An updated stratigraphic and environmental framework for the distribution of Silurian vertebrates on Gotland

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Abstract. In this work, previously published occurrences of vertebrates from the latest Llandovery to end-Ludlow successions of Gotland, Sweden, are gathered and summarized in an updated stratigraphic framework, which also incorporates facies differences of sedimentary units. Even though the taxonomy of vertebrates from Gotland is in need of revision, their occurrences are here reported on a group level in order to give preliminary indications of where the focus of continued sampling should lie. Indeed, there are parts of Gotland that are poorly represented by the samples at hand and others that have been extensively sampled but still have not yielded any vertebrates. Preliminary investigations of new samples indicate that the lack of vertebrates in older sediments of Gotland may be because of sampling bias, while the reasons for a complete absence of vertebrates in other parts remain unknown. Our results also emphasize a sudden appearance of acanthodians on Gotland in the early Ludfordian. To investigate these preliminary results, complementary sampling and more confined facies-categorization will be needed. Combined with a higher taxonomical resolution, this will also help us understand how the vertebrate faunas were affected by the events coupled with extinctions that have been identified on Gotland and on a global scale. One of these events has been shown to affect the Gotland vertebrates before. Our results indicate that this may be true for several of the events. When an increased understanding of the vertebrate faunas of Gotland has been established, the goal is to use up-to-date correlations to compare Gotland with other parts of the Baltic Basin to render a better picture of early vertebrate evolution during the Silurian.

Key words: vertebrate distribution, stratigraphy, facies, Silurian events, Gotland, Sweden.

INTRODUCTION

Gotland, Sweden, has relatively complete and accessible sequences of Silurian sedimentary rocks (Fig. 1), from latest Llandovery to latest Ludlow, and a documented record of vertebrates throughout most of it (Fredholm 1988a, 1988b, 1989, 1990). Gotland is therefore ideal for increasing our understanding of basic patterns of vertebrate diversity in the Silurian, including temporal, geographical and environmental constraints. The first vertebrate remains from Gotland were reported and described during the second half of the 19th century (von Volborth 1861; Rohon 1893; Lindström 1895) and have subsequently been reported by numerous authors until the present time (Spjeldnaes 1950; Martinsson 1966, 1967; Gross 1968a, 1968b; Janvier 1971, 1978; Ørvig 1979; Fredholm 1988a, 1988b, 1989, 1990; Märss 1992, 1996, 2001; Blom et al. 2002; Eriksson et al. 2009). Although some of the taxonomy is out of date and needs revision, the studies of microvertebrate remains by Fredholm (1988a, 1988b, 1989, 1990) are still the best summary and source of knowledge on vertebrates from Gotland. Much progress regarding Gotland geology and stratigraphy has been made in recent years, giving implications for the timing of vertebrate occurrences. However, little has been done regarding the taxonomy of the Gotland vertebrates since Fredholm's works.

In the current study, all available published data have been gathered and placed in an updated stratigraphy that also incorporates facies variation of the units. This will form the basis for an extensive study of vertebrate biostratigraphy on Gotland, which will place emphasis on faunal variations coupled to differing environments.

STRATIGRAPHIC AND ENVIRONMENTAL FRAMEWORK

Since Fredholm's works, much progress has been made in unravelling the correlations and relationships of the different sedimentary units on Gotland (Fig. 1), which subsequently has implications for the temporal distribution of vertebrates on Gotland. The Högklint Formation has been restricted to a narrow strip along the northwestern coast of Gotland, not reaching further northeast than the

bay Kappelshamnsviken (Jeppsson 2005). The sediments previously referred to the Högklint Formation northeast of that bay are now referred to both the Tofta Formation at Svarven 1, Saxriv 1 and Bläse 1, as well as several localities on Fårö (see Jeppsson 2005), and the relatively newly described Hangvar Formation at Ar 1, Vialms 1, Källdurssivshagen 2 and 3 and Kalbjergaträsk 1 (Jeppsson 2008). This fills in the previously presumed gap between Högklint unit c and Slite unit c in this area (Jeppsson 2005, 2008). The coeval strata of the Hangvar Formation in the southwest were previously described as Slite units a and b (for details see Jeppsson 2008). Following this, the thelodont scales reported by Martinsson (1967) from Svarvarhuk (Svarven 1) belong in the younger Tofta Formation, rather than Högklint unit b. The siliciclastic Fröjel Formation, which is only found in the southwestern part of Gotland, has been shown to represent the topmost part of the Slite Group (Calner 1999). This unit is missing in northeastern parts of Gotland, except for on the island of Ytterholmen, because of the erosive contact with the overlying Bara Member of the Halla Formation (Calner 1999; Calner & Säll 1999; Calner et al. 2004a). Using conodont-based correlations between Gotland and Saaremaa (Estonia), Jeppsson et al. (1994) demonstrated that the former units a, b and c of the thick Hemse Group on Gotland include two separate sequences. These were subsequently divided into one older and one younger set of units a, b and c (Jeppsson et al. 1994).

The stratigraphic framework (Fig. 2) used in this study is the one presented by Jeppsson et al. (2006). It is largely based on conodont zonation resulting from several previous studies of conodont biostratigraphy and extensive sampling on Gotland. This forms a rigid backbone for stratigraphical subdivisions, which also makes lateral correlations of previously problematic units possible (Jeppsson et al. 2006). This also has implications for the stratigraphical succession, e.g. the previously separate units d and f of the Slite Group have been shown to mostly represent the same interval, informally referred to as the broskogs formation by Jeppsson et al. (2006). Furthermore, the reefal unit g of the upper Slite Group is composed of two different reef-generations separated by a marly interval, informally referred to as the eskelhem formation by Jeppsson et al. (2006).

Numerous works have also dealt with the facies distribution of the sediments of Gotland (e.g. Samtleben et al. 1996, 2000). The facies model in this stratigraphy is largely based on the one presented by Erlström et al. (2009). However, the facies categories presented here are somewhat simplified with four main facies that incorporate several subfacies. Distal and proximal shallow shelf sediments are grouped in the 'Shallow shelf' facies, which also incorporates the somewhat shallower sediments of the Botvide Member. The reef front, reef core, interreef, shoal and back-reef environments are represented by the 'Reef' facies, distal and proximal lagoonal sediments are grouped in the 'Lagoon' facies and 'Shoreface' represents the two main siliciclastic units of Gotland, namely the Gannarve Member of the Fröjel Formation and the lower part of the Burgsvik Formation, i.e. the Burgsvik Sandstone.

A number of events coupled with variations in lithology, stable isotopes and extinctions have also been identified on Gotland since Fredholm's works (indicated by grey boxes to the right in Fig. 2). Of these, the Ireviken, Mulde and Lau events have been recognized globally (e.g. Märss 1992; Jeppsson 1993, 1998; Märss et al. 1998; Jeppsson & Aldridge 2000; Calner et al. 2004b). The Lau Event was described on Gotland as a stepwise event with faunal turnovers that affected the conodonts and some other fossil groups (Jeppsson 1993; Jeppsson & Aldridge 2000). Prior to this, Märss (1992) identified faunal turnovers and extinction events among vertebrates in South Wales, Severnaya Zemlya, the Central Urals, Timan-Pechora Region, the East Baltic and on Gotland, which she named the *Andreolepis hedei* Event. This faunal reorganization among Gotland vertebrates was later confirmed and studied in more detail by Eriksson et al. (2009).

VERTEBRATE TAXONOMY OF GOTLAND

Since Fredholm (1988a, 1988b), little has been done in vertebrate taxonomy on Gotland. Nilsson (2005) revised some of the taxonomy of vertebrates from the uppermost Hemse Group to the lower Hamra Formation and Blom et al. (2002) revised the fragmentary remains of anaspids from Gotland. However, the acanthodians, thelodonts and osteostracans from the majority of the Gotland stratigraphy are still in need of taxonomic review and revision. Since this is outside the scope of this study, the occurrence of individual taxa is reported on a group level in order to give a preliminary overview of vertebrate distribution on Gotland in the context of an updated stratigraphic and environmental framework. In order to see where the occurrences and the diversity of vertebrate groups may be the result of sampling and study biases, the total number of samples that were targeted for vertebrates is displayed to the right in each facies column.

DISCUSSION

The column with the total diversity of Gotland vertebrates in Fig. 2 shows an apparent increase in diversity over time, with the upper parts being richer than the lower

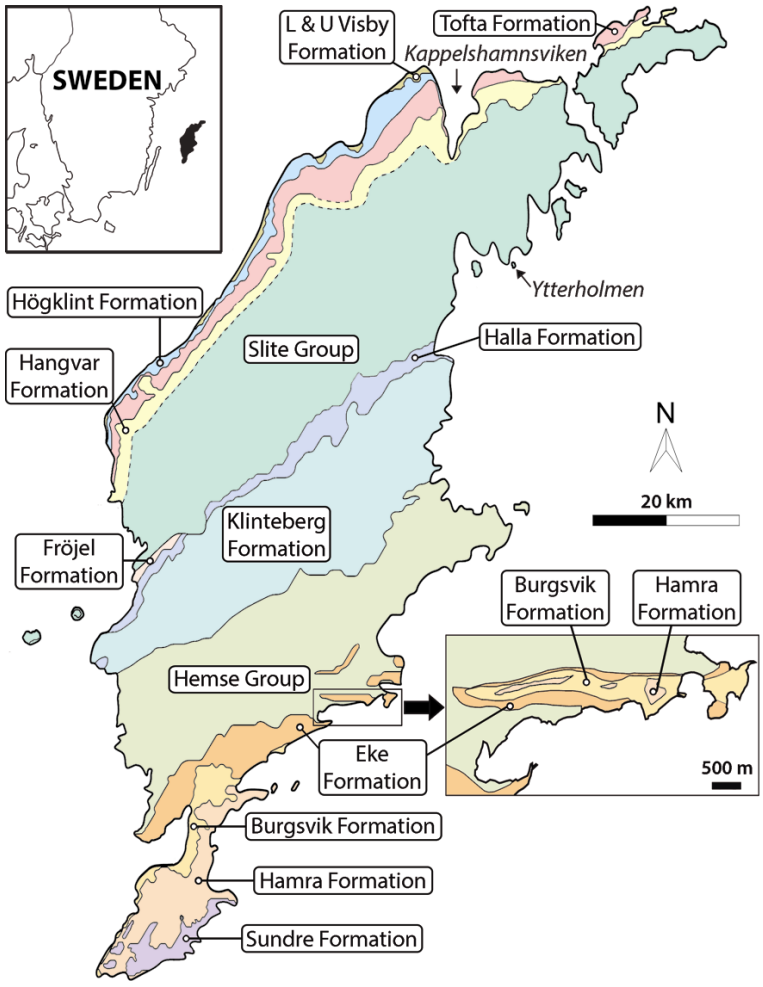

Fig. 1. Geological map of Gotland with the main stratigraphical units in colours; the colours correspond to the stratigraphical units in Fig. 2. Modified from Eriksson & Calner (2005).

parts. The lower units of the Gotland stratigraphy show low or no occurrence of vertebrates, but the poor sampling in some of these parts is evident in Fig. 2. Preliminary analyses of new samples show vertebrate occurrences in these lower units, indicating that the scarcity may be the result of sampling bias. Other parts of the section have been exceedingly sampled, but have still not produced any vertebrates.

The Gotland vertebrates have previously been demonstrated to be affected by the *A. hedei* Event (Märss 1992, 1998; Eriksson et al. 2009), identified as the Lau Event among other fossil groups on Gotland (Jeppsson 1993; Jeppsson & Aldridge 2000). The column with total diversity of vertebrates through the stratigraphy in Fig. 2 shows that the vertebrate fauna is also influenced by at least the Mulde and Linde events. The effect of the Valleviken Event is not as evident on vertebrate group level and more data are needed to investigate the effects of the Ansarve and Ireviken events. Another peculiarity highlighted by the data at hand is the sudden appearance of several acanthodian taxa in the När Formation on Gotland.

Future studies will include more detailed taxonomic divisions with the aim of seeing intra-group differences between environments, as well as understanding how the vertebrate faunas were affected by the events. The facies model will also be expanded upon by creating subdivisions within each assigned facies to potentially see more subtle differences and if some of the variations in vertebrate diversity can be the result of environmental differences. By complementary sampling in both temporal and lateral parts of Gotland that are poorly represented by the data presented here, we hope to fill in the gaps and investigate the patterns that we see. A thorough taxonomic and biostratigraphical revision of the Silurian vertebrates of Gotland will also work as a model from which inferences can be drawn about how vertebrate radiation patterns relate to facies boundaries and environmental history. With the aid of up-to-date correlations of the sediments on Gotland to other parts of the Baltic Basin, the patterns identified will be extrapolated and compared to other areas outside Gotland.

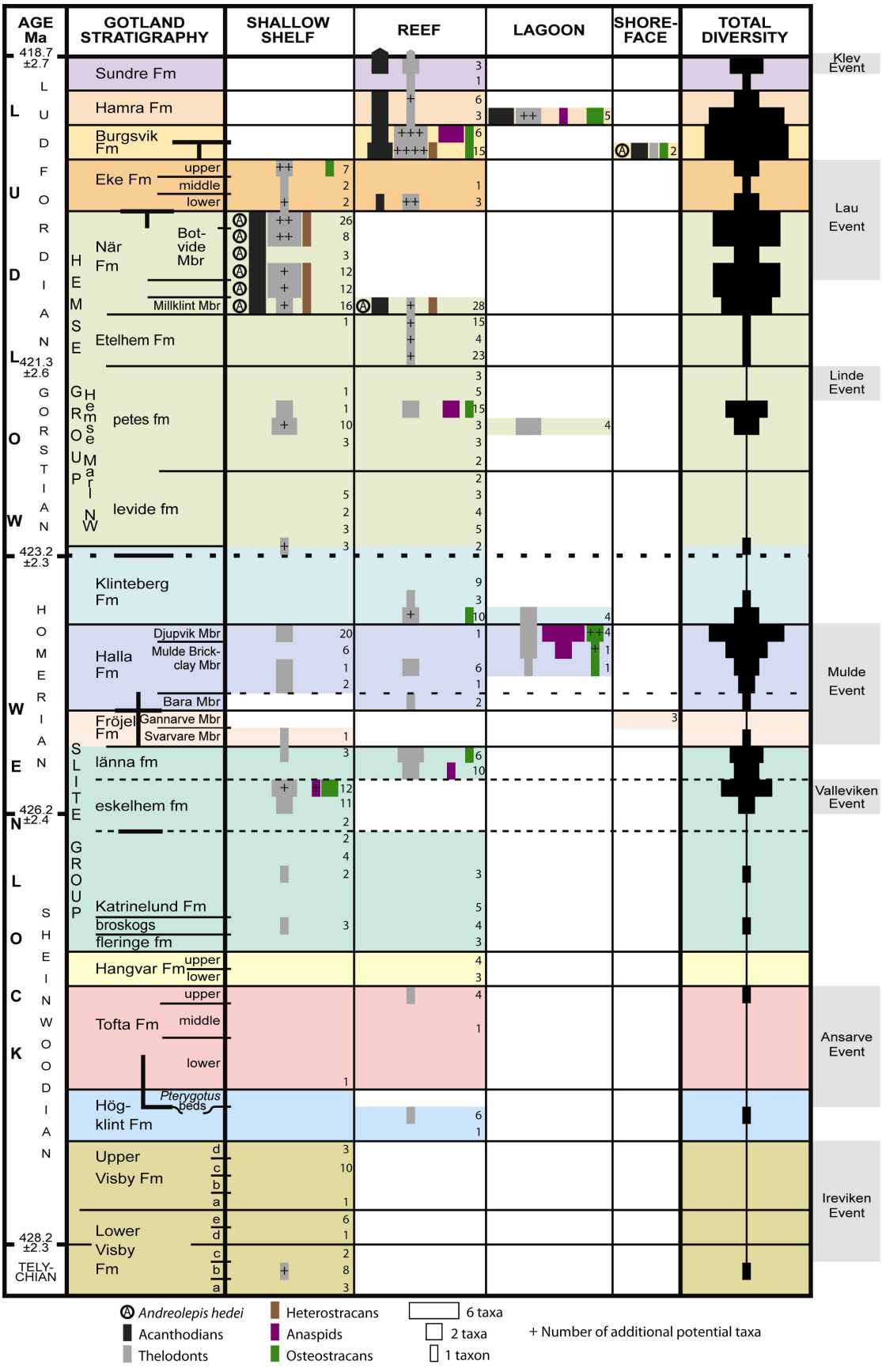
AGE Ma
GOTLAND STRATIGRAPHY
SHALLOW SHELF
REEF
LAGOON
SHORE-FACE
TOTAL DIVERSITY
Sundre Fm
Hamra Fm
Burgsvik Fm
Eke Fm
upper
middle
lower
När Fm
Bot-vide Mbr
Millklint Mbr
Etelhem Fm
Hemse Group
petes fm
levide fm
Klinteberg Fm
Halla Fm
Djupvik Mbr
Mulde Brick-clay Mbr
Bara Mbr
Fröjel Fm
Gannarve Mbr
Svarvare Mbr
Slite Group
länna fm
eskelhem fm
Katrinelund Fm
broskogs
fleringe fm
Hangvar Fm
Tofta Fm
Högklint Fm
Pterygotus beds
Upper Visby Fm
Lower Visby Fm
Klev Event
Lau Event
Linde Event
Mulde Event
Valleviken Event
Ansarve Event
Ireviken Event
Andreolepis hedei
Acanthodians
Thelodonts
Heterostracans
Anaspids
Osteostracans
6 taxa
2 taxa
1 taxon
+ Number of additional potential taxa

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Fig. 2. Vertebrate group occurrence and diversity through the Silurian of Gotland. Most taxa are represented by different colours and *Andreolepis hedei* is represented by the letter A (see key in Fig. 2). The thickness of the taxon symbol determines how many taxa of a particular group are present in the four different facies. The 'Total diversity' column shows the total, definite diversity of all vertebrate groups in Gotland through time, disregarding facies. The colours of the stratigraphic units correspond to those on the geological map of Gotland from Fig. 1. Thick horizontal and vertical lines in the column 'Gotland stratigraphy' mark unconformities. Numbers to the right in the columns show the total number of samples that were targeted for vertebrates. The thickness of the stratigraphical units does not reflect the true thickness of the formations, i.e. they are not in scale. Stratigraphy is based on Jeppsson et al. (2006), formations with lowercase letters have not been formally described.

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