are large or medium sized.

About 200 collections produced c. 100 000 elements from the interval analysed herein. The yield varies from several hundreds per kg in some När Fm. samples to 4 in 31 kg of a silty clay (Eke Fm., sample G95-4LJ from Härdarve 1). Resampling of the Hemse/Eke boundary interval included c. 10 samples per metre at Botvide 1 (2.25 m of Hemse Group exposed) and Nyan 2 (1.07 m of Hemse Group exposed). The sample size, c.10 kg, was calculated to yield at least 3000 specimens/collection, which has been shown to be sufficient in the Lower Visby Fm. to include all taxa, except possibly the two rarest ones (Jeppsson 1997a, 1998; Jeppsson & Männik 1993). However, in the Botvide Member many important taxa turned out to have a frequency <1‰. Hence, most recorded range-ends have an uncertainty of one to a few decimetres, despite the fact that sample size was later increased to c. 30 kg. Most samples from younger strata were less productive.

Conodont zonation

A local zonation is of limited use; hence, revisions below are based on all published records of Ludlow conodont ranges and own studies of most published larger collections, in order to make the zonation useful globally for high-precision stratigraphy (for space reasons, only the Gotland data base is discussed herein). The P. siluricus Zone. - Walliser (1964) defined this zone, based on the range of Polygnathoides siluricus at Cellon, Austria. Ancoradella ploeckensis ranges above its own zone, into the lowermost P. siluricus Zone there and in many other areas. Being zone fossils, every record of these taxa has been assumed to be coeval with these zones. At Cellon, the first A. ploeckensis co-occurs with Kockelella variabilis variabilis and Ozarkodina n. sp. A of normal size, in Walliser's sample C18 (the K. variabilis specimen in C16A represents another subspecies). That co-occurrence may be real, or A. ploeckensis may be restricted to the upper part of the sampled interval and the other two taxa to the lower part. On Gotland the oldest P. siluricus (one specimen) co-occurs with the youngest records of K. v. variabilis and typical O. n. sp. A during the earliest Linde Event (at Alsvik 2, in G02-164LJ, 102.9 kg). As for the Cellon find, co-occurrence in one collection does not prove co-occurrence in time. Independent of that, the find predates the interval with A. ploeckensis on Gotland when P. siluricus was absent. P. siluricus became regular only well after A. ploeckensis had disappeared. The find in the upper part of the British Upper Bringewood Fm. (Aldridge in Jeppsson & Aldridge 2000), may be coeval with that on Gotland. P. siluricus has been reported as low as in the S. chimaera graptolite Zone (Klapper & Murphy 1975), but this needs confirmation (Uyeno 1981; similarly the isotope data of Saltzman (2001) indicate errors in the assumed relationship of different sets of collections). The discontinuous occurrence of P. siluricus through time hence needs to be analysed.

Platform-equipped taxa are only intermittently present through the Wenlock-early Devonian, and when present, they are mostly rare. Thus, in many areas the niche for taxa with a platform element may frequently have been too 'narrow' to permit splitting between two populations large enough to reproduce. A model with species of Kockelella, Polygnathoides and Ancoradella competing for this niche explains the known records of P. siluricus as follows. Through the early Ludlow other taxa with platform elements dominated this niche. Competition relaxed briefly early during the Linde Event, permitting P. siluricus to visit some areas, but only during the Havdhem Primo Episode did oceanic conditions favour P. siluricus for a longer period of time. It became widespread and, after a transition interval, completely replaced Kockelella and Ancoradella in many areas. During the early Lau Event, oceanic conditions again favoured Kockelella, which could compete successfully with and nearly replaced P. siluricus in some areas.

The intermittent, rare, early *P. siluricus* record results in the oldest find in some areas considerably pre-dating the earliest find elsewhere. Hence, another definition of the base of *P. siluricus* Zone is necessary. On Gotland there is a distinct faunal change when *Ozarkodina confluens confluens* (=ssp. *cornidentata* Viira, 1983) and *Silurognathus maximus* sp. nov. (see Appendix) appeared, and *Coryssognathus dubius* and *P. siluricus* became regular. The base is preliminary placed there, although further studies are required in order to give the best definition. När Fm. strata correlate with the Upper Leintwardinian (Martinsson 1967); hence the *P. siluricus* Zone is late Early Ludfordian in age. Abundant and diverse condont faunas characterise this zone globally (Jeppsson 1975). The zone includes three distinct faunas on Gotland. That with *S. maximus* is oldest; the main part of the zone lacks that taxon, but *P. siluricus* remained regular.

The topmost part of this zone is distinct, and is here distinguished as the Upper *P. siluricus* Subzone. At least on Gotland identification of its base requires closely spaced large collections

Z	Conodont Cones and	Conodont faunas	Grap- tolites	Oceanic state (severity)	Lithostrati- graphy on Gotland		Sediments NE SW	Thickness metres
	Subzones						(proximal) (distal)	NE SW
(O. s <i>najdri</i> Zone	moderate diversity	Pm. lati- lobus im- pover- ished fauna diverse, with N. kozlowski	Hoburgen Secundo	Hamra Fm. (lower part)		oncolitic lst., marl	Hamra + Sundre c.100 (88-124)
(1	ower part)			Episode	Burgsvik Fm.		oolite sandstone	29.83? 47.22
I c r c c c c c c c c c c c c c c r c c c r c c c r c	Upper Icrio- dontid Subzone	one species strongly dominating		L a (6.2) u E v (4) e	Eke Fm.	Upper Eke	oncolitic oncolitic lst. + marl mudstone	10? L+M+U Eke 31.3? <i>13.90</i> L+M Eke 19.95 >10 2.55
	Middle Icriodontid Subzone	impover- ished, with P. equicostatus				Middle Eke	oncolitic oncolitic Ist. + marls rare lst. beds	
	Lower Icrio- dontid Subzone	impover- ished fauna				Lower Eke	oncolitic marl dolomitic oncolitic mudstone, crinoid lst. rare lst. beds	
	<i>O. excavata</i> fauna	rapid			H e s När e Fm. G r o u p	Botvide Member	Shaleria coquinas mudstone	0.21
	Upper P. siluricus Subzone	stepwise extinctions		(3) t (2)			DayiaDayiacoquinas,coquinas,dolomiticdolomitic mudst.,Ist. and marlrare lst. beds	2.1
	Main part of the Zone	very diverse; platform conodonts		Havdhem Primo Episode		main part of the När Fm. Millklint Lst. Mbr	lst. mudstone, crinoid lst. alt. lst. beds	30+ 65+ Hemse c. 200 (250?)

Fig. 2. The sequence and correlation of the revised conodont zones, conodont faunal characteristics, the graptolite zonation (Urbanek 1997), the oceanic state (Jeppsson & Aldridge 2000), the severity on the severity scale for Silurian events (Jeppsson 1998; identified on the conodont faunal changes), the revised lithostratigraphy, typical lithologies and some thickness data. Note that the Millklint Limestone Member is only found east of the other sediments listed; i.e. it is lateral to, not below (today), the marls of the main member. Two different thicknesses are given for Eke and Burgsvik: italics as published by Hede (1921) and roman based on his identified range of *Daiya navicula* (see Hede 1919) and conclusion about its range (Hede 1921 p. 69) – see the text for details.

through the boundary interval; over 3000 conodonts in each are desirable (see Botvide Member, below for details). The base is exposed at c. -2.15 m at Botvide 1.

The Icriodontid Zone. - The extinction of P. siluricus was followed by impoverished faunas. This widespread zonal interval is characteristic and needs a name. Walliser (1964) distinguished a zone based on what now is Pedavis latialata. Where found, that species is mostly so rare that the oldest local find may well considerably post-date the immigration into that area. Hence, a reliable synchronous lower boundary must be based on the extinctions (compare the globally useful earliest Wenlock zones; Jeppsson 1997b). The best level is the extinction of the last one of Polygnathoides and Kockelella. In the Cellon section, Walliser drew the top of his *I. latialata* Zone above bed C30, i.e. at least c. 2.2 m above the last *Pe. latialata* (his table 2, II, just below the first O. crispa) or just below that bed (his Plate 1). However, icriodontids do continue into the succeeding zone (see e.g. Burgsvik below), and the top of the zone as here defined is lower down, probably below his sample C28. The zone is here renamed the Icriodontid Zone since locally different icriodontids are found in it.

Three subzones can be distinguished across the facies belts. The reappearance of the slender form of *Panderodus equicostatus* marks the base of the Middle Icriodontid Subzone. That taxon has not been recorded on Gotland between the late Wenlock and this subzone. The Upper Icriodontid Subzone is characterised by an extreme dominance of a single species. On Gotland, that *Pa. equicostatus* form reached frequencies of 90% – the *Pa. equicostatus* fauna of Jeppsson (1998). In other areas, another taxon may dominate, e.g. in Skåne (Scania) *Oz. scanica* reaches similar frequencies (the younger *H. scanica* fauna of Jeppsson 1975).

The O. snajdri Zone. – Walliser (1964) named a 'snajdri-Horizont' and suggested that it may be high in the P. siluricus Zone. The holotype is from the Mušlovka quarry in Bohemia, where O. snajdri appeared c. 5 m above the last P. siluricus (Kříž & Schönlaub 1980). O. snajdri appeared during the Early Ludlow, low in the Hemse on Gotland and in the Paadla in Estonia (Jeppsson et al. 1994; Viira & Aldridge 1998). I have now large collections of that early Ludlow form from Gotland and some specimens and fragments through succeeding zones and have seen similar specimens elsewhere, e.g. in Schönlaub's sample 19 from Mušlovka (Kříž & Schönlaub 1980), from the Middle Icriodontid Zone. However, extinctions due to the Lau Event (Jeppsson 1993; Jeppsson & Aldridge 2000) evidently vacated enough niche space to permit it and some other survivors to become widespread and regularly present, often in good frequencies, once environmental conditions improved after the event. Thus, the zone is useful, but its base must be redefined - as at the appearance of a diverse, reasonably balanced fauna, including O snajdri, directly after the low diversity interval (see above). The faunal change was abrupt - the incoming diverse fauna is found immediately above the low diversity fauna in the section Bjärsjölagård 2b in Skåne, where this zone was previously known as the O. wimani fauna (Jeppsson 1975). O. wimani similarly had a long, strongly faciesrestricted history (at least from the early Wenlock; Jeppsson et al. 1995). At least a lower part of the O. snajdri Zone correlates with the Upper Whitcliffe Fm. (Jeppsson & Aldridge 2000). In the international type section for the base of the Pridoli, the Ludlow continues with the succeeding O. crispa Zone (O. crispa, too, had a long prehistory) and, as now known, a thin post-O. crispa interval (Kříž et al. 1986). The Silurian of Gotland continues above O. crispa.

Correlation with the graptolite zonation. – In Poland a fauna with *Neocucullograptus kozlowskii* is followed by, in order, c. 25 m with impoverished graptolite faunas (included by Urbanek 1997 in the *N. kozlowskii* Zone) and a fauna with *Pseudomonoclimacis latilobus* – (the *M. balticus/P. latilobus* Zone = a lower part of the *M. formosus* Zone). These three intervals approximately correlate with the *P. siluricus*, the Icriodontid, and the *O. snajdri* zones, respectively (cf. Jeppsson & Aldridge 2000); the exact relationship of their boundaries remains to be documented.

The succession of strata and faunas

The Hemse Group

As delimited by Hede (1921, p. 56, 1925, 1927, pp. 24, 27), the Hemse Group on central Gotland includes three distinct units:

1. A lower marl unit (= the Hemse Marl Northeastern Part). The oldest fauna, from Urgude 2, includes *K. crassa* and *O. b. bohemica*; that subspecies occurs with the graptolite *N. nilssoni* in Bohemia (Walliser 1964, p. 97). In the När 1 core *N. nilssoni* is found down to 155.70 m, possibly to 168.40/168.30 m (Jaeger 1991). Conodonts indicate that the base of the Hemse Group may be as deep as 180 m (*P. gracilis, Pa. panderi?, O. bohemica* ssp. indet., etc.) but not below 190 m (*Pa. equicostatus, O. excavata*) and prove that this unit continues at least to 50 m (not to 40 m). Thus, this marl unit is somewhere between 105.7 and 150 m thick, probably between 130 and 150 m. Its thickness is probably similar along the western coast of Gotland considering the faunal and lithological similarities. Coeval strata on eastern Gotland mostly consist of argillaceous limestones.

2. Limestone (\approx 30 m in the Linde area) dominates in the middle unit, except on western Gotland where there is only marl and argillaceous limestones.

3. The upper marl unit, here included in the När Fm. (new name), is ≥ 65 m, see below.

Combining the known maximum of each unit in the same way as Hede (1960), the Hemse Group as now delimited is at least 200 m, possibly 250 m, in thickness. The difference from Hede's (1960) 100 m is mainly due to the addition of När core data. The dip of the basal Hemse, from the exposures NNE of Etelhem (c. 50 m above sea level) to the När core (\approx 14 km; ground level 1.39 m a.s.l.), is \approx 16 m/km. Assuming the same thickness along the coast as in these cores, and that strata coeval with the limestone unit are much thinner, the average 'dip along the coast' is c. 10 m/km (true NW–SE-dip is higher).

The När Formation

Hede (1921, p. 62, 1925, 1927) distinguished the upper Hemse marl (Hemse Marl, Southeastern Part in later literature) as a distinct unit. It is developed as interbedded marls and argillaceous limestones across western and central Gotland. Some coeval strata in the NE were described as the Millklint Limestone. These two units are here referred to a new formation, the När Fm. It includes three distinct conodont faunas. The Millklint and Botvide members are named, but the main part of the marl is informally referred to as the 'main part' pending studies of whether or not the change behind the faunal difference between its older and younger parts also caused enough lithological changes to distinguish two members.

The main part of the När Fm. and the Millklint Member

Lithologies. - The main part of the När Fm. is well delimited both lithologically and faunally. Rounded intraformational pebbles are found at some levels, and rare graptolites occur at many places, especially on western Gotland (Hede 1942). Hede (1927) mapped its base, using macrofossils, only on the geological map 'Hemse' (the youngest sheet with that boundary), but also identified its characteristic fauna on the Hoburgen sheet, from Nisse 1 and southwards (Hede 1921). Similarly, Martinsson (1967) recorded the Neobeyrichia lauensis-N. scissa brachiopod fauna on that sheet at Sigers and Källder in Havdhem parish. I have correlated Hede's boundary on the 'Hemse' map with the conodont faunal sequence and then used conodonts for identification elsewhere. In the northeastern part of the outcrops, the Millklint Limestone Member (Hede 1929) caps some hills; finds of Silurognathus maximus show that this crinoidal limestone represents only a low part of the När Fm.

The lowermost 65.18 m in the Burgsvik core (Burgsviksborrningen 1, Fig. 1) is coeval with the Hemse strata exposed between Nisse 1 and Bodudd (Hede 1919) on the western coast. The main part of the P. siluricus Zone is found at Nisse 1. Conodonts show that the När Fm. reaches still further northwards, at least to Mjauviken 2 and Hallbenarve 1 where the S. maximus fauna occurs. If the macrofaunas also permit separating these localities, and dip is the same along the coast, then 5 to c. 30 m is to be added; plus an unknown thickness of undrilled strata with the Nisse-Bodudd macrofauna. The total thickness on western Gotland may thus be 70 m or more. In the När core, the base of the När Fm. is between 40 m (with an older conodont fauna) and 30.15/30.10 m (with the fish Andreolepis hedei; Fredholm 1988). Lithology indicates that it may be at 30.15 or possibly at 35.55 m (based on data in an unpublished Geological Survey report by Szabo & Skoglund 1967). At both levels, the lithology changes abruptly from more calcareous to more argillaceous, like in the outcrops on western Gotland. The core started only a few metres below the top of the När Fm. Hence, the strata thin to the NE.

Conodonts. – A combination of two or more of four taxa is characteristic for the När Fm. – O. c. confluens, P. siluricus, Coryssognathus dubius, and Silurognathus maximus (the last one only in the lower part of the formation). Over 20 taxa have been

found in this formation (based on c. 100 collections aggregating many tens of thousands of specimens). O. c. confluens is the most frequent taxon in most collections. Panderodus serratus and Pa. aff. serratus are the most frequent taxa with coniform elements in the marl area and Pa. greenlandensis n. ssp. in the limestone area. A few scattered specimens in the most proximal marl area represent the latter, but *Pa. serratus* is widespread. *O. excavata* and *C.* dubius are frequent everywhere. Rare but regularly encountered are Polygnathoides siluricus (in all lithologies) and Pa. panderi (at least in the marl area). S. maximus is facies-independent but confined to a part of this zone, see above. Oulodus s. siluricus and Kockelella cf. sardoa seem to be similarly restricted but are exceedingly rare. Pa. gracilis is frequent at the southwesternmost localities but very rare or absent in the eastern marly area. Decoriconus sp., Pseudooneotodus beckmanni, Belodella sp., and B. mira seem to have a similar distribution and preference, but their elements are small and rare except in collections from the finest grained lithologies (obtained on a 63 µm screen) or fragile. Aldridgeodus minimus is similarly small and fragile. It has been found in both marl and limestone areas, although its rarity prevents identification of environmental preferences. Oul. excavatus is similarly rare except in the limestone area. The När Fm. correlates with the N. kozlowskii graptolite interval.

Localities. – The part (member?) with *S. maximus* has been identified at: Mjauviken 2 in G89-776LJ, Hallbenarve 1 in G89-773LJ, Hulte 3 in G86-112LJ, Kodings 2 in G86-110LJ, Västlaus 1 in G82-31LJ, Mattsarve 1 in G85-20LJ, Gogs 1 in e.g. G67-54LJ, Snausarve 1 in G93-940LJ, Tuten 1 in G81-51LJ, and Ljugarn 1 in G79-50LJ from the fissure filling mapped by Watkins (1975). In the coeval Millklint Member, *S. maximus* occurs at Millklint 1 at -0.30/-0.15 m in G96-4LJ and at +0.25/0.35 m in G96-3LJ, at Gannes 3 at -0.2 m in G84-88LJ, at $-0.12/\pm0.00$ m in G84-316DF, at +1.16/1.22 m in G85-13LJ, at +1.70/1.80 m in G84-14LJ, and at +3.60/3.80 m in G84-2LJ, at Sysne 1 in G81-44LJ, Kuppen 1 in G81-44LJ, and Kuppen 3 in G91-16LJ.

The part without *S. maximus* but with *P. siluricus* and *C. dubius* has been identified at Klasård 1 in G71-150LJ, Vaktård 3 in G71-148LJ, Linviken 2 in G71-147LJ, Nisse 1 in G87-445LJ, (questionably Nisse 4 in G71-145LJ), Gläves 3 in G82-34DF, Gläves 1 in G75-30LJ, När 2 in G82-326DF, Gannor 3 in G71-125LJ, Fie 4 in B48BS, Fie 1 in G71-128LJ, and lowermost at Botvide 1. The similar collection G69-36LJ from the Millklint Member at Millklint 3 is too small to tell if the absence of *S. maximus* is significant.

C. dubius is the most frequent of the characteristic species and the sole indicator of the När Fm. in small collections from Snippsnyte 1 in G86-114LJ, Stora Kruse 1 in G82-29LJ, Alva 1 in G86-113LJ, Hemse 1 in R97-BS, and Lau Gård 1 in G84-10LJ. In the Millklint Member such small collections are available from Millklintdalen 2 in G77-44LJ, Herrgårdsklint 1 in G71-80LJ, Östergarnsholm1 in G78-19CB, and Östergarnsholm 2 in G78-20CB. However, rare *C. dubius* appeared slightly lower down, at Tälleby 1 in G91-86LJ; Hede (1921) used the macrofauna there as an example of the fauna in the northwestern (lower) Hemse marl.

P. siluricus without other characteristic species occurs in the limestones at Tjängdarve 1 in G82-30LJ, Lyrungs 1 in G91-88LJ, Lyrungs 2 in G79-216LJ, and in outliers (mostly hill tops) NW of the continuous area at Broträskkröken 1 in G-LJ, Garde 1 in G92-440LJ, and Rudvier 1 and 87-420LJ from the lowest exposed (c. -1.3/-0.9 m, crinoid lst below the clay shale) and in

G84-53LJ from +1.45/1.65 m. These limestones seem to predate *S. maximus*, although their stratigraphic position requires further study.

G89-771LJ from Snauvalds 2 yielded *P. siluricus, K. ortus* group and *O. cf. posthamata* (most elements; together with and clearly distinct from normal *O. excavata*; hence a distinct species). No similar fauna has as yet been found on the area of the Hemse geological map; hence, it is uncertain if this fauna occurs in the strata included by Hede (1921) in his 'younger part of the Hemse Group', now the När Fm.

The Botvide Member, the Upper P. siluricus Subzone

Lithologies. - The upper part of the När Fm. has been referred to as the Davia flags (Munthe 1910) because of frequent coquinas of the brachiopod Davia in some beds, and the higher weathering resistance than subjacent strata, resulting from the high dolomite content (Munthe 1902, p. 272-273). A distinct lithologic boundary occurs 0.49 m below the top of the Hemse at Nyan 2. Similarly, when the Botvide 1 section had been rejuvenated in 1993 (the road was widened), the uppermost part of the Hemse appeared yellowish-brownish grey and dirty, with older strata being bluish grey. The first conodont faunal changes predate that change (see below). Probably for such a reason, Laufeld (1974a) distinguished a slightly thicker unit, the Hemse Marl 'uppermost part', or 'Top Part' in some literature, here formally named the Botvide Member. Its lower boundary is coeval with the first faunal change. The member is c. 2.15 m thick at Botvide 1, the only locality where its base is identified. Several very rusty contact surfaces (weathered pyrite layers) occur in the Botvide Member, e.g. Nyan 2 at -0.38, -0.24, -0.09 and 0 m, and at Botvide 1 at -0.81 and locally at -0.76 m.

Typical *Dayia* flags are limited to the eastern marl area, but coeval strata at Bodudd 1, the southwesternmost exposure, are similar enough to be identified. There the member consists of more or less shaly calcareous mudstones and limestones, including at least one 0-15 mm thick *Dayia* coquina bed, somewhat above a distinct 26 mm bed of pale argillaceous dolostone (grains of dolomite are locally frequent on Gotland; some beds are dolomitic, but this may be the only dolostone).

The contact with the Eke Fm. is exposed and has been sampled in several sections (approximate distance from Bodudd 1 within brackets): Bodudd 1, Malms 1 (23 km), Kärne 3 (27 km), Burgen 4 (28 km), Gannor 1 and 2 (33 km), Hallsarve 1 (35 km), Botvide 1 (37 km) and Nyan 2 (38 km, but 4 km SE of Botvide). Exposures with only Botvide Member include Bodudd 3 in G71-151LJ, Hörte 1 in G82-329DF, När 2 in G82-328DF from +0.31/0.34 m, and Öndarve 1 in G83-5LJ. The first three contain *Pa. panderi*, which disappears between collections from -0.90/-0.87 and -0.6/-0.7 m at Botvide 1, and between -0.96/-0.93 and -0.81/-0.78 m at Nyan 2; hence these represent a lower part of the Botvide Member. Strata at Millklint 1 (13 km NE of Botvide) are older, see above.

Conodonts. – Stepwise extinctions characterize the Upper *P. siluricus* Subzone and c. 50% of the taxa do not continue into the succeeding Icriodontid Zone. Initially the conodont faunas remained essentially the same as in the main part of the *P. siluricus* Zone, although large collections reveal some differences. *Pa. gracilis*, which in older strata had a strong distal (SW) preference, occurs regularly even in the eastern marl area at Botvide 1 and Nyan 2. In spite of many 10 000's of specimens extracted

from this member, *P. siluricus* is represented in only four or five collections. Either it was present only extremely briefly, having an intermittent Lazarus range, or, if continuously present, its average frequency was in the 0.01–0.1‰ range.

Through the När Fm., the robust O. c. confluens is usually better represented than O. exavata. However, conodonts are rarer, small specimens dominant, and O. exavata more frequent than O. c. confluens in most collections from the interval between -0.21 and 0 m at Nyan 2 (Andrew Simpson first found this kind of fauna in Australia; hence I looked for it on Gotland). At Nyan 2 these strata are thin-bedded, dolomitic and hard (slabs up to 0.5×0.4×0.02–0.04 m are strong enough to be collected and transported). This "Lilliput fauna" is also found in the topmost Hemse at Hallsarve 1, Gannor 2, Burgen 4, and Kärne 3, Thus, slightly before the beginning of erosion (see below), environmental conditions changed to those that favoured O. excavata. What kind of change is yet unknown, but *O. excavata* is found on Gotland in even higher frequencies (between c. 90 and c. 98%) in both the Fröjel Fm. and the Mulde Tegelbruk Member; perhaps due to a slight freshening of the water (Jeppsson & Calner 2003). Further, the topmost decimetre(s) of the Hemse Group include coquinas of Shaleria aff. ornatella (see Bassett & Cocks 1974) at Gannor 1, Hallsarve 1, Nyan 2, Maldes, etc. (Munthe 1902). Neither coquinas of this type (Munthe 1902) nor the O. excavata fauna have been found at Botvide 1. At Malms 1, the O. exavata fauna was not found, the Shaleria frequency is unstudied, and the conglomerate is unusually well developed. At Bodudd 1 sampling was not detailed enough to find that conodont fauna.

The Eke Formation

Oncoids are widespread in the Eke and have sometimes been used as the only defining character of the formation. However, Hede (1919, 1921) drew the lower boundary between clay shale and unbedded marl, 1.57 m below the first oncoids in the Burgsvik core. Similarly, at Bodudd 1, there is c. 2.55 m (Sandström pers. comm.) of more or less unbedded dolomitic mudstones between the Botvide Member and the first oncolites. Conodonts identify these strata as lower Eke. These sequences are the two most distal ones. Härdarve 1 is another distal locality, in an area mapped as Burgsvik (Munthe 1921; probably before the quarry was opened). Silty claystones with and without oncolites are interbedded in the 4.5 m deep quarry, with oncolites as close as 1 m below ground level (Laufeld 1974b); conodonts also indicate Eke for the topmost strata (see below). This reclassification simplifies the geological map when, as would be expected from the direction of the dip, it is Eke instead of Burgsvik at Härdarve (≈ 0.7 km W of the upper Eke at Ronnings 1; see Fig. 1). Evidently, oncolitic facies began later, was interrupted now and then, and may have ended earlier more distally. Hence, discriminating characters other than being oncoidal are needed. Here I use the top of the typical Botvide Member as the lower boundary and provisionally the replacement of the characteristic upper Eke fauna (see below for the upper boundary). Cherns (1983) reported Eke at Millklint 1. However, the presence of S. maximus above the presumed boundary identifies the strata as the Millklint Member (see above). The Eke includes three distinct faunas. There seem to be enough lithological differences to identify the corresponding strata as members. Regarding thickness, see Burgsvik Fm., below.

The Lower Icriodontid Subzone, the lower Eke

Lithologies. - The basal contact of the Eke Fm. on eastern Gotland is a submarine discontinuity-surface with phosphorite and glauconite coatings (Spjeldnaes 1950). The basal beds are conglomeratic with rounded pebbles of Hemse Marl (Munthe 1902). The basal part (1.1 to several meters) consists of oncoidal crinoidal limestone at Malms 1, Kärne 3, Burgen 4, Gannor 1 and 2, Hallsarve 1, Botvide 1, and Nyan 2. Being farther offshore and slightly deeper, the sequence at Bodudd 1 would be expected to be more complete. The sequence agrees well with this; no conglomerate and no crinoid limestone were found. Features interpreted as palaeokarst affecting the lowermost Eke Fm. have been documented (Cherns 1982). The crinoidal limestone is overlain by marl (Härdarve 3, Härdarve 1, and Lau Backar 1). From the shore section Bodudd 1 to the Burgsvik core, the base of the Eke Fm. dips on average 8.37 m/km [63.50-8.25 m (Hede 1921, p. 63) /6.6 km; the disturbance marked on Fig. 1 may, however, have influenced this average]. The altitudes of Botvide 1 and Lau Backar 1 indicate a lower Eke thickness of ≥ 10 m.

Conodonts. – On Gotland, the first low-diversity conodont fauna is characterised by O. confluens, O. excavata and Pa. unicostatus. Ps. beckmanni and Decoriconus sp. are also found. C. dubius, Pa. gracilis and Pa. serratus occur at +0.10/0.13 m at Malms 1, i.e. close to the base of this interval. C. dubius is also found at Botvide 1, but the other two are not found elsewhere at this level. Some of these specimens may derive from Hemse Marl pebbles, although the surface of the Malms sample lacked visible pebbles (frequent in the sample below). Alternatively, the absence of Pa. serratus and C. dubius at Botvide and När may be due to winnowing – they are rather small, and these strata are less argillaceous than those at Malms.

P. serratus returned later. Collections from Lau Backar 1 include *O. confluens*, *O. excavata*, *Ps. beckmanni*, and *Pa. serratus*. These plus *Decoriconus* sp. were also found at Bodudd 1 in sample G93-928LJ from +0.28/0.35 m (small collection from 40 kg) and in an old collection from nearby. A larger collection (from 37 kg) from -0.05/0.00 m is similar, except that *O. excavata* dominates and that there is no *Panderodus*.

The Härdarve 1, 2 quarry is now water-filled, and sample G95-3LJ is from ground level, i.e. the top of the former section. Sample G95-4LJ from Härdarve 3 was taken 1.5–1.7 m above a distinctly harder bed (below the bottom of the pond, not accessible for sampling). Together, these samples (31 kg each) produced about 50 mostly juvenile and fragmentary conodonts. The fauna – *O. excavata* and *Pa. serratus* (at Härdarve 3) – is known neither from the Burgsvik nor from the upper Eke but is closest to those from the lower Eke.

The Middle Icriodontid Subzone, the middle Eke

Lithologies. – At Bodudd 1, more and less easily weathered strata are interbedded. The first oncolites may mark the boundary; they appear at +0.52 m above the upper auxiliary reference level, 0.15 m above sampled lower Eke (see above) and 0.15 m below sampled middle Eke.

Conodonts. – Pa. equicostatus reappeared (absent since late Homerian) and characterises this interval. It was found with *O. confluens, O. excavata*, and *Pa. serratus* at Sunnkyrke 2 on eastern Gotland and, with the first two of these together with *Ps. beckmanni, Decoriconus* and rare *Belodella* sp. at Bodudd

1 in G93-930LJ from +0.65/0.70 m and in G93-929LJ from +1.16/1.20 m.

The Upper Icriodontid Subzone, the upper Eke

Lithologies. – Argillaceous limestones and marls of the upper Eke occur in many surface exposures, but none of these is a substantial section. If Hede's (1921) conclusion regarding the disappearance of *Dayia* is correct (see Burgsvik, below), the upper Eke in the Burgsvik core would include part or all of the 10.15 m between the last *Dayia* and 33.40 m (see below).

Conodonts. – The upper Eke fauna differs considerably from the preceding ones but closely resembles those of the 'middle' Upper Visby Fm. and the Bara Oolite Member (Jeppsson 1998; Jeppsson & Calner 2003). In all three faunas the lineage of *Pa. equicostatus* with slender elements is strikingly dominant (typically >90%). Other coniforms – *Decoriconus* and *Ps. beckmanni* – make up a large part of the rest of the upper Eke collections. *Oulodus* sp. is found in all three intervals; it is the most frequent species with ramiform elements in the upper Eke Fm. *O. cf. scanica, Dapsilodus obliquicostatus* (Ronnings 1), and *Icriodus* sp. (Ronnings 1 and, based only on a coniform, at Petsarve 14) are rare and/or intermittent.

Localities. – Bodudd 2 in G02-140LJ from the distinctly less easily eroded limestone layer the upper surface of which is the reference level, Kutård 1 in G03-381LJ, Olsvenne 5 in G02-141LJ, a loose block from Lingmyr, Ronnings 1 in G94-34LJ etc., Petsarve 2 in G77-34CB, Petsarve 3 in G92-438LJ, Petsarve 14 in G92-439LJ, Petsarve 15 in G77-33CB, Kullunde 2 in G71-17LJ, and Ronehamn 2 in G75-24LJ.

The Burgsvik Formation

Lithologies. – The Burgsvik Fm. consists of sandstone and intercalated sandy claystones, intercalated with or overlain by oolite towards the top (Hede 1921). In the Burgsvik core Hede (1919) found oolite as low as 7.18 m below the top of the formation. He (1921, p. 71) reported 47.22 m (from –49.60 to –2.38 m) of Burgsvik, drawing the lower boundary above the last oncolites. The youngest find of *Dayia navicula* was at 43.55 m (Hede 1919), in the Burgsvik. Later he described its range as up through the lower Eke but not higher (1921 p. 69; 1925, p. 25). However, Hurst (1975) reported two specimens from the Burgsvik at Hoburgen 2 (L. Gustavsson pers. comm.). Hence, the *Dayia* find in the Burgsvik core is not evidence for a higher boundary in that core. (The Burgsvik *Dayia* may need a restudy being intermediate in age to the Pridoli *D. n. bohemica* Bouček 1941, by Havliček and Štorch 1990 treated as a distinct species).

Conodonts. – Most collections from the Burgsvik Fm. are from the northeastern outcrops. A major abrupt conodont faunal change is evident above the Eke Fm. *Ozarkodina. wimani*, *O. snajdri*, *O. confluens*, *Oul. novoexcavatus*, and *Pa. equicostatus* are all well represented in the first Burgsvik fauna. *Ps. beckmanni* and *Decoriconus* are less frequent. *O. scanica*, icriodontid fragments (Burgen 9 in G91-31LJ from +1.05/1.20 m and in G91-32LJ from +2.75 m), and *Dapsilodus obliquicostatus* (Glasskär 1 in 82-15CB) are less widespread or rarer (only small, mostly old collections are available). *O. excavata* and other species of *Panderodus* are notably absent even in larger collections but, most collections are far too small for absences to be considered significant. *O. excavata* returned later and occurs even in some small collections from the topmost Burgsvik.

Localities. - O. excavata is absent in collections from: Uddvide 2 in G67-44LJ, Burgen 7 in G94-29LJ, Kapellet 1 in G83-16LJ, Närshamn 1 in G83-11LJ, Närshamn 2 in G83-12LJ, Närshamn 3 in G83-13, G83-14LJ, 4 G83-15LJ, Glasskär 1 in G72-18LJ, Glasskär 2 in G72-19LJ, and Glasskär 3 in G82-18CB. (The collection G83-21LJ, which should be from -0.50/-0.40 m at Burgen 7 contains Pa. serratus, A. minimus and Belodella sp. About the same level was recollected, G94-29LJ, yielding only the normal Burgsvik fauna, indicating a probable error in the former collection.) Some of these collections are too small to tell whether the absence of O. excavata is significant or not. Loose material from Hägvide 3 (G82-321DF, Fredholm 1989) was previously referred to Eke because of its position (Fig. 1), but additional data about Eke and younger fish faunas redate it as Burgsvik (Eva Nilsson pers. comm. 2005); the conodonts fit with this.

O. excavata or *O.* cf. *excavata* occurs at Hoburgen 2 in G67-47LJ, G67-48LJ and G69-40LJ, Kättelviken 1 in G02-134 LJ, Sibbenarve 1 in G82-33LJ, Burgen 9 in G94-30LJ (0–0.2 m below the quarry floor) and G94-32LJ (from the topmost layer, 2.75 m above the floor), and Kroken 2 in G72-21LJ. These localities seem to represent the upper(most?) Burgsvik.

The Hamra Formation

Lithologies. – The Hamra Fm. consists of more or less oncolitic strata followed by marls and marly limestones in more distal areas (in the S) and, more proximally, reefs and associated sediments (Munthe 1921). The lower boundary of the succeeding Sundre Fm. was drawn at the appearance of red crinoid debris. However, red-colouring is due to secondary weathering (see Jeppsson & Laufeld 1987 for a discussion and references). The depth of weathering would hence be expected to vary, and a better defined boundary is probably needed.

The base of the Hamra Fm. is c. 5 m above sea level near Grumpvik. 2.4 km to the ESE, 500 m NNE Vamlingbo church, the land surface is 15 m a.s.l. and the base of the Hamra c. 40 m below it (Munthe 1921). If 'c. 40 m' = 40 ± 5 m, the average dip is between 10.4 and 14.6 m/km. If the dip is constant, the base would then be between 88 and 124 m below sea level at Salmundsudd on the eastern coast, 8.5 km from Grumpvik. The thickness of the Hamra+Sundre, therefore, seems thicker than the frequently quoted 40+10 m, perhaps twice as thick.

Some localities. – Strands 1, Bankvät 1, and Skradarve 1 in G02-139LJ.

Conodonts. – In addition to the fauna listed above from the Burgsvik Fm., collections from the Hamra Fm. include several other surviving taxa, e.g. *Pa. unicostatus*. New lineages appear higher up, e.g., *Oul.* n. sp. aff. *Oul. elegans* and *Ctenognathodus confluens*. As yet there is no biostratigraphic subdivision of the Hamra-Sundre interval, but conodont studies in progress indicate that Hamra a, b, c, and undivided Sundre do not adequately reflect age relationships.

Acknowledgements. – Discussions with Richard J. Aldridge, Mikael Calner, Lena Gustavsson, Karin Högdahl, Maurits Lindström, Anders Martinsson, Ruth Mawson, Eva Nilsson, Andrew J. Simpson, and John A. Talent influenced the content. Hans Peter Schönlaub and Otto Walliser kindly permitted studies of their collections and the references herein to the conclusions thereof. Ann-Sofi Jeppsson typed several of the drafts and critically read several versions. Jonas Brane, Scanphoto, photographed the specimen in Fig. 3. Rikard Anehus, Lena and Åsa Erlfeldt assisted with parts of the fieldwork, and Git Klintvik Ahlberg and Rikard processed and picked many of the condont collections. Claes Bergman (CB) and

Doris Fredholm gave access to conodonts from some quoted collections (DF and b48BS, collected by Björn Sundquist). Richard J. Aldridge and Peep Männik as referees provided lots of useful comments and so did Mikael Calner and Mats Eriksson. The Swedish Research Council and its predecessor, the Swedish Natural Science Research Council, funded much of my field and laboratory work, especially conodont extraction.

References

- Bassett, M.G. & Cocks, L.R.M., 1974: A review of Silurian brachiopods from Gotland. Fossils and Strata 5, 56 pp.
- Bouček, B., 1941: Geologické vyletvdo okolí prazškého, Melantrich 1–201
- Cherns, L., 1982: Paleokarst, tidal erosion surfaces and stromatolites in the Silurian Eke Formation of Gotland, Sweden, Sedimentology 29, 819-833.
- Cherns, L., 1983: The Hemse-Eke boundary. Facies relationships in the Ludlow
- Series of Gotland, Sweden. Sveriges Geologiska Undersökning C800, 1–45. Eriksson, M.E., Bergman, C.F. & Jeppsson, L., 2004: Silurian scolecodonts. *Review of Palaeobotany and Palynology 131*, 269–300.
 Fåhraeus L., 1969: Conodont zones in the Ludlovian of Gotland and a correlation
- with Greath Britain. Sveriges Geologiska Undersökning C639, 33 pp
- Fredholm, D., 1988: Vertebrate biostratigraphy of the Ludlovian Hemse Beds of Gotland, Sweden. Geologiska Föreningens i Stockholm Förhandlingar 110, 237-253
- Fredholm, D., 1989: Silurian vertebrates of Gotland. Lund Publications in Geology 76, 47 pp
- Havlíček, V. & Štorch, P., 1990. Silurian brachiopods and benthic communities in the Prague Basin (Czechoslovakia). Rozpravy Ústrědního Ústavu Geologického 48, 1–125.
- Hede, J.E., 1919: Djupborrningen vid Burgsvik på Gotland 1915. Paleontolo-
- gisk-stratigrafiska resultat. Sveriges Geologiska Undersökning C298, 1-59. Hede, J.E., 1921: Gotlands Silurstratigrafi. Sveriges Geologiska Undersökning
- C305, 100 pp. Hede, J.E., 1925: Berggrunden (Silursystemet). In H. Munthe, J.E. Hede & L von Post: Beskrivning till kartbladet Ronehamn, 14-51. Sveriges Geologiska Undersökning Aa156.
- Hede, J.E., 1927: Berggrunden (Silursystemet). In H. Munthe, J.E. Hede & L. von Post: Beskrivning till kartbladet Hemse, 15-56. Sveriges Geologiska Undersökning Aa164.
- Hede, J.E., 1929: Berggrunden (Silursystemet). In H. Munthe, J.E. Hede & G. Lundqvist: Beskrivning till kartbladet Katthammarsvik, 14-57. Sveriges Geologiska Undersökning Aa170.
- Hede, J.E., 1942: On the correlation of the Silurian of Gotland. In Lunds Geo-logiska Fältklubb, 1892-1942, 205–229. [Also in: Meddelanden från Lunds Geologisk-Mineralogiska Institution 101].
- Hede, J.E., 1960: The Silurian of Gotland. In G. Regnéll & J.E. Hede: The Lower Palaeozoic of Scania. The Silurian of Gotland. International Geological Congress XXI. Session Norden. Guidebook Sweden d. Stockholm. 89 pp. [Also as Publications of the Institutes of Mineralogy, Palaeontology and Quaternary Geology of the University of Lund 91].
- Hurst, J.M., 1975: Some observations on brachiopods and the level-bottom community ecology of Gotland. Geologiska Föreningens i Stockholm Förhandlin-gar 97, 250–264.
- Jaeger, H., 1991: New standard graptolite zonal sequence after the "big crisis" at the Wenlockian/Ludlovian boundary (Silurian). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 182, 303-354.
- Jeppsson, L., 1975: Aspects of Late Silurian conodonts. Fossils and Strata 6, 79 pp.
- Jeppsson, L., 1983: Silurian conodont faunas from Gotland. In Taxonomy, ecology and identity of conodonts. Proceedings of the ECOS III Symposium Lund 1982. Fossils and Strata 15, 121–144. [Also in Lund Publications in Geology 181.
- Jeppsson, L., 1990: An oceanic model for lithological and faunal changes tested on the Silurian record. Journal of the Geological Society, London 147, 663-674.
- Jeppsson, L., 1993: Silurian events: the theory and the conodonts. Proceedings of the Estonian Academy of Sciences 42, 23–27.
- Jeppsson, L., 1997a: The anatomy of the mid-Early Silurian Ireviken Event. In C. Brett & G.C. Baird (eds.): Paleontological Events: Stratigraphic, Ecological, and Evolutionary Implications, 451-492. Columbia University Press, New York.
- Jeppsson, L., 1997b: A new latest Telychian, Sheinwoodian and Early Homerian (Early Silurian) Standard Conodont Zonation. Transaction of the Royal Society of Edinburgh Earth Sciences 88, 91-114.
- Jeppsson, L., 1998: Silurian oceanic events. Summary of general characteristics. In E. Landing & M.E. Johnson (eds.): Silurian cycles: Linkages of dynamic stratigraphy with atmospheric, oceanic and tectonic changes, 239-257. New York State Museum Bulletin 491.
- Jeppsson, L., 2005: Biases in the recovery and interpretation of micropalaeontological data. Special Papers in Palaeontology 73, 57-71.

- Jeppsson, L. & Aldridge, R.J., 2000: Ludlow (late Silurian) oceanic episodes and events. Journal of the Geological Society, London 157, 1137-1148.
- Jeppsson, L. & Anehus, R., 1995: A buffered formic acid technique for conodont extraction. Journal of Palaeontology 69, 790-794.
- Jeppsson, L. & Anehus, R., 1999: A new technique to separate conodont elements from heavier minerals. Alcheringia 23, 57-62
- Jeppsson, L. & Calner, M., 2003 (for 2002): The Silurian Mulde Event and a scenario for secundo-secundo events. Transaction of the Royal Society of Edinburgh Earth Sciences 93, 135-154.
- Jeppsson, L. & Laufeld, S., 1987: The Late Silurian Öved-Ramsåsa Group in Skåne, southern Sweden. Sveriges Geologiska Undersökning Ca 58, 1-45. [Also as Lund Publications in Geology 55]
- Jeppsson, L. & Männik, P., 1993: High-resolution correlations between Gotland
- and Estonia near the base of the Wenlock. *Terra Nova 5*, 348–358.
 Jeppsson, L., Aldridge, R.J. & Dorning, K.J., 1995: Wenlock (Silurian) oce-anic episodes and events. *Journal of the Geological Society, London* 152, 487-498.
- Jeppsson L., Anehus, R. & Fredholm, D., 1999: The optimal acetate buffered acetic acid technique for extracting phosphatic fossils. Journal of Paleontology 73, 957-965.
- Jeppsson, L., Viira, V. & Männik, P., 1994: Silurian conodont-based correlations between Gotland (Sweden) and Saaremaa (Estonia). Geological Magazine 131 201-218
- Klapper, G. & Murphy, M.A., 1975: Silurian-Lower Devonian conodont se-quence in the Roberts Mountains Formation of central Nevada. University of California Publications in Geological Sciences 111, 1-87. Kříž, J., Jaeger, H., Paris, F. & Schönlaub, H.P., 1986: Přídolí – the fourth subdi-
- vision of the Silurian. Jahrbuch geologische Bundesanstalt 129, 291-360.
- Kříž, J. & Schönlaub, H.P., 1980: Stop 1. Daleje Valley, Mušlovka Quarry section. In H.P. Schönlaub (ed.): Second European Conodont Symposium-ÉCOS II. Guide book - Abstracts, 153-157. Abhandlungen Geologische Bundesanstalt 35.
- Laufeld, S., 1974a: Silurian Chitinozoa from Gotland. Fossils and Strata 5, 1 - 130
- Laufeld, S., 1974b: Reference localities for palaeontology and geology in the Silurian of Gotland. Sveriges Geologiska Undersökning C705, 1-130
- Martinsson, A., 1962: Ostracodes of the family Beyrichiidae from the Silurian of Gotland. Publications of the Palaeontological Institute, University of Uppsala 41, 369 pp. Uppsala. [Also as Bulletins of the Geological Institute, University of Uppsala 41]
- Martinsson, A., 1967: The succession and correlation of ostracode faunas in the Silurian of Gotland. Geologiska Föreningens i Stockholm Förhandlingar 89, 350-386
- Munthe, H., 1902: Stratigrafiska studier öfver Gotlands silurlager. Geologiska Föreningens i Stockholm Förhandlingar 24, 272–273.
- Munthe, H., 1910: On the sequence of strata within southern Gotland. Geologiska Föreningens i Stockholm Förhandlingar 32, 1397–1453.
- Munthe, H., 1921: Beskrivning till kartbladet Burgsvik jämte Hoburgen och Yt-terholmen. Sveriges Geologiska Undersökning Aa152. 172 pp.
- Salzman, M.R., 2001: Silurian 813C stratigraphy: A view from North America. Geology 29, 671-674.
- Spjeldnaes, N., 1950: On some vertebrate fossils from Gotland with some comments on the stratigraphy. Arkiv för Mineralogi och Geologi 1 (8), 211–218.
- Sundblad, K., Gyllencreutz, R. & Flodén, T., 1998: The Precambrian crust beneath the Baltic Sea. In Eurobridge-98. Geophysical Journal, Kyiv [Kiew] 1998, 121–124.
- Talent, J.A., Mawson, R., Andrew, A.S., Hamilton, P.J. & Whitford, D.J., 1993: Middle Palaeozoic extinction events: faunal and isotopic data. Palaeogeography, Palaeoclimatology, Palaeocciogy 104, 139–152. Urbanek, A., 1997: Late Ludfordian and early Prídolí monograptids from the
- Polish Lowland. In A. Urbanek & L. Teller (eds.): Silurian graptolite faunas in the East European Platform: stratigraphy and evolution. Palaeontologica Polonica 56, 23–57
- Uyeno, T.T., 1981 (1980): Stratigraphy and conodonts of Upper Silurian and Lower Devonian rocks in the environs of the Boothia Uplift, Canadian Arctic Archipelago. Part II, Systematic study of conodonts. Geological Survey of Canada Bulletin 292, 39–75.
- Viira, V., 1983: Spatognatodus (konodonti) verznego Silur Estonii [Upper Silurian Spathognathodus (conodonts) from Estonia]. In E. Klaamann (ed.): Paleontology of early Paleozoic of the East Baltic and Podolia, 41-71. Academy of Sciences of the Estonian Institute of Geology [in Russian]
- Viira, V. & Aldridge, R.J., 1998: Upper Wenlock to Lower Přídolí (Silurian) conodont biostratigraphy of Saaremaa, Estonia, and a correlation with Britain. Journal of Micropalaeontology 17, 33–50.
- Walliser, O.H., 1964: Conodonten des Silurs. Abhandlungen des Hessischen Landesamtes für Bodenforschung zu Wiesbaden 41, 106 pp., 4 tab., 32 pls.
- Watkins, R., 1975: Silurian brachiopods in a stromatoporoid bioherm. Lethaia 8, 53-61.

Appendix, Taxonomy

Silurognathus maximus Jeppsson, herein

Fig. 3

Spathognathodus n. sp. A – Fåhraeus 1969, pl. 1:7–8. Gen. et sp. indet. – Jeppsson 1983, p. 126, fig. 1G–J.

Derivation of name. – From Silurian, the name of the period, *gnathus*, jaw, and *maximus* alluding to this species having the largest sp (Pa) element of any Ludlow conodonts I know of.

Holotype. - LO 9594T (Fig. 3) from Mattsarve 1, in G85-20LJ.

Material. – Over 50 elements and fragments including the base of the cusp or the basal cavity tip, and many other fragments (see Jeppsson 1983 & Fåhraeus 1969 for further illustrations).

Diagnosis. – Basal body firmly fused to the rest of the element; distinctive, often variable denticulation.

Description. – Denticles relatively low, deeply seated with rounded cross sections. Basal body usually so firmly attached that even fragments retain it. The sp (Pa) element is the most distinct. Its two processes are closely similar and separating them is difficult. Distally they often curve markedly downwards. Basal cavity lips extended strongly laterally. Few specimens found are complete enough to tell the total length; the nearly complete holotype is slightly over 3.6 mm in length. The oz (Pb) element (Jeppsson 1983, fig. 1G) has narrow ledges. No ne (M) element has yet been identified. The posterior process of the hi (Sc) element (Jeppsson 1983, fig. 1H) curves strongly inwards and, from the 4th denticle, strongly outwards. The anterior-lateral process is directed nearly obliquely inwards. The pl (Sb) and tr (Sa) elements have the general shape shown in fig 11 of Jeppsson (1983), with the pl being asymmetrical.

Known range. – *S. maximus* had a very short known range; on Gotland it is limited to a middle part of the *P. siluricus* range.

Discussion. – The robust elements were constructed for heavyduty work, but the forces on them often exceeded their strength. Thus their shape varies markedly due to breakage and repair of different denticles and groups of denticles. A large part of the strength relied on the organic matter in the basal body; now when that is degraded the elements are brittle, and many finds consist of minor pieces of a process – easily identified by their construction (see Jeppsson 1983, fig 1I) and by being from a very large element.

The orientation and curvature of the processes of the S elements resemble those of their homologous in *Kockelella*. and in *Oulodus*. Many *Kockelella* specimens have a characteristic

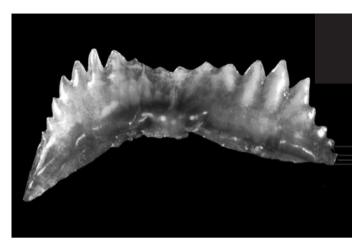


Fig. 3. Silurognathus maximus. Holotype, LO 9594T. Lateral view of the slightly over 3.6 mm long sp (Pa) element from Mattsarve 1; the very tip of the 'right' end is lost.

pattern of small spots and short streaks of white matter below the denticles, especially shown in the sp elements. One sp element of *S. maximus* shows a similar spottiness between the denticles. *Kockelella* may be the closest relative, although *S. maximus* is distinct from all Wenlock and Ludlow *Kockelella* species, and the last common ancestor must have been at least far back in the Llandovery. The large variation in the denticulation distinguishes *S. maximus* and so does the robustness. There is no similar taxon in older strata on Gotland, and *S. maximus* likely evolved somewhere else and immigrated to the Baltic Basin when conditions became favourable for such a large taxon.

S. maximus is coeval with a part of the range of the ostracode *Neobeyrichia lauensis*, 'the largest beyrichiid described' (Martinsson 1962); its females reached a hinge length of 4.05 mm and a sulcal height of 2.65 mm. *N. lauensis* survived longer; however, the co-occurrence may indicate that conditions were generally favourable for gigantism or that there were a more direct dependence, e.g. did some conodonts prey on beyrichiids? If so, and if *S. maximus* specialised on large beyrichiids, then the frequent damage to its elements and quick disappearance of the species could indicate that the carapace strength of *N. lauensis* increased faster than the conodont elements could evolve.