

Untangling a Darriwilian (Middle Ordovician) palaeoecological event in Baltoscandia: conodont faunal changes across the ‘Täljsten’ interval

Johanna I. S. Mellgren and Mats E. Eriksson

Department of Earth and Ecosystem Sciences, Division of Geology, Lund University, Sölvegatan 12, SE-223 62 Lund, Sweden

Email: Johanna.Mellgren@geol.lu.se; Mats.Eriksson@geol.lu.se

ABSTRACT: Conodont faunal dynamics and high-resolution biostratigraphy in the lithologically and faunally anomalous ‘Täljsten’ succession, which spans the Darriwilian *Lenodus variabilis*–*Yangtzeplacognathus crassus* Zone boundary, were investigated in a 2.5 m-thick section on Mt Kinnekulle that includes an interval yielding fossil meteorites and extraterrestrial chromite. The previous interpretation that this interval reflects a regression is consistent with the occurrence and abundance patterns of some conodont taxa. The disappearance of e.g., *Periodon*, suggests that the regression began prior to the deposition of the grey ‘Täljsten’. The transition from red to grey limestone coincides with a conspicuous faunal re-arrangement. The lower half of the ‘Täljsten’ reflects a gradual shallowing favourable for some taxa, such as *Lenodus*, and the immigration of *Microzarkodina* cf. *ozarkodella* and *Histiodela holodentata*. In the middle of the ‘Täljsten’ interval, coinciding with the appearance of abundant cystoids, conditions became less hospitable for conodonts, resulting in a low diversity and low abundance fauna, which occurs to the top of the interval. The overlying red limestone, apparently deposited during a deepening event, marks a return to pre-‘Täljsten’ conditions with a re-organised fauna. The close correlation between the lithologic shifts and conodont faunal changes demonstrates the usefulness of conodonts as environmental indicators.



KEY WORDS: Biostratigraphy, Conodonts, faunal association, high resolution, palaeoecology, Sweden

When working on different aspects of the Middle Ordovician strata at Mount Kinnekulle in Västergötland, Sweden, one cannot help noticing the conspicuous grey band that extends through the impressive units of red orthoceratite limestone. For a long time, this interval has colloquially been known as the ‘Täljsten’ (Jaanusson 1982) (Fig. 1a, b). Adding to its peculiarity is a unique bed largely built up of cystoids, which is clearly distinguishable mid-way through the interval (Fig. 1c). Lithological correlations have shown that the ‘Täljsten’ can be traced to the Degerhamn quarry at southern Öland and to the Tartu drill core, southeastern Estonia. Furthermore, the ‘oolite beds’ of the Sillaoru and Obukhovo formations in Estonia and Russia supposedly seem to correspond to these conspicuous layers (Dronov *et al.* 2001). Another aspect that has drawn much attention to this particular sequence is the discovery of more than 50 fossil meteorites and a high concentration of extraterrestrial chromite grains in and around the ‘Täljsten’, which have confirmed that a major asteroid disruption event took place about 470 Ma (Schmitz *et al.* 2001, 2003, 2008; Schmitz & Häggström 2006).

Even though the limestone deposits of Kinnekulle have been studied since the mid 18th century (e.g. Kalm 1746; Linnæus 1747; Hisinger 1828; see modern references below), little work has been done to determine how this superficially anomalous interval differs from the red strata above and below in terms of faunal content. The primary aim of this present paper is to describe and discuss the conodont faunal dynamics through

the ‘Täljsten’ interval in order to add to the understanding of the environmental and depositional conditions in which these layers were formed. This will reflect how the palaeoecological event represented by the ‘Täljsten’ influenced this group of animals and, in addition, will facilitate fine-scale correlations with, and identification of, stratigraphically analogous strata elsewhere. The study is based on a comprehensive bed-by-bed sampling in the Hällekis quarry section on the NW slope of Mount Kinnekulle, where this interval is easily accessible. The focus has been on comparing the red and the grey limestone, as well as individual beds within the ‘Täljsten’, with emphasis on conodont element abundance, relative frequency changes of major genera, and species characteristics.

1. Geological setting and previous studies

The Ordovician strata in the Baltoscandian region were deposited in an epicontinental sea covering extensive parts of the palaeocontinent Baltica. The sedimentation rate was exceedingly low and the cool water conditions restricted carbonate production, resulting in average net accumulation rate estimated at 1–9 mm/1000 years for Sweden and the Baltic countries and 3–12 mm/1000 years in the Oslo area (Nielsen 2004). Separate composite facies belts (referred to as Confacies Belt (CB)) with specific sedimentological and palaeontological characteristics were recognised by Jaanusson (1976), who sub-divided the Baltoscandian deposits into the North

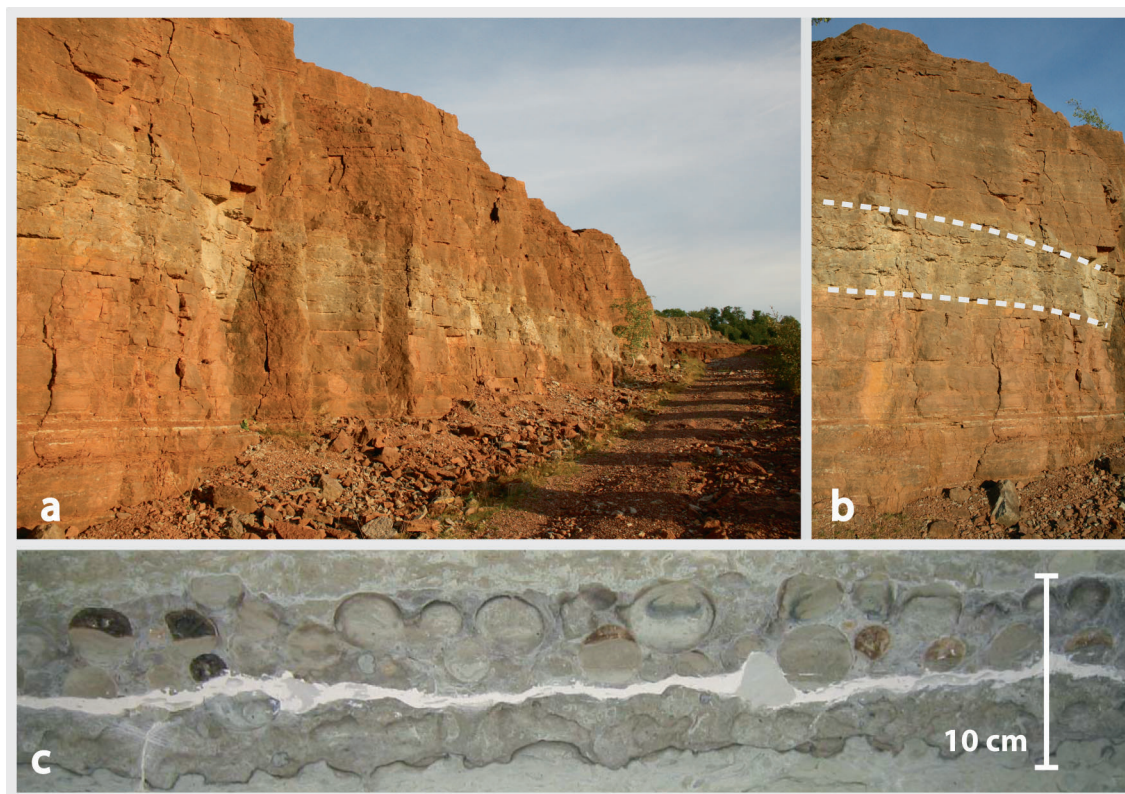


Figure 1 (a) Photograph of the 'Täljsten' interval and enclosing red strata of the Lanna and Hølen limestone, at the Hällekis quarry, Sweden. (b) Photograph indicating the lower and upper boundaries of the 1.3 m thick 'Täljsten'. (c) Close-up on a polished surface of the cystoid-rich Blymåkka bed from the adjacent Thorsberg quarry (note that the thin whitish layer in the middle of the slab is a seam of cement gluing the piece together).

Estonian CB, the Central Baltoscandian CB, and the Scanian CB (Fig. 2a). Generally, the North Estonian CB is considered to represent the shallowest water setting and the Scanian CB the deepest, thus making the Central Baltoscandian CB intermediate (Jaanusson 1976, 1995). However, regarding the water depth, the opinions have long been known to differ, especially for the limestones of the Central Baltoscandian CB. These, which are collectively referred to as 'orthoceratite limestone', were considered by Jaanusson (1976) and Nielsen (1992, 1995) to be of shallow-water origin and formed under the influence of sea-level oscillations and periods of non-deposition. On the other hand, Lindström (1963, 1971, 1979, 1984, 1988) and Chen & Lindström (1991) have argued for slow sedimentation rates at a considerable water depth, perhaps hundreds of metres.

The Middle Ordovician orthoceratite limestone on Kinnekulle was deposited at the margin between the Central Baltoscandian CB and the Scanian CB (Fig. 2a & b), and is typically bioclastic, red to variegated in colour and has abundant hardgrounds. The tripartite division of this sequence made by Jaanusson (1982) was based on colour differences, where the 1.3-m-thick grey 'Täljsten' separates the underlying pale-red Lanna limestone from the overlying red Hølen limestone (topostratigraphical units).

Generally, the base of the 'Täljsten' is considered to mark the base of the Hølen limestone. At Hällekis, the Lanna and Hølen limestones together comprise approximately 27 m of strata (Tinn & Meidla 2001). For regional and global correlations, see Figure 3.

The stratigraphy of the now classic section at the Hällekis quarry was first described briefly by Thorslund & Jaanusson (1960) in the guide for the International Geological Congress excursions in 1960. The conodont zonation in the uppermost Lanna through the Hølen limestone was outlined by Zhang

(1998a), who in this interval recognised, in stratigraphically ascending order, the upper *Lenodus antivariabilis* Zone, the *L. variabilis* Zone, the *Yangtzeplacognathus crassus* Zone, and the *Microzarkodina hagetiana* and *M. ozarkodella* Subzones of the *Eoplacognathus pseudoplanus* Zone (Fig. 3). Tinn & Meidla (2001) and Tinn *et al.* (2006) studied and described the ostracod fauna through the Lanna and Hølen limestones, with implications on palaeoecology, sea-level changes, and stratigraphy. Schmitz *et al.* (2003) and Schmitz & Häggström (2006) sampled the Arkeologen and Golvsten beds (see Fig. 4), as well as a 9-m interval below the Arkeologen bed, in search for extraterrestrial material. While the pre-Arkeologen samples yielded insignificant amounts, high concentrations of extraterrestrial chromite grains were found in the other beds, with especially high values in the Arkeologen bed (see Schmitz *et al.* 2003, table 1; Schmitz & Häggström 2006, table 1; Schmitz *et al.* 2008).

2. Materials and methods

When referring to the separate beds of the investigated interval (Figs 4, 5), the terminology used follows that of Schmitz *et al.* (2001), that is, traditional quarry names that refer to individual beds with specific lithological characteristics. The 'Täljsten' consists of eight such beds, including those of transitional character. In ascending order, these are the Golvsten, Botten, Gråkartan, Blymåkka, Fjällbotten, Likhall, Flora and Mumma beds. Below the 'Täljsten' is the Arkeologen bed and above it lies the Rödkartan bed (Figs 4, 5).

Twenty-six bed-by-bed samples, together spanning an interval from the lowermost Arkeologen bed to the top of the Rödkartan bed were collected for the present study. The sampled interval was selected to include the entire grey

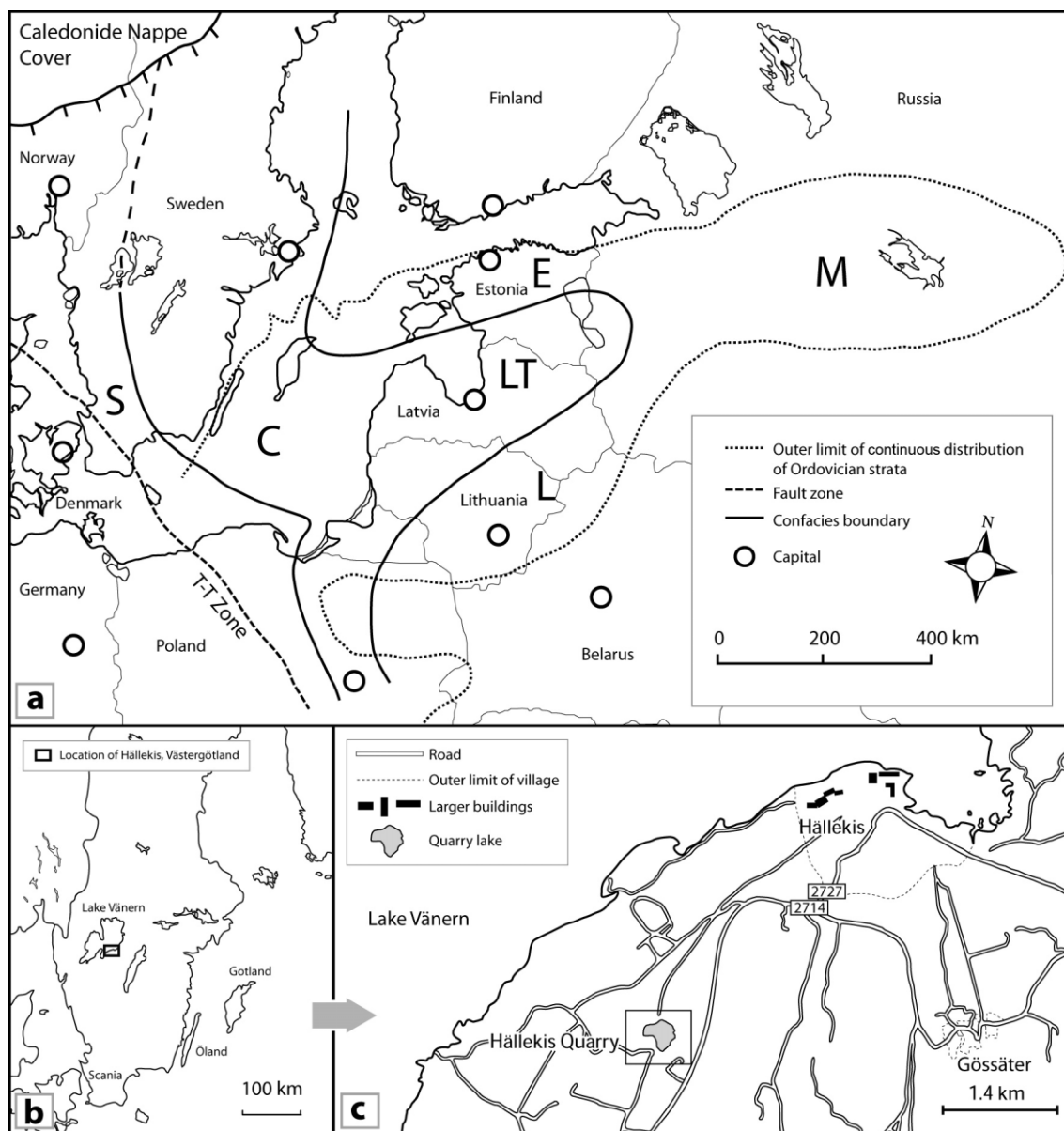


Figure 2 (a) Map of the Baltoscandian region. Confacies boundaries modified from Jaanusson (1995) and Rasmussen *et al.* (2007). Abbreviations: C=Central Baltoscandian Confacies belt; E=North Estonian Confacies belt; L=Lithuanian Confacies belt; LT=Livonian Tongue; M=Moscow basin; S=Scanian Confacies belt. (b) Map of southern Sweden with the location of Hällékis indicated. (c) Close-up of the Hällékis area.

‘Täljsten’ interval as well as the adjacent red limestone above and below it. The samples were processed with dilute, buffered acetic acid and buffered formic acid, and the residues separated in heavy liquids according to the techniques described by Jeppsson *et al.* (1999). The acid-resistant residues were washed through a 0.063-mm sieve, dried, and the conodont elements were electrostatically hand-picked under a binocular microscope. In order to facilitate picking, the dried sample residues were split into three different size fractions (≥ 0.125 mm, 0.125–0.090 mm and 0.090–0.063 mm). The two finest fractions were only picked completely in eight samples selected for statistical analyses (marked by an asterisk in Fig. 5). In these eight samples, all conodont elements ≥ 0.063 with the base and part of the cusp intact were picked, sorted and counted. Large numbers of P and M elements of *Microzarkodina* were retrieved from the finest fractions in all of these samples. These elements are more often preserved complete, compared to elements derived from genera with larger-sized elements, and they were therefore positively biased in the picking and counting process, resulting in the relatively high values of

Microzarkodina throughout the investigated interval (Fig. 5). Samples that were not completely picked in the case of the finest fraction were used primarily for the purpose of biostratigraphy and taxonomic identification. In total, more than 100 000 conodont elements were included in the present study.

The state of preservation is generally good through the sampled interval. Especially in the grey ‘Täljsten’ interval, it can be regarded as excellent. The CAI value is 1 (thermally unaltered; Epstein *et al.* 1977) for all elements investigated.

All figured elements (repository number LO – for Lund Original) are stored in the type collection at the Department of Earth and Ecosystem Sciences, Lund University.

3. The conodont fauna

The conodont taxa retrieved from the investigated interval are typical of the Middle Ordovician *L. variabilis*–*Y. crassus*–*E. pseudoplanus* Zonal interval of Baltoscandia (e.g. Löfgren

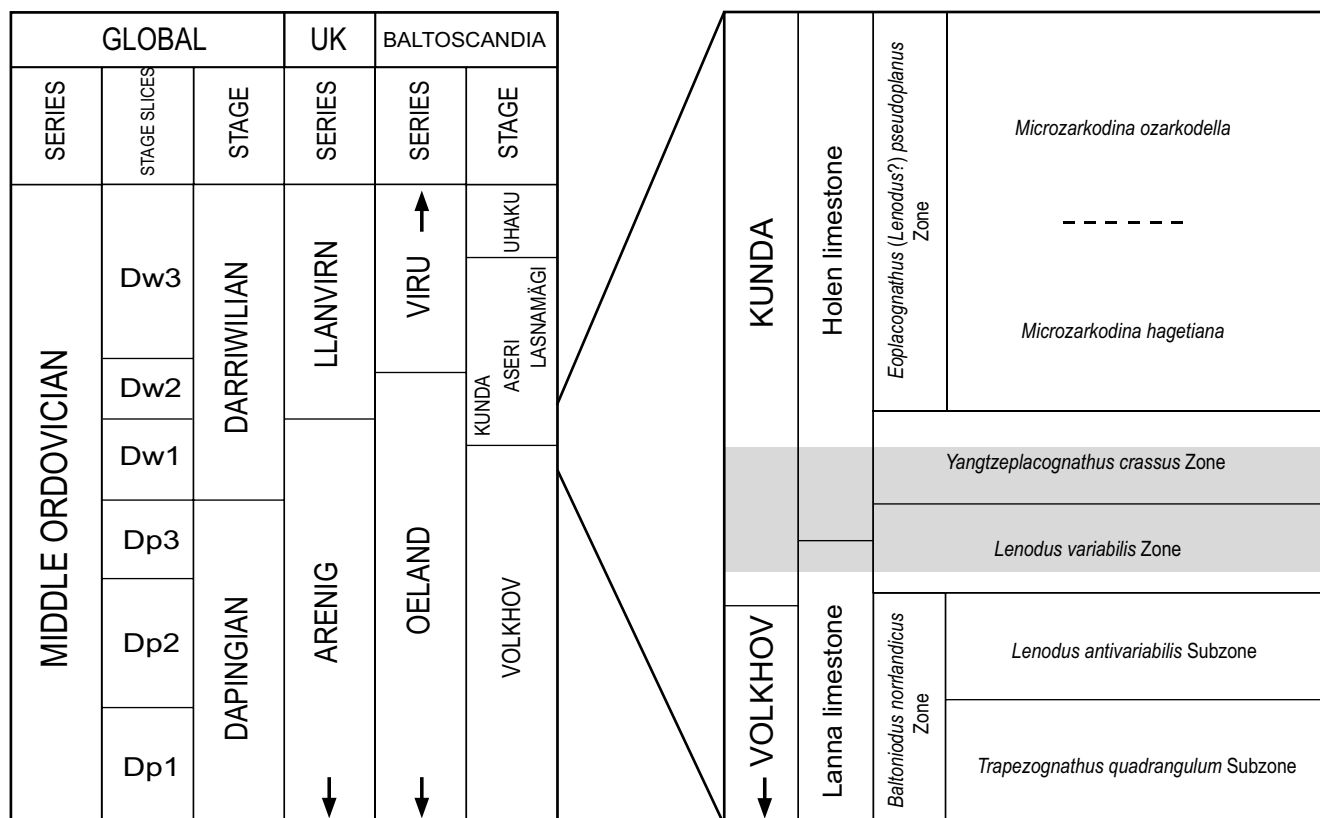


Figure 3 Middle Ordovician chronostratigraphical chart with stage slices, correlating the global series and stages with corresponding UK and Baltoscandian units (modified from Bergström *et al.* 2009). To the right is the conodont zonation of the topmost Volkhov and Kundan (modified from Zhang 1998a; Löfgren & Zhang 2003) with the sampled interval shaded grey.

2003, 2004). The most frequent genera include *Microzarkodina*, *Baltoniodus*, *Protopanderodus*, *Semiacontiodus*, *Drepanoistodus*, *Drepanodus*, *Scalpellodus*, *Decoriconus*, and the platform genera *Lenodus* and *Yangtzeplacognathus*. Other, less common, genera include *Periodon*, *Histiodela*, *Costiconus*, *Dzikodus*, *Ansella*, *Pygodus*, and *Panderodus* (collectively referred to as 'others' in Appendix).

When studying the succession of conodonts throughout the 2.5-m sequence (Figs 4, 5), obvious differences in taxonomical composition, relative frequency and element abundance can be noted. The differences are most noticeable between the red and the grey limestone, but the grey 'Täljsten' interval also proved to be surprisingly heterogeneous. Due to the detailed sampling, it is possible to follow the gradual response of the conodonts to the shifting environmental conditions and to identify levels of more abrupt faunal changes. In order to emphasise this, the investigated sequence has been sub-divided into four conodont faunal associations, which in stratigraphically ascending order are the *Periodon–Scalpellodus*, the *Semiacontiodus davidi–Microzarkodina cf. ozarkodella*, the *Histiodela*, and the *Yangtzeplacognathus–Dzikodus*. These associations are distinguished by differences in taxonomic composition, and the occurrence and frequency patterns of the conodonts.

Significant faunal patterns at the genus and species levels were used for describing and discussing the associations below, whereas the composition of the entire conodont fauna and ranges of individual species are shown in Figure 4. Some taxa are synoptically treated as they occur in the associations, while others are more ambiguous and are therefore discussed in more detail in section 3.2.

3.1. Conodont faunal associations

3.1.1. The *Periodon–Scalpellodus* association. The stratigraphically lowermost conodont association in the sampled

interval at Hällekis occurs in the 0.85 m-thick interval of strata of the Arkeologen and Golvsten beds, including the approximately 0.10 m-thick unit of transitional red-to-grey coloured strata of the Golvsten bed (Fig. 4). Abundances are calculated based on samples HÄ08-Ark4 and HÄ07-2 (Fig. 5). Generally, the Arkeologen bed is characterised by a few dominating taxa that are accompanied by smaller numbers of other species. This trend, however, changes upwards in the succession, and in the Golvsten bed (sample HÄ07-2 from the lower level), the relative frequencies between taxa becomes more equal, concurrent with increasing species diversity (Fig. 5).

The lowermost level of the Arkeologen bed has a notable abundance of *Periodon macrodentata* (= *P. aculeatus* of Zhang 1998a; Fig. 6A–B) and *Scalpellodus gracilis* (Fig. 6F–G). Mid-way through the Arkeologen bed (sample HÄ08-Ark3), however, *Periodon* drastically decreases in abundance to finally disappear in the Golvsten bed. *Scalpellodus*, on the other hand, remains abundant throughout the Arkeologen bed and, after the decrease of *Periodon*, elements of this genus outnumber the rest of the fauna (Fig. 5) with the exception of *Microzarkodina* spp., whose occurrence per kg – although high – in fact can be regarded as normal in this study (see Appendix). In the upper part of the Arkeologen bed *Costiconus costatus* (= *Walliserodus ethingtoni* in Zhang 1998a; included in 'others' in the Appendix; Fig. 6D–E) temporarily becomes slightly more common, only to return subsequently very sporadically and in extremely low numbers in the lower part of the 'Täljsten'.

Drepanoistodus is also fairly common throughout the interval of the association, and the complete dominance of forms possessing large geniculate (M) elements with a low cusp-to-base ratio, is noteworthy (Fig. 7A–E, G–J, M, N).

As shown in Figures 4 and 5, the Golvsten bed (samples HÄ07-2 and HÄ07-3) represents the transitional interval from red to grey limestone and it coincides with an overall increase

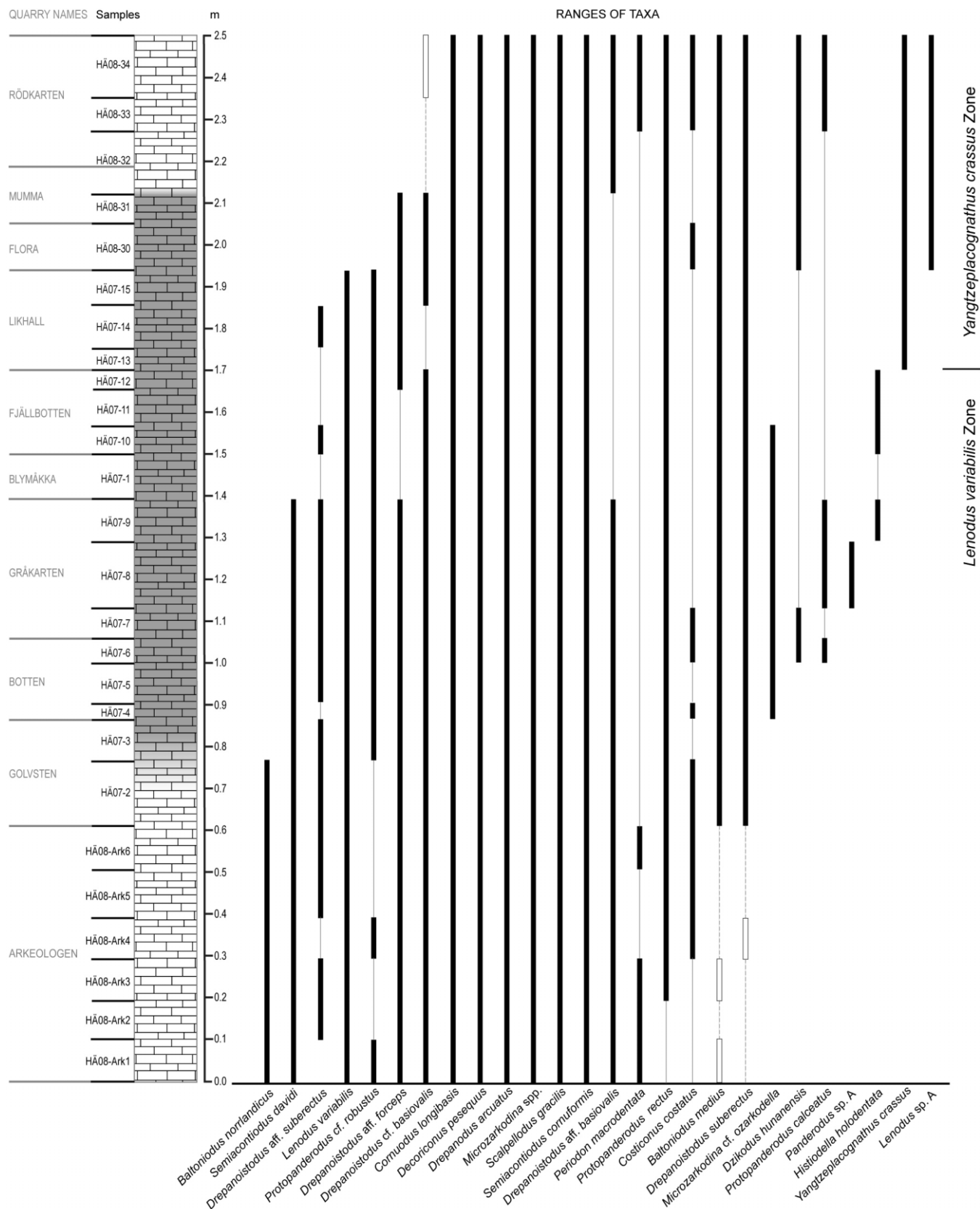


Figure 4 Sampled section at Hälleki with traditional quarry names, level and thickness of samples, and the observed stratigraphical ranges of the conodont taxa recorded. Open bars represent uncertain identifications. The 'Täljsten' interval is shaded grey. The base of the *Yangtzeplacognathus crassus* Zone is shown to the right.

in conodont abundance. The most prominent abundance increase is in species of *Microzarkodina* and *Baltoniodus* that together represent 58% of the conodonts in sample HÄ07-2. *Scalpellodus*, on the other hand, markedly decreases in abundance to 8% of the fauna. In this transitional interval,

Baltoniodus norrlandicus (Fig. 6Q, R) is replaced by its descendant *B. medius* (Fig. 6S, T). Due to the minimal stratigraphical overlap of these two species (Fig. 4), this faunal shift is believed to be ecologically controlled. Their brief co-occurrence could explain the short-term increase of

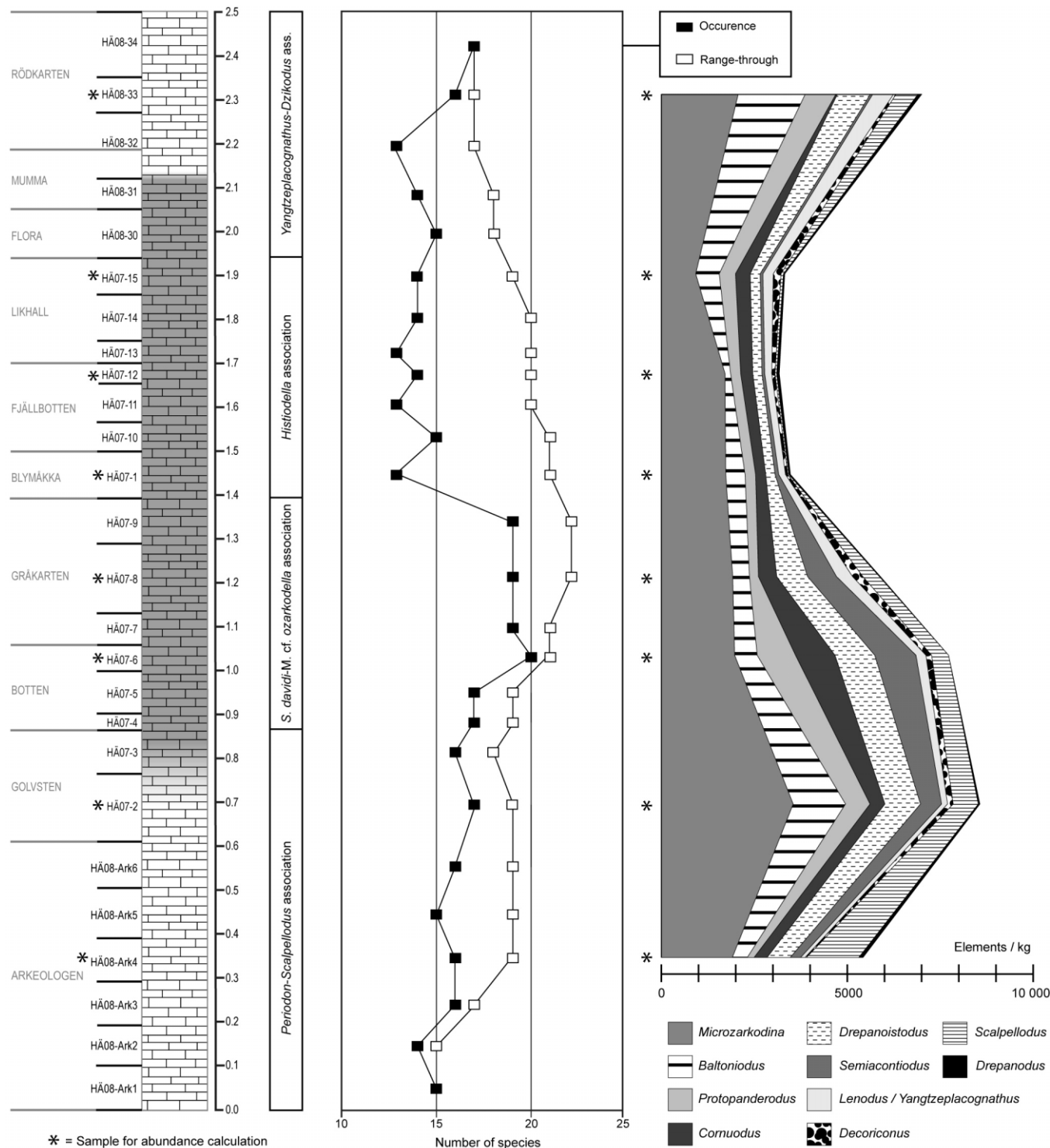


Figure 5 From left to right: Sampled section at Hällekis with the ‘Täljsten’ interval shaded grey, samples used for abundance calculations indicated by an asterisk (*). Distribution of the conodont faunal associations recognised. Conodont diversity plot, expressed as total diversity based on specific occurrence in a sample and as range-through; first to last occurrence, with boxes correlated to the centre of each sample indicated in the log. Element abundance (elements/kg rock) of selected genera.

Baltoniodus in the red-to-grey transition interval (Fig. 5). Also at the base of the ‘Täljsten’ interval is a changing co-occurrence pattern between the two recorded species of *Semiacontiodus*. In the middle of the Arkeologen bed, the ratio between *S. davidi* (Fig. 6W, X) and *S. cornuformis* (Fig. 6O, P) is approximately equal (54% *S. davidi* and 46% *S. cornuformis* in sample HÄ08-Ark4). However, at this red-to-grey transition level, the ratio changes significantly (92% *S. davidi* and 8% *S. cornuformis*).

3.1.2. The *Semiacontiodus davidi*-*Microzarkodina* cf. *ozarkodella* association. This faunal association roughly corresponds to the lower 0.50 m of the ‘Täljsten’ and includes the Botten and Gråkartan beds (Fig. 4). Abundances are calculated based on samples HÄ07-6 and HÄ07-8. Overall, and despite the clearly improved element preservation compared to that in the subjacent red layers, the Botten-Gråkartan interval shows a gradually decreasing trend in conodont abundance. The diversity, on the other hand, continues to increase (Fig. 5).



Figure 6 (A–B) *Periodon macrodentata* (Graves & Ellison, 1941): (A) LO 10604t, $\times 60$, sample HÄ08-Ark2; (B) LO 10605t, $\times 55$, same sample as (A). (C) *Decoriconus pesequus* Löfgren, 1998, LO 10606t, $\times 59$, sample HÄ07-5. (D–E) *Costiconus costatus* (Dzik, 1976): (D) LO 10607t, $\times 74$, sample HÄ08-Ark6; (E) LO 10608t, $\times 74$, same sample as (D). (F–G) *Scalpellodus gracilis* (Sergeeva, 1974): (F) LO 10609t, $\times 76$, sample HÄ08-Ark4; (G) LO 10610t, $\times 81$, same sample as (F). (H–I) *Cornuodus longibasis* (Lindström, 1955): (H) LO 10611t, $\times 61$, sample HÄ07-5; (I) LO 10612t, $\times 84$, same sample as (H). (J–K) *Drepanodus arcuatus* Pander, 1856: (J) LO 10613t, $\times 51$, sample HÄ08-Ark6; (K) LO 10614t, $\times 63$, sample HÄ07-8. (L–M) *Panderodus* sp. A: (L) LO 10615t, $\times 105$, sample HÄ07-8; (M) LO 10616t, $\times 110$, same sample as (L). (N) *Histiodela holodentata* Ethington & Clark, 1982, LO 10617t, $\times 90$, sample HÄ07-10. (O–P) *Semiacontiodus cornuiformis* (Sergeeva, 1963): (O) LO 10618t, $\times 57$, sample HÄ08-30; (P) LO 10619t, $\times 119$, sample HÄ07-6. (Q–R) *Baltoniodus norrlandicus* (Löfgren, 1978): (Q) LO 10620t, $\times 80$, sample HÄ07-2; (R) LO 10621t, $\times 78$, sample HÄ08-Ark4. (S–T) *Baltoniodus medius* Dzik, 1976: (S) LO 10622t, $\times 81$, sample HÄ08-30; (T) LO 10623t, $\times 54$, sample HÄ07-15. (U–V) *Dzikodus hunanensis* Zhang, 1998b: (U) LO 10624t, $\times 52$, sample HÄ08-30; (V) LO 10625t, $\times 62$, sample HÄ08-34. (W–X) *Semiacontiodus davidi* Löfgren, 1999a: (W) LO 10626t, $\times 52$, sample HÄ07-5; (X) LO 10627t, $\times 64$, same sample as (W). (Y) *Protopanderodus rectus* Lindström, 1955, LO 10628t, $\times 49$, sample HÄ07-5. (Z) *Protopanderodus calceatus* Bagnoli & Stouge, 1997, LO 10629t, $\times 46$, sample HÄ07-8. (AA) *Protopanderodus* cf. *robustus* (Hadding, 1913), LO 10630t, $\times 59$, sample HÄ07-15. (AB–AC) *Microzarkodina* M-elements: (AB) LO 10631t, $\times 69$, sample HÄ07-7; (AC) LO 10632t, $\times 95$, sample HÄ07-2. (AD) *Microzarkodina* Sa-element, LO 10633t, $\times 97$, sample HÄ07-14. (AE) *Microzarkodina* sp. A, LO 10634t, $\times 96$, sample HÄ08-Ark4. (AF–AG) *Microzarkodina* cf. *ozarkodella* (Lindström, 1971): (AF) LO 10635t, $\times 76$, sample HÄ07-7; (AG) LO 10636t, $\times 73$, same sample as (AF). (AH) *Microzarkodina* Sa-element, LO 10637t, $\times 104$, sample HÄ07-2. (AI) *Microzarkodina* M-element, LO 10638t, $\times 70$, sample HÄ07-11. (AJ) *Microzarkodina hagetiana* Stouge & Bagnoli, 1990, LO 10639t, $\times 91$, sample HÄ08-Ark4. (AK) *Microzarkodina* cf. *bella* Löfgren, 2000, LO 10640t, $\times 69$, sample HÄ08-30.

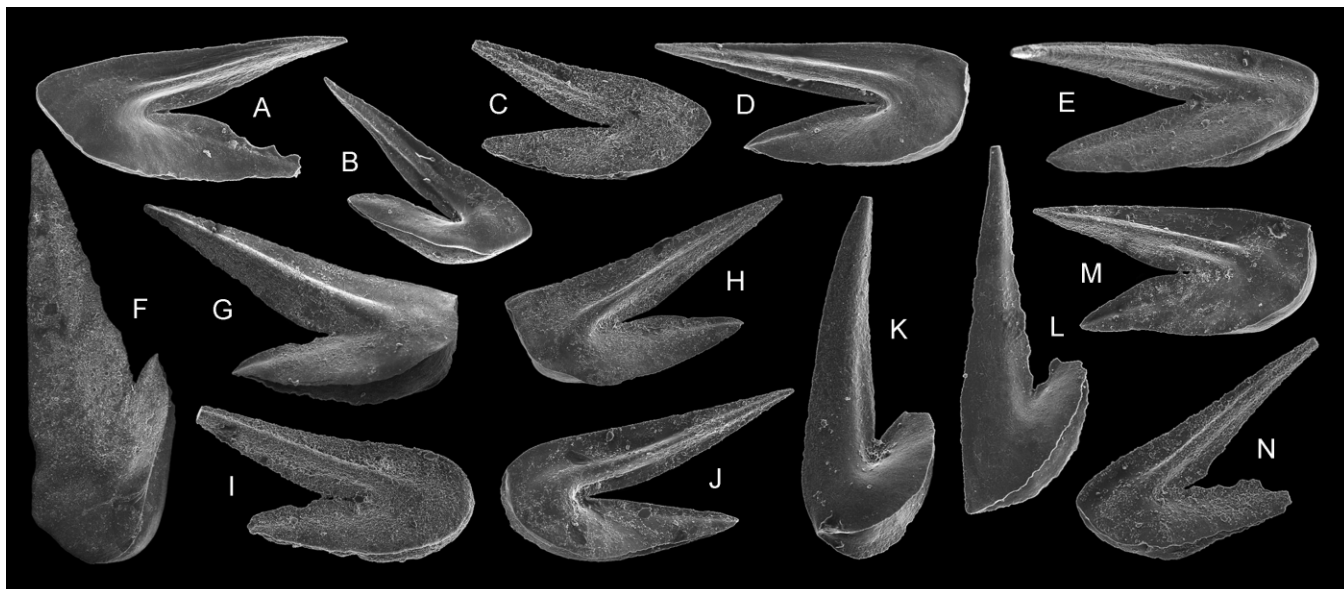


Figure 7 Represented forms of *Drepanoistodus* geniculate M (oistodontiform) elements. (A–C) *Drepanoistodus* aff. *forceps* (Lindström, 1955): (A) LO 10641t, $\times 91$, sample HÄ07-6; (B) LO 10642t, $\times 65$, sample HÄ07-15; (C) LO 10643t, $\times 74$, sample HÄ07-2. (D) *Drepanoistodus* cf. *basiovalis* (Sergeeva, 1963), LO 10644t, $\times 88$, sample HÄ07-6. (E) *Drepanoistodus* aff. *basiovalis* (Sergeeva, 1963), form with an oval antero-basal outline and nearly equally long base and cusp, LO 10645t, $\times 66$, sample HÄ07-8. (F) *Drepanoistodus* aff. *suberectus* (Branson & Mehl, 1933), LO 10646t, $\times 55$, sample HÄ08-Ark6. (G–H) *Drepanoistodus* aff. *basiovalis* (Sergeeva, 1963), forms with particularly sharp antero-basal corners: (G) LO 10647t, $\times 64$, sample HÄ08-Ark3; (H) LO 10648t, $\times 63$, sample HÄ08-Ark4. (I–J) *Drepanoistodus* aff. *basiovalis* (Sergeeva, 1963), ‘*D. stougei*-like’ forms: (I) LO 10649t, $\times 80$, sample HÄ08-Ark6; (J) LO 10650t, $\times 69$, same sample as (I). (K) *Drepanoistodus* cf. *suberectus* (Branson & Mehl, 1933), LO 10651t, $\times 81$, sample HÄ07-6. (L) *Drepanoistodus* aff. *suberectus* (Branson & Mehl, 1933), with pointed antero-basal outline, LO 10652t, $\times 90$, sample HÄ07-6. (M) *Drepanoistodus* aff. *basiovalis* (Sergeeva, 1963), LO 10653t, $\times 65$, sample HÄ07-2. (N) *Drepanoistodus* cf. *basiovalis* (Sergeeva, 1963), LO 10654t, $\times 73$, sample HÄ08-Ark2.

Furthermore, the relative frequency of individual genera is now even more equal than at the end of the interval of the previous association.

Characteristic for the Botten bed is an equal and high abundance of *Protopanderodus* spp. (Fig. 6Y–AA), *Cornuodus longibasis* (Fig. 6H, I), *Drepanoistodus* spp., and *Semiacontiodus* spp. (representing 14% each of the total fauna in sample HÄ07-6). The relative frequency then changes to some extent between the Botten and the Gråkarten (sample HÄ07-8) beds as the total element abundance drops by almost 2000 elements/kg (Fig. 5; Appendix). The fact that some genera (e.g. *Protopanderodus* and *Drepanoistodus*) markedly decrease in abundance, whereas others remain constant; signals that various taxa responded differently to the changing environment in this interval. For example, the platform genus *Lenodus* (Fig. 8A–G, I–AA, AE, AK) doubles its abundance from sample HÄ07-6 to sample HÄ07-8. It seems as if the yet unknown ecological triggering mechanism that began acting during the transition from red to grey limestone became even more efficient within the interval of this association, and favoured the existence of conodont taxa with this type of platform.

At the species level, the strong dominance of *Semiacontiodus davidi* over *S. cornuiformis*, which was initiated in the Golvsten bed, prevails throughout the interval of the association with an approximate 90% to 10% ratio (Appendix). The ‘Täljsten’ interval was in fact chosen as type stratum for *S. davidi* because it occurs there in great abundance (see Löfgren 1999a). Perhaps the most noticeable difference between the *S. davidi*–*M. cf. ozarkodella* association and the previous one is in the *Microzarkodina*-fauna, which becomes completely dominated by forms possessing two anterior denticles in front of the cusp (*M. cf. ozarkodella*; Fig. 6AF, AG), co-occurring with *M. cf. bella* (Fig. 6AK); see also section 3.2. In the Arkeologen

and Botten beds no such forms were recorded, which suggests a sudden and environmentally controlled immigration.

The restricted occurrence of *Panderodus* sp. A (Fig. 6L, M) in sample HÄ07-8, a taxon never previously recorded in Middle Ordovician strata of Kinnekulle, is another indication of species immigration during this interval.

3.1.3. The *Histiodela* association. The interval of the third association begins in the cystoid-rich Blymåkka bed and extends through the Fjällbotten and Likhall beds, both of which contains additional, minor horizons of cystoids. In the Blymåkka bed, conodont diversity plunges to the lowest level seen throughout the investigated interval, and the association as a whole demonstrates consistently lowered element abundance values of <3500 elements/kg (Fig. 5). Although this infrequency can, to some degree, be explained by an increased depositional rate and the obvious fact that the presence of cystoids reduces the conodont-yielding matrix in the samples, some conodont taxa evidently were more severely affected than others during this interval. As shown in Figure 5 and in the Appendix, *Semiacontiodus*, *Scalpellodus*, and *Drepanoistodus* are markedly reduced in abundance, while *Baltoniodus* and *Protopanderodus* on the contrary show a slight increase. For *Semiacontiodus*, this decrease is largely caused by the disappearance of *S. davidi*. Thus, stratigraphically upwards, *S. cornuiformis* remains as the sole representative of the genus. *Scalpellodus gracilis*, which decreased in abundance in the lowermost ‘Täljsten’, is strongly subordinate numerically in the *Histiodela* association.

The *Histiodela* association also shows a faunal shift within *Drepanoistodus*, the outcome of which becomes evident higher up the succession. This is expressed by a marked decrease of forms with low cusp-to-base ratio of the M-element that dominated the previous two associations. Yet another faunal shift is seen in the *Microzarkodina* fauna; the frequency of

M. cf. ozarkodella changes from completely dominating to only sporadic, while *M. cf. bella* becomes the most common species.

Within this interval of low diversity and abundance, *Histiodela holodentata* (= *H. tableheadensis* in Stouge 1984; Fig. 6N) occurs in small numbers (samples HÄ07-9, HÄ07-10–HÄ07-12). The presence of this species allows correlation to the North American conodont faunal province.

3.1.4. The *Yangtzeplacognathus*–*Dzikodus* association. The last faunal association recognised herein occurs in the uppermost 0–55 m of the grey/green-to-red strata of the Flora through Rödkarten beds. The conodont fauna of this interval reflects the ending of the ‘Täljsten’ event and the return of environmental conditions of pre-‘Täljsten’ character.

Despite being directly contiguous to the Likhall bed, the Flora bed proved to be substantially different in terms of element abundance (estimated to be c. 7000 elements/kg in sample HÄ08-30). In addition, the sample residues of both samples HÄ08-30 and HÄ08-31 (lower Mumma bed) are weakly greenish in colour instead of white/hyaline. The most noticeable difference compared to the *Histiodela* association is the sudden appearance of large and numerous specimens of *Dzikodus humanensis* (Fig. 6U, V), suggesting changed ecological conditions, presumably a result of increased water depths: Zhang (1998b) placed *Dzikodus* in her ‘*Walliserodus*’ (= *Costiconus*) biofacies on the Yangtze platform in south-central China, indicative of fairly deep environments (see also Löfgren 2003). Otherwise, in the greenish Flora and Mumma beds, the relative frequency of the major genera represented are similar to those of the previous association, e.g. with *Scalpellodus gracilis* occurring in very low frequencies.

In the overlying red Rödkarten bed (samples HÄ08-32 to HÄ08-34), the relative frequencies distinctly change, as that of *Cornuodus longibasis*, which has been fairly constant at 8–14% of the fauna throughout the ‘Täljsten’, suddenly drops to merely 1% (sample HÄ08-33; Fig. 5). Considering that abundance values for *C. longibasis* were also comparably low in the *Periodon*–*Scalpellodus* association (5–6%), its retrogression could be consistent with the return of pre-‘Täljsten’ conditions. This is also supported by the re-occurring *M. hagetiana*-dominated *Microzarkodina* fauna, the increasing abundance of *S. gracilis* (8% in sample HÄ08-33), and the sporadic occurrence of *Periodon macrodentata* and *Costiconus costatus*. Furthermore, *Baltoniodus* reaches its highest observed abundance in the entire sequence and so do the platform conodonts (Fig. 5; Appendix). As to the latter (in this part of the interval represented by both *Lenodus* and *Yangtzeplacognathus*), this rules out the possibility that the low number of *Lenodus* in the *Periodon*–*Scalpellodus* association, which is followed by higher numbers in the *S. davidi*–*M. cf. ozarkodella* association, could be due to differences in preservation. In sample HÄ08-33 the platform conodonts comprise 8% of the fauna, just as in the Gråkartan bed where these conodonts become noticeably abundant.

The outcome of the faunal shift in *Drepanoistodus*, which begins during the interval of the previous association, becomes more apparent here due to the increased number of elements. Some of the taxa that were dominant in the interval up until the *Histiodela* association still prevail (Fig. 4), but they are notably fewer and smaller. In comparison with the three previous associations, *D. cf. suberectus* (Fig. 7K) becomes a more prominent faunal element in the *Drepanoistodus*-fauna.

3.2. Comments on selected taxa

Although generally well known, the Middle Ordovician conodont faunas of Baltoscandia include a number of taxonomically unclear taxa with incompletely known intraspecific

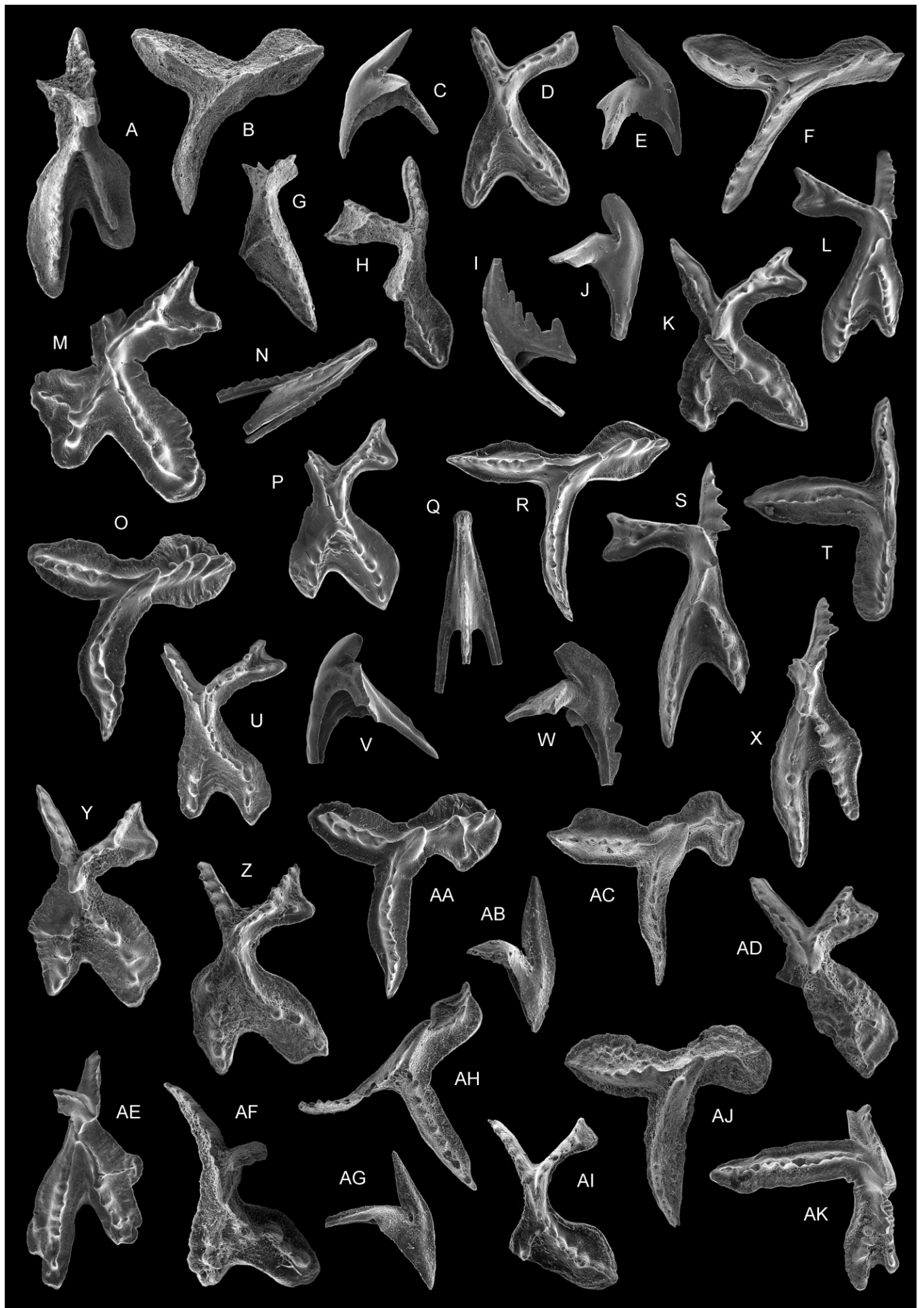
variability. Despite the fact that the present material comes from a single section, the very large collection of excellently preserved specimens forms a good basis for discussions of some of the problematic taxa.

3.2.1. *Drepanoistodus*. Species of *Drepanoistodus* are mainly separated based on their geniculate M (oistodontiform) elements, while the non-geniculate S (drepanodontiform) elements are more difficult to use for species identification (e.g. Stouge & Bagnoli 1990, p. 15; Rasmussen 2001, p. 71; Viira *et al.* 2001, p. 714). Obviously, the description of distinct species is obstructed by the problems of recognising the complete apparatus architecture. This could, moreover, be a contributing source of discrepancy when discussing the intra-specific variability of the geniculate element. For example, a comparison of the geniculate elements of *D. basiovalis* illustrated by Stouge & Bagnoli (1990, pp. 38–39, pl. 5, figs 22, 23) with those illustrated by Löfgren (2004, p. 516, fig. 11n, o) demonstrates that quite disparate elements have been assigned to this same species.

Zhang (1998a) assigned most elements of *Drepanoistodus* from Hällekis to *D. basiovalis*. However, the large number of morphologically variable geniculate elements recorded in this study suggests that more than one species may be present. As most of these elements are identifiable based on published literature on Middle Ordovician conodonts, they were provisionally grouped and treated as separate taxa in Figure 4. A significant part of the *Drepanoistodus* fauna (particularly in the lower half of the interval investigated) includes taxa with variable geniculate elements, which share the characteristics of a generally low cusp-to-base ratio and a distinct inner carina. These include *Drepanoistodus cf. basiovalis*, *Drepanoistodus aff. forceps* and *Drepanoistodus aff. basiovalis* (Fig. 4). Elements referred to as *D. cf. basiovalis* (Fig. 7D, N) are morphologically closest to *D. basiovalis* (Sergeeva, 1963). Open nomenclature is used because the bases of the Hällekis specimens tend to be longer than that of the holotype from the Leningrad region (Sergeeva 1963, p. 97, fig. 3). The same is the case in elements of *D. aff. forceps* (Fig. 7A–C), which otherwise are morphologically comparable to the stratigraphically older *D. forceps* (Lindström, 1955).

The range of *D. aff. basiovalis* (Fig. 4) collectively includes four distinguished morphotypes. The most abundant type (Fig. 7M) is probably the same as the elements referred to as *Drepanoistodus aff. basiovalis* by Rasmussen (2001, pl. 5, fig. 17). This type is accompanied by forms similar to *D. stougei* Rasmussen, 1991 (Fig. 7 I, J), i.e. with perfectly rounded antero-basal margins, as well as forms with a very sharp antero-basal corner (Fig. 7G–H), and elements with a more oval outline and with the base and cusp of almost equal length (Fig. 7E).

By contrast, *Drepanoistodus* with a high cusp-to-base ratio are referred to as *Drepanoistodus cf. suberectus* or *Drepanoistodus aff. suberectus*, which are separated mainly on the basis of cusp inclination and base morphology. *D. cf. suberectus* (Fig. 7K) has a rounded antero-basal outline whereas *D. aff. suberectus* (Fig. 7F) has a more erect cusp and a particularly small base, giving the antero-basal part a rather oblong outline. The latter form also bears similarities to *Drepanoistodus contractus* (Lindström, 1955) but differs from this species in cusp inclination and the tendency of having an inverted basal cavity, a character not described for *D. contractus*. This type of element was referred to as *D. basiovalis* by Löfgren (2003, fig. 7AA) and *D. cf. basiovalis* by Stouge & Bagnoli (1990, plate 5, fig. 15A). In addition, a few elements with a more pointed antero-basal outline have been recorded (Fig. 7L; see also *D. cf. basiovalis* of Stouge & Bagnoli 1990, plate 5, fig. 14) and these are also included in *D. aff. suberectus* (Fig. 4).



Zhang (1998a) recorded *Drepanoistodus? venustus* 1.5 m above the 'Täljsten' interval. *Drepanoistodus venustus* (Stauffer, 1935) is a taxon of North American Midcontinent affinity and Baltoscandian elements similar to this species have long been considered problematic (e.g. Rasmussen 2001, pp. 76–78; Löfgren 2006, pp. 16–18). Small geniculate elements with almost equally long cusps and bases are commonly referred to as '(*Oistodus*) *Drepanoistodus* (cf./aff.) *venustus* (Stauffer)' (e.g. Stouge & Bagnoli 1990; Viira *et al.* 2001; Viira 2008). However, Löfgren (2006) re-assigned such elements from Baltoscandian populations to a new genus and species; *Venoistodus balticus* Löfgren, 2006, and included a rather wide range of variability into this new taxon (see Löfgren 2006, p. 17, figs. 3A–G, L, Q, W, Y–AA).

Many of the elements identified in the material at hand (from the *Drepanoistodus*-rich levels below the Blymäkka bed) generally agree with the description and several of the figured elements of *V. balticus*. However, following Löfgren (2006, p. 18) they should not be assigned to that species because of their relatively large size, as the description of *V. balticus* was based on small elements "compared to the normal size of adult elements of *Drepanoistodus forceps* and *D. basiovalis*". Differences in size could be influenced by palaeoecological factors, and because the interval studied suggests anomalous environmental conditions, these may have promoted enlargement (and numerical dominance) of these forms. The fact that this type of element is scarcer and notably smaller in the red layers above the 'Täljsten' interval supports this interpretation.

3.2.2. Microzarkodina. Species of *Microzarkodina* are generally distinguished on their P-elements, although the S-elements (especially Sa) may also be characteristic. The M-elements are more often considered difficult to identify at the species level (e.g. Löfgren 2000). Therefore, the discussions below refer to the P-elements, unless stated otherwise.

Zhang (1998a) reported only one *Microzarkodina* species from the *L. variabilis*–*Y. crassus* interval at Hällekis, *M. hagetiana* Stouge & Bagnoli, 1990 from the lower/middle part of the 'Täljsten' and the 5 m-thick interval above. Indeed, through the present study, representatives of this genus are more variable and a number of separate forms are recognised. *M. hagetiana* (Fig. 6AJ) is most common in the red strata

below and above the 'Täljsten' interval. At those same levels it co-occurs with a form that, although superficially resembling *M. hagetiana* (Fig. 6AE; *Microzarkodina* sp. A), differs in having a more flexed antero-basal part and posterior denticles of alternating lengths (as opposed to a straight antero-basal part and denticles that decreases away from the cusp; see description of *M. hagetiana* by Stouge & Bagnoli 1990, p. 20). In addition, another *Microzarkodina*-form most commonly found in the top half of the 'Täljsten' interval (see above) is distinguished by a tall carinate cusp, one single anterior denticle on the front of the cusp, and short posterior denticles (Fig. 6AK). Its basic morphology fits both that of the stratigraphically older *Microzarkodina parva* Lindström, 1971 and of the younger *Microzarkodina bella* Löfgren, 2000, but due to a better stratigraphical correspondence with the latter species, this form is herein referred to as *M. cf. bella*. The taxonomic uncertainty is due mainly to the appearance of the basal cavity that tends to be deeper than that described for *M. bella*. Also, it is currently not clear whether the cusps of *M. bella* carry a carina or a costa (cf. Löfgren 2000; Löfgren & Tolmacheva 2008). Nevertheless, a direct ancestor–descendant relationship between *M. parva* and *M. bella* seems plausible. The same supposed relationship between *M. parva* and *M. hagetiana*, suggested by Löfgren & Tolmacheva (2008), seems doubtful due to their apparent morphological dissimilarities.

The last form of *Microzarkodina* recognised herein is the one mentioned above (in section 3.1.2), whose elements are easily distinguished by having two (rarely three) anterior denticles (Fig. 6AF, AG). This characteristic of possessing more than one anterior denticle is particularly distinguishing of *Microzarkodina ozarkodella* Lindström, 1971. Löfgren (2000, 2003, 2004) also assigned this character to *M. bella* and to *M. hagetiana*, and mentioned that it was developed in those taxa in the uppermost *Lenodus variabilis* Zone and the *Yangtzeplacognathus crassus* Zone. However, recently *M. bella* was re-described as rarely having more than one anterior denticle (Löfgren & Tolmacheva 2008).

According to Löfgren (2004) and Löfgren & Tolmacheva (2008), *M. ozarkodella* probably evolved from *M. hagetiana*. Thus, stratigraphically early '*M. ozarkodella*-type' forms should be referred to as *M. cf. hagetiana* and be regarded as

Figure 8 (A–G) *Lenodus variabilis* (Sergeeva, 1963), *sensu lato* based on apparatus description of Löfgren & Zhang (2003): (A) sinistral Pa element, LO 10655t, $\times 42$, sample HÄ07-2; (B) sinistral Pb element, LO 10656t, $\times 80$, same sample as (A); (C) M element, LO 10657t, $\times 71$, sample HÄ07-10; (D) dextral Pa element (juvenile), LO 10658t, $\times 75$, sample HÄ07-5; (E) M element (juvenile), LO 10659t, $\times 71$, sample HÄ07-8; (F) sinistral Pb element, LO 10660t, $\times 91$, sample HÄ07-8; (G) LO 10661t, $\times 70$, sample HÄ08-Ark6. (H) *Yangtzeplacognathus?* element, LO 10662t, $\times 63$, sample HÄ08-Ark6. (I–T) *Lenodus variabilis* (Sergeeva, 1963), *sensu lato*: (I) ScA element, LO 10663t, $\times 49$, sample HÄ07-8; (J) M element, LO 10664t, $\times 55$, sample HÄ07-1; (K) dextral Pa element (note the non-belonging element debris at the cusp), LO 10665t, $\times 64$, sample HÄ07-8; (L) sinistral Pa element (juvenile), LO 10666t, $\times 64$, sample HÄ07-1; (M) dextral Pa element (with secondary postero-lateral process), LO 10667t, $\times 50$, sample HÄ07-6; (N) Sb element, LO 10668t, $\times 47$, sample HÄ07-8; (O) sinistral Pb element (broad platform type), LO 10669t, $\times 50$, sample HÄ07-11; (P) dextral Pa element, LO 10670t, $\times 69$, sample HÄ07-1; (Q) Sa element, LO 10671t, $\times 44$, sample HÄ07-12; (R) sinistral Pb element (gracile type), LO 10672t, $\times 62$, sample HÄ07-11; (S) sinistral Pa element (gracile type), LO 10673t, $\times 82$, sample HÄ07-8; (T) dextral Pb element, LO 10674t, $\times 51$, same sample as (S). (U) '*Lenodus variabilis?*' (Sergeeva, 1963), dextral Pa element with a crooked posterior process, LO 10675t, $\times 75$, sample HÄ07-13. (V–Y) *Lenodus variabilis* (Sergeeva, 1963), *sensu lato*: (V) M element, LO 10676t, $\times 52$, sample HÄ07-11; (W) M element (with a denticulated anterior margin), LO 10677t, $\times 54$, sample HÄ07-8; (X) sinistral Pa element (gracile type), LO 10678t, $\times 67$, sample HÄ07-10; (Y) dextral Pa element (with secondary postero-lateral process), LO 10679t, $\times 56$, sample HÄ07-13. (Z) '*Lenodus variabilis?*' (Sergeeva, 1963), dextral Pa element with a crooked posterior process, LO 10680t, $\times 67$, sample HÄ07-12. (AA) *Lenodus variabilis* (Sergeeva, 1963), *sensu lato*, sinistral Pb element (broad platform type), LO 10681t, $\times 43$, sample HÄ07-14. (AB–AC) *Yangtzeplacognathus crassus* Zhang, 1998a, *sensu lato* based on apparatus description of Löfgren & Zhang (2003): (AB) M element, LO 10682t, $\times 107$, sample HÄ07-15; (AC) sinistral Pb element, LO 10683t, $\times 62$, sample HÄ08-31. (AD) *Lenodus?* sp. A, dextral Pa element, LO 10684t, $\times 49$, sample HÄ08-30. (AE) *Lenodus variabilis* (Sergeeva, 1963), *sensu lato*, sinistral Pb element (broad platform type), LO 10685t, $\times 40$, sample HÄ07-13. (AF) *Yangtzeplacognathus crassus* Zhang, 1998a, dextral Pa element, LO 10686t, $\times 90$, sample HÄ08-33. (AG–AI) *Yangtzeplacognathus crassus* Zhang, 1998a: (AG) M element, LO 10687t, $\times 78$, sample HÄ08-33; (AH) sinistral Pb element, LO 10688t, $\times 71$, sample HÄ08-34; (AI) dextral Pa element (juvenile, early type), LO 10689t, $\times 81$, sample HÄ07-14. (AJ) *Lenodus?* sp. A, sinistral Pb element, LO 10690t, $\times 52$, sample HÄ08-34. (AK) *Lenodus* sp., dextral Pa element (with split posterior process), LO 10691t, $\times 41$, sample HÄ08-31.

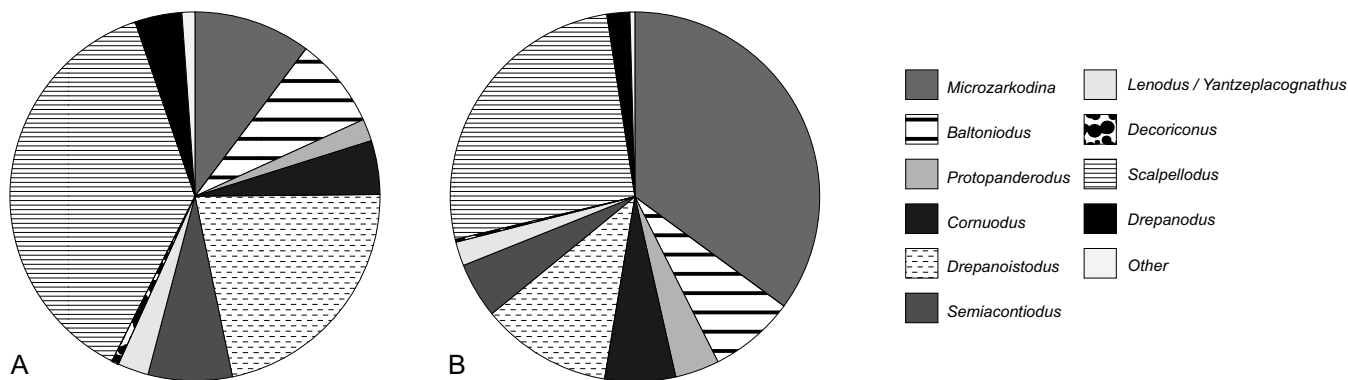


Figure 9 Pie-charts showing the relative frequency (%) in sample HÄ08-Ark4: (A) Distribution after picking all elements in fractions ≥ 0.125 mm; (B) Distribution including all elements in fractions ≥ 0.063 mm.

intermediates. By contrast, however, Löfgren & Tolmacheva (2008) referred to some of their illustrated *M. cf. hagetiana* elements as being of '*M. ozarkodella*-type', while simultaneously treating them as "early, probable homeomorphs of *Microzarkodina ozarkodella*" (Löfgren & Tolmacheva 2008, p. 39). It is noteworthy that the *M. cf. hagetiana* elements of Löfgren & Tolmacheva (2008, figs 9 X, Z; 10 A, B) were collected from the same level of the 'Täljsten' interval (sample HK88-2; see Löfgren 2003, p. 421) as the form carrying two anterior denticles described in the present paper.

While the likelihood that more than one species developed this character certainly exists, the form found in the study interval at Hällekis does not support a *M. hagetiana*–*M. ozarkodella* relationship. After comparing its overall element morphology (e.g. denticulation, cusp inclination and basal cavity depth) to stratigraphically older representatives of *Microzarkodina* with only one anterior denticle, it is evident that this form is closest to the stratigraphically older *Microzarkodina flabellum* (Lindström 1955). However, the presence of two anterior denticles indubitably makes them in this respect most similar to the stratigraphically younger *M. ozarkodella*, and they are here referred to as *M. cf. ozarkodella*.

In Figure 4, specimens of *Microzarkodina* are only separated on the basis of having one or several anterior denticles and are referred to as *Microzarkodina* spp. and *Microzarkodina cf. ozarkodella*, respectively.

3.2.3. The platform genera *Lenodus* and *Yangtzeplacognathus*. Zhang (1998a) established the conodont zonation in Hällekis based on the platform-equipped genera *Lenodus*, *Yangtzeplacognathus* and *Eoplacognathus*. The *L. variabilis* and *E. pseudoplanus* zones of Zhang (1998a) are a modification of the *Amorphognathus variabilis* Zone of Lindström (1971) and the *Eoplacognathus? variabilis* and *E. suecicus* zones of Löfgren (1978), whereas the *Y. crassus* Zone was established by Zhang (1998a, b) based on the range of the nominal species. These zones have subsequently been used as standard units in the conodont biozonation in Baltoscandia (Viira *et al.* 2001; Löfgren 2003, 2004; Löfgren & Zhang 2003; Stouge & Nielsen 2003; Schmitz *et al.* 2003; Schmitz & Häggström 2006; Rasmussen *et al.* 2007), except in areas where these genera are too scarcely represented (e.g. Norway; Rasmussen 2001).

The base of the *Y. crassus* Zone has been placed at slightly different levels in the Hällekis section. Both Zhang (1998a, p. 7, fig. 2) and Stouge *in Villumsen* (2001) placed the first appearance datum of *Y. crassus* at the base of the Rödkarten bed. Löfgren & Zhang (2003), on the other hand, assigned their sample HK88-2 to the *Y. crassus* Zone. The precise level of this sample is not given, but due to the high abundance of *S. davidi*, it is reasonable to assume that it was retrieved from within the grey 'Täljsten' interval below the Blymåkka bed. In

a review of this sample, no Pa elements of *Y. crassus* were encountered, which makes it difficult to confirm its presence, as these elements are the most characteristic for this species. The small collection in question, mainly containing *L. variabilis*, contains a dextral Pa element with a crooked posterior process that could be mistaken for *Y. crassus*. Such elements are relatively common in the material at hand (Fig. 8U, Z), but they are more common in the upper half of the 'Täljsten'. The posterior processes of these Pa elements may be crooked in various ways, but never form an arc together with the anterior process as described in *Y. crassus* by Zhang (1998a, p. 63). Aside from this attribute, these elements closely resemble those of *L. variabilis* in the angles between processes, development of postero-lateral process, and point of bifurcation on the anterior process (see descriptions by Zhang 1998b; Löfgren & Zhang 2003), and they are therefore provisionally included in *L. variabilis* in Figure 4. The similarities (and differences) are easily recognised, as these elements are found together with 'true' *L. variabilis*, in which the lateral- and posterior processes of the dextral Pa element form a fairly straight line and give the element an X-shape (Fig. 8D, K). It seems likely that further detailed studies will reveal a number of different morphotypes of *L. variabilis*-like taxa in this interval.

Small elements belonging to *Y. crassus* with certainty (Fig. 8AI) are first recorded in the upper part of the 'Täljsten' (the Likhall bed; sample HÄ07-13), and are here considered to mark the base of the *Yangtzeplacognathus crassus* Zone in Hällekis. These elements gradually become larger and more developed, as well as more abundant, in the greenish Flora and Mumma beds and in the red strata above.

Another observation has been made regarding the variability of the platform elements (i.e. sinistral and dextral Pa- and Pb elements) of *Lenodus* in the 'Täljsten' interval. Generally, two forms can be distinguished. The first one has more restricted platforms and more pointed distal ends of the platforms, making the elements appear more gracile (Fig. 8P, R, S). The second type has broader platforms and more blunt distal ends, commonly a branching posterior process of the Pb elements (Fig. 8O, AA), and in some elements there is a small secondary process on the postero-lateral process of the Pa elements (Fig. 8M, Y, AE). Some of the elements of this latter type are comparable with the elements of *E. pseudoplanus* illustrated by Viira *et al.* (2001), Löfgren & Zhang (2003) and Löfgren (2004). Löfgren & Zhang (2003) discussed a temporal variation in *L. variabilis* and noted that the stratigraphically younger specimens were more "*E. pseudoplanus*-like". In the material at hand, however, such '*E. pseudoplanus*'-like specimens co-occur with the 'typical' *L. variabilis* *sensu* Sergeeva (1963). In Figure 4, both types are included in the morphological range of *L. variabilis*, as the majority of these elements can

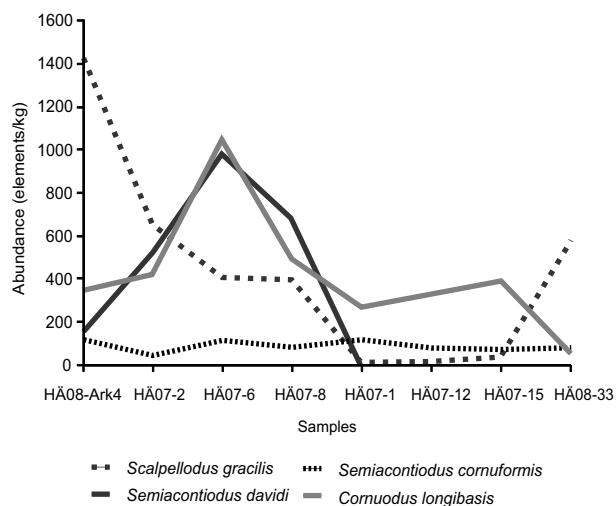


Figure 10 Graph showing the varying abundance of four conodont species from the material at hand.

be assigned to this species. In this present study, the stratigraphic range of *L. variabilis* ends when the more gracile type disappears, which is concurrent with the first appearance of *Lenodus?* sp. (Fig. 8AD, AJ) and the definite establishment of larger elements of *Y. crassus* (Fig. 8AF).

A close study of the zone index platform conodonts through the 'Täljsten' interval, preferably covering a longer stratigraphical range than the one dealt with here, is likely to give valuable clues as to the evolution and relationships of *Lenodus*, *Yangtzeplacognathus* and *Eoplacognathus*. As shown here, their taxonomy may be more complex than that commonly indicated when they are used as biostratigraphical markers. This is supported by the number of *Lenodus* species distinguished by Rasmussen (2001), and the discussion regarding the intraspecific variability of *L. variabilis* by Löfgren & Zhang (2003, p. 730).

4. Palaeoecology and correlations

The palaeoecology of conodonts is commonly related to their depth-preferences. These, in turn, are based on the nature and composition of the strata in relation to the presence/absence of certain taxa and the inferred sea-level (and concurrent inner-outer/shelf-slope environment). Limiting factors, such as temperature, salinity, oxygen, and food resources (Barnes & Fåhræus 1975) are not exclusively linked to bathymetry and could probably explain some conodont occurrences that seemingly contradict depth-models. For the Middle Ordovician of Baltoscandia, sea-level interpretations based on conodont occurrences have occasionally been presented in the literature (e.g. Lindström 1984). The most recent attempt to combine sedimentological analysis with conodont faunal composition was made by Rasmussen & Stouge (1995), who recognised a number of distinct conodont biofacies based on data from the Stein Fm (of the Scanian CB) and linked them to contemporary sea-level fluctuations in Baltoscandia (e.g. Nielsen 1992).

There are potential problems with establishing, and subsequently applying, these types of models. If the laboratory methods and picking criteria (e.g. smallest fraction dealt with, and the degree of breakage accepted) are not specified in detail, comparisons and interpretations may be biased. For example, there is a significant difference in both element abundance and relative frequency of taxa if samples are picked down to 0.090 mm or 0.063 mm, as shown in Figure 9. Also the laboratory technique, and consequently the element preservation and yield, has improved vastly over the years

(e.g. Jeppsson 2005). Nevertheless, the biofacies model of Rasmussen & Stouge (1995), as well as other relevant studies, is considered in the interpretations below.

The lithological interpretation of the 'Täljsten' interval made by Dronov *et al.* (2001), and the ostracod data of Tinn & Meidla (2001), both suggest that this sequence corresponds to a shallowing event. This scenario is supported by the conodont data of this present study. The sudden rise in conodont abundance, combined with the grey-to-greenish colour change from the Likhall to the Flora bed, indicates quite different environmental and depositional conditions, as does the presence of numerous specimens of *Dzikodus humanensis*. This is consistent with a subsequent deepening of the basin, an interpretation in agreement with that of Dronov *et al.* (2001), who recognised a transgressive surface at the top of the 'Täljsten'. It is possible that the apparent bed-to-bed differences between sample HÄ07-15 and HÄ08-30 is due to a depositional break.

Instead of regarding the 'Täljsten' as a single unit, this present study makes it possible to further untangle a stepwise progression of the regression and subsequent transgression. At the same time, a few conodont occurrence patterns are in conflict with the regression hypothesis. This may suggest that the palaeoecological significance assumed for these particular taxa is in need of reassessment. However, *Periodon* and *Costiconus* are both considered reliable indicators of relatively high sea-levels and/or a greater influence of oceanic waters (e.g. Barnes & Fåhræus 1975; Lindström 1976; Pohler 1994; Rasmussen & Stouge 1995). Thus, their occurrence pattern through the investigated interval suggests that the enclosing red strata reflect deeper/more oceanic water conditions compared to the 'Täljsten'. The high abundance of *Periodon* in the lowermost Arkeologen, followed by its sudden decrease midway through the same bed, suggests that the regression was initiated some time before the deposition of the grey layers.

Additional taxa with occurrence patterns indicating an ecological shift are *Semiacontiodus* and *Microzarkodina*. The former genus, represented here by *S. davidi* and *S. cornuformis*, was recognised by Löfgren (1999a, 2003, 2004) as being associated with the shallowest settings represented in her sections (Central Baltoscandian CB). Löfgren (1999a), however, also noted that there might be a difference in ecological preference between these two species, related to something other than water depth alone. The sudden increase of *S. davidi*, followed by its complete and permanent disappearance at the cystoid-rich Blymäkka level, certainly supports this observation (Figs 4, 10). The disappearance of *S. davidi* was likely due to the same ecological factor that promoted a sudden mass occurrence of cystoids; perhaps a change in temperature and salinity. As for *Microzarkodina*, it is now established that the separate forms recognised here have disparate ecological preferences. The temporary invasion of *M. cf. ozarkodella* could have come from shallower parts of the basin, as what is likely the same taxon was common in coeval strata at Gillberga, Öland (Löfgren 2000, p. 325). The disappearance of *M. cf. ozarkodella* at approximately the same level as *S. davidi* is conspicuous and ecologically interesting. This particular form seems to have had a rather narrow ecological preference, slightly distinct from that of *M. cf. bella*, which persisted through the *Histiodellella* faunal association interval.

The declining conodont abundance curve (samples HÄ07-2–HÄ07-9; Fig. 5) could be interpreted as due to gradually increasing depositional rates and/or solidification of the bottom substrate due to a progressively shallower setting. The latter scenario is supported by the presence of cystoids in the interval where conodont abundance are lowest (samples HÄ07-1, HÄ07-11–HÄ07-15; Fig. 5). In this interval, here

considered to reflect the peak regression, the conodont diversity and occurrence patterns suggest that it was a time of less favorable conditions for conodonts in general and certain taxa in particular. However, the record of *Histiodella holodontata* – a species of North American Mid-Continent affinity – in this interval suggests that these conditions were suitable for this particular taxon. The first immigration of *H. holodontata* at Steinsodden (Norway) in the basal Llanvirn was considered by Rasmussen & Stouge (1995) as being indicative of a transgression. Similarly, Löfgren (2004) regarded occurrences of *Histiodella* spp. as related to transgressions. In view of its occurrence in the Hällekis section, an alternative interpretation could be that immigration took place during a brief period of lowered sea levels, and/or shifting oceanic currents, allowing an easier relocation of taxa across the Iapetus Ocean. The subsequent dispersal of *H. holodontata* in Baltoscandia could then have been promoted by the following transgression. Nevertheless, the elements found in the material at hand represent one of the earliest populations of the species in Baltoscandia, since the ‘Täljsten’ interval is contemporaneous with, or even slightly older than, the first record of the species from Steinsodden and Andersön (see Rasmussen 2001).

Other taxa with interesting occurrence patterns are *Scalpellodus gracilis* and *Cornuodus longibasis*. According to Rasmussen & Stouge (1995), high relative frequencies of *Scalpellodus* are indicative of a comparably shallow setting in the more western part of the Baltoscandian basin. In this present study, the abundance of *Scalpellodus* is highest in the red layers below the ‘Täljsten’, then decreases when entering the ‘Täljsten’ and almost completely vanishes in the parts interpreted as the shallowest (Fig. 5). However, Löfgren (2003) considered *Scalpellodus* as having a comparably narrow depth-preference range, and almost certainly, the shallowest settings in the reference sections of Rasmussen & Stouge (1995) correspond to deeper environments at Hällekis. It is therefore likely that the highest abundances of *Scalpellodus* during the deposition of the ‘Täljsten’ were found further westwards, and that they subsequently returned in connection with the post-‘Täljsten’ transgression. Noteworthy for future ecological interpretations is that the relative increase of *S. davidi* coincides perfectly with the relative decrease of *S. gracilis* in the Arkeologen to Botten interval (Fig. 10).

Cornuodus longibasis had its peak abundance in the lower half of the ‘Täljsten’. It was considered by Löfgren (1999b) as being indicative of ‘medium depths’ as it occurred in all her Central Baltoscandian CB sections. This taxon was not included in the biofacies analysis of Rasmussen & Stouge (1995). If depth is the key limiting factor for the distribution of *C. longibasis*, its marked decline in the post-‘Täljsten’ strata supports the idea that these layers reflect a significantly deeper water setting compared to that of the ‘Täljsten’, as well as the red subjacent strata. Thus, unusually high abundances, or even the presence, of this genus in the western Central Baltoscandian CB or the Scanian CB, respectively, could be indicative of a relative shallowing.

4.1. Potential high resolution correlations

There is clearly potential for precise conodont-based correlations between the study interval at Hällekis and contemporary strata elsewhere in Baltoscandia. For example, the conodont succession of the upper member of the Komstad Limestone at Fågelsång, Scania, southernmost Sweden (Stouge & Nielsen 2003, fig. 5 and table 1), seems practically correlative on a bed-by-bed basis. The last occurrence of *S. davidi* at Fågelsång is just below the single bed occurrence of *H. holodontata* (= *H. tableheadensis* in Stouge & Nielsen 2003), which indicates correlation to the Blymåkka–Fjällbotten–Likhall

(cystoid-bearing) interval. This is further supported by the lithological change shown by Stouge & Nielsen (2003, fig. 5), which is expressed as an alteration from bedded to nodular limestone. Other biostratigraphical markers following the ‘Täljsten’-pattern include the disappearance of *B. norrlandicus* c. 0.5 m below the supposed Blymåkka interval, and the appearance of *Y. crassus* less than a metre above it.

Because samples collected solely for biostratigraphical purposes are often more spaced than those of the present study, it is difficult to make confident high-resolution correlations based only on the conodont faunas described. There are, however, sections that may prove to be of interest for further investigations of this interval in Baltoscandia, some of which are outlined below.

4.1.1. Degerhamn, Isle of Öland, Sweden. As mentioned above, the ‘Täljsten’ interval with its individual beds has been lithologically correlated to the Degerhamn quarry, south-western Öland. Stouge (2001) briefly summarised the conodont biostratigraphy of this region, confirming that the strata of interest lie within the *L. variabilis*–*Y. crassus* interval. Thus, a study similar to the one presented here would give clues on how a more shallow-water adapted conodont fauna responded to this event.

4.1.2. Kårgårde, central Sweden. The Kårgårde section was one of several localities briefly described by Löfgren (2004) regarding the conodont fauna of the *E. pseudoplanus* Zone. Although seemingly too high stratigraphically, the pattern of the last occurrence of *S. davidi* and the first appearance of *H. holodontata* strongly resembles that observed at Hällekis and Fågelsång. The samples of interest (H11–H9 from Kårgårde) also seem to be associated with a lithology change of red-grey variegated limestone (Löfgren 2004, pp. 509–510).

4.1.3. Stein Formation, Norway. Some of Rasmussen’s (2001) sections should have potential for high resolution correlation with Hällekis, judging from the conodont faunas reported from coeval strata. For example, the range chart from the Herram and Steinsodden sections (Rasmussen 2001, p. 31, fig. 26) suggests that the ‘Täljsten’-equivalent interval is to be found in between samples 69629–69643 (uppermost *B. norrlandicus*/*D. stougei*–*B. medius*/*H. holodontata* zones). This particular interval holds, with few exceptions, the same taxa as found in the interval investigated in the present paper.

To examine if this event had effects outside of Baltoscandia, long-distance correlations are necessary. Obviously, the longer the distance the greater the risk that the conodont faunas are too dissimilar for correlation. However, there is a good chance for detailed correlations with the Yangtze platform in China. Zhang (1998a) showed that more than 90% of the Middle Ordovician conodont species found in south-central China occur also in the Baltoscandian area. Furthermore, the restricted ‘minimound’-interval that disrupts the more ‘normal’ limestone on the Yangtze platform (Zhang 1998b; Schmitz *et al.* 2008) is certainly anomalous in the same way as the ‘Täljsten’ in Hällekis. Localities of particular interest are the Fenxiang and Puxi River sections, where the conodont biostratigraphy (Zhang 1998b), combined with the presence of extraterrestrial chromite at Puxi (Schmitz *et al.* 2008), suggests a close stratigraphic correspondence between the ‘minimound’ interval and the ‘Täljsten’ interval.

5. Conclusions

Conclusions drawn from conodont distribution and abundance patterns support previous interpretations that the grey ‘Täljsten’ interval at Kinnekulle is the outcome of a marked sea-level fluctuation that temporarily changed the living

premises of the fauna, and interrupted the normal sedimentary conditions. This event did not cause any substantial extinction amongst the conodonts, but is rather distinguished by a reorganisation in the faunal composition, partly due to the temporary immigration of (for this setting) atypical faunal elements. Through bed-by-bed studies, the progress of this event has been established, and in turn, this has given additional indications of the ecological (depth) preferences of different conodont taxa. Furthermore, the high resolution biostratigraphy obtained has good potential for correlation to coeval strata within Baltoscandia, as demonstrated by the identification of the 'Täljsten'-equivalent layers at Fågelsång, southern Sweden.

The regression initiated already in the pre-'Täljsten' strata (lower Arkeologen bed) shown by the disappearance of *Periodon*. This was followed by the disappearance of other taxa here regarded as indicative of deeper waters in relation to the 'Täljsten', e.g. *Scalpellodus*, *Costiconus* and the *M. hagetiana*-type *Microzarkodina* fauna. Concurrently, the overall faunal structure changed to become more and more equally distributed between taxa, as well as more diversified. In the increasingly shallower basin of the lower half of the 'Täljsten' there was a change in the relative frequency of taxa, as well as the temporary immigration of a new *Microzarkodina*-fauna dominated by *M. cf. ozarkodella* and accompanied by *M. cf. bella*. Also, elements of *Panderodus* sp. A are found within this interval. The latter, presumably new, species will be described elsewhere.

For the upper half of the grey interval, the cystoid-rich Blymåkka bed initiates what is regarded as the maximum regression, which likely resulted in changed ecological conditions. This new environment promoted the establishment of cystoids on the sea-floor, but seemingly affected the frequency of conodonts negatively (not only because of a lowered amount of conodont-bearing matrix), and this interval is also characterised by a lowered diversity. However, at the same time, a minor population of *Histiodella holodentata* entered the basin, suggesting that the conditions were apt for this species of North American affinity.

The remaining part of the investigated interval reflects the end of the 'Täljsten' regressional event and the return of

relatively deeper water conditions. The first indications of a transgression are found in the topmost, green-coloured part of the 'Täljsten', by markedly higher abundance values and the immigration of numerous specimens of *Dzikodus humanensis*. In the overlying red layers, the taxonomical composition of the conodonts resembles that found below the 'Täljsten' but with some important differences, for instance the different *Drepanoistodus* fauna.

The mechanisms behind this sea-level fluctuation and the formation of the 'Täljsten' are not entirely clear and cannot be determined from faunal studies alone. Complementary data from, e.g., geochemical and petrological analyses could help give further clues to if this was climatologically induced, or connected to another event of a more cataclysmic nature, e.g. volcanism or meteoritic impacts. Moreover, data from 'Täljsten'-equivalent strata elsewhere are central in trying to understand the underlying cause. The high-resolution biostratigraphy provided in the present paper, as well as the demonstrated faunal reorganisations and occurrence patterns, have shown to have a clear potential to facilitate bed-by-bed correlations.

6. Acknowledgements

The authors are grateful to 'Kungliga Fysiografiska Sällskapet i Lund' for funding parts of the equipment used. Mats Eriksson is grateful to the Swedish Research Council for funding his research. The authors would especially like to thank Birger Schmitz, Lund, for being a driving force behind the project and for assistance in the field. He and Anita Löfgren, Lund, read an early draft of the manuscript. Johan Olsson, Lund, Mario Tassinari, Vinninga, and Stig M. Bergström, Columbus, are thanked for assistance in the field. Bergström also critically read and improved the manuscript significantly. Oliver Lehnert, Erlangen, and Stephen Leslie, Harrisonburg, acted as referees for the journal and provided very useful comments to the manuscript. Git Klintvik-Ahlberg and Carsten Tell are thanked for valuable laboratory and sample processing assistance. Finally, we would like to express our gratitude to Svend Stouge, Copenhagen, for valuable discussions on different conodont matters.

7. Appendix

Number of conodont elements and calculated ratios (in percent) for the major conodont taxa in samples used for abundance calculations.

Sample	HÄ08-Ark4	HÄ07-2	HÄ07-6	HÄ07-8	HÄ07-1	HÄ07-12	HÄ07-15	HÄ08-33
	Number of elements/kg and percentage							
Taxa								
<i>Microzarkodina</i>	1922 35	3576 41	1966 25	1915 32	1717 50	1711 54	913 28	2062 29
<i>Baltoniodus</i>	412 8	1463 17	599 8	449 8	521 15	136 4	625 19	1822 26
<i>Protopanderodus</i>	212 4	651 7	1050 14	262 4	310 9	299 10	470 14	833 12
<i>Cornuodus</i>	339 6	416 5	1056 14	490 8	261 8	327 10	385 12	40 1
<i>Drepanoistodus</i>	628 12	959 11	1087 14	831 14	243 7	230 7	261 8	882 14
<i>Semiacontiodus</i>	266 5	568 6	1106 14	773 13	120 3	82 3	75 2	83 1
<i>Lenodus/Yangtzeplacognathus</i>	115 2	176 2	273 4	457 8	180 5	191 6	292 9	547 8
<i>Decoriconus</i>	13 0	149 2	163 2	271 5	61 2	88 3	211 6	67 0
<i>Scalpellodus</i>	1440 26	658 8	413 5	402 7	18 0	22 1	43 1	575 8
<i>Drepanodus</i>	110 2	65 1	12 0	39 1	26 1	74 2	34 1	94 1
Others	24 0	22 0	2 0	4 0	1 0	9 0	0 0	13 0
Sum number of elements	5481	8703	7727	5893	3458	3169	3309	7018
Sum percentage	100	100	100	100	100	100	100	100

Number of elements and calculated ratios (in percent) for *Semiacontiodus davidi* and *Semiacontiodus cornuiformis* in samples used for abundance calculations.

Sample	HÄ08-Ark4	HÄ07-2	HÄ07-6	HÄ07-8	HÄ07-1	HÄ07-12	HÄ07-15	HÄ08-33
	Number of elements/kg and percentage							
Taxa								
<i>Semiacontiodus davidi</i>	144 54	521 92	989 89	688 89	0 0	0 0	0 0	0 0
<i>Semiacontiodus cornuiformis</i>	122 46	47 8	117 11	85 11	120 100	82 100	75 100	83 100
Sum number of elements	266	568	1106	773	120	82	75	83
Sum percentage	100	100	100	100	100	100	100	100

8. References

- Bagnoli, G. & Stouge, S. 1997. Lower Ordovician (Billingenian–Kunda) conodont zonation and provinces based on sections from Horns Udde, north Öland, Sweden. *Bollettino della Società Paleontologica Italiana* **35** (2), 109–63.
- Barnes, C. R. & Fähræus, L. E. 1975. Provinces, communities, and proposed nektonic habit of Ordovician conodontophorids. *Lethaia* **8** (2), 133–49.
- Bergström, S. M., Chen, X., Gutiérrez-Marco, J. C. & Dronov, A. 2009. The new chronostratigraphic classification of the Ordovician System and its relations to major regional series and stages and to δ^{13} chemostratigraphy. *Lethaia* **42**, 97–107.
- Branson, E. B. & Mehl, M. G. 1933–1934. Conodont studies. *Missouri University Studies* **8**, 1–349.
- Chen, J.-Y. & Lindström, M. 1991. Cephalopod septal strength indices (SSI) and depositional depth of Swedish orthoceratite limestone. *Geologica et Palaeontologica* **25**, 5–18.
- Dronov, A., Holmer, L., Meidla, T., Stuessen, U., Tinn, O. & Ainsaar, L. 2001. Detailed litho- and sequence stratigraphy of the 'Täljsten' Limestone unit and its equivalents in the Ordovician of Baltoscandia. In Harper, D. A. T. & Stouge, S. (eds) *WOGOGO-2001 Abstracts*, 8–9. Copenhagen: Geological Museum of Copenhagen and Geological Survey of Denmark and Greenland.
- Dzik, J. 1976. Remarks on the evolution of Ordovician conodonts. *Acta Palaeontologica Polonica* **21**, 395–455.
- Epstein, A. G., Epstein, J. B. & Harris, L. D. 1977. Conodont color alteration – an index to organic metamorphism. *US Geological Survey Professional Paper* **995**, 1–27.
- Ethington, R. L. & Clark, D. L. 1982. Lower and Middle Ordovician conodonts from the Ibex area, western Millard County, Utah. *Brigham Young University Geological Studies* **28** (2), 1–155.
- Graves, R. W. & Ellison, S. 1941. Ordovician conodonts of the Marathon Basin, Texas. *University of Missouri, School of Mines & Metallurgy Bulletin, Technical Series* **14** (2), 1–26.
- Hadding, A. R. 1913. Undre dicellograptusskiffern i Skåne jämte några därmed ekvivalenta bildningar. *Lunds Universitets Årsskrift. N. F., Avd 2* **9** (15), 1–90.
- Hisinger, W. 1828. Anteckningar i Physik och Geognosie under resor uti Sverige och Norrige **4**, 1–260. Stockholm: P. A. Norstedt & Söner.
- Jaanusson, V. 1976. Faunal dynamics in the Middle Ordovician (Viruan) of Balto-Scandia. In Bassett, M. G. (ed.) *The Ordovician System: Proceedings of a Palaeontological Association Symposium, Birmingham, September 1974*, 301–26. Cardiff: University of Wales Press and National Museum of Wales.
- Jaanusson, V. 1982. Ordovician in Västergötland. In Bruton, D. L. & Williams, S. H. (eds) *Field Excursion Guide, IV International Symposium on the Ordovician System. Paleontological Contributions from the University of Oslo* **279**, 164–83.
- Jaanusson, V. 1995. Confacies differentiation and upper Middle Ordovician correlation in the Baltoscandian Basin. *Proceedings of the Estonian Academy of Sciences* **44** (2), 73–86.
- Jeppsson, L. 2005. Biases in the recovery and interpretation of micropalaeontological data. *Conodont Biology and Phylogeny: Interpreting the Fossil Record* **73**, 57–71.
- Jeppsson, L., Anehus, R. & Fredholm, D. 1999. The optimal acetate buffered acetic acid technique for extracting phosphatic fossils. *Journal of Paleontology* **73**, 964–72.
- Kalm, P. 1746. *Pehr Kalms Västgötha och Bohusländska resa förrättad år 1742*, 330 pp. Stockholm: Salvius.
- Lindström, M. 1955. Conodonts from the lowermost Ordovician strata of south-central Sweden. *Geologiska föreningens i Stockholms Förhandlingar* **76**, 517–604.
- Lindström, M. 1963. Sedimentary folds and the development of limestone in an Early Ordovician sea. *Sedimentology* **2**, 243–92.
- Lindström, M. 1971. Lower Ordovician conodonts of Europe. *Geological Society of America Memoir* **127**, 21–61.
- Lindström, M. 1976. Conodont palaeogeography of the Ordovician. In Bassett, M. G. (ed.) *The Ordovician System: Proceedings of a Palaeontological Association Symposium, Birmingham, September 1974*, 501–22. Cardiff: University of Wales Press and National Museum of Wales.
- Lindström, M. 1979. Probable sponge borings in Lower Ordovician limestone of Sweden. *Geology* **7** (3), 152–5.
- Lindström, M. 1984. Baltoscandic conodont life environments in the Ordovician: sedimentologic and paleogeographic evidence. *Geological Society of America Special Paper* **196**, 33–42.
- Lindström, M. 1988. Conodont palaeobiology. *Lethaia* **21**, 291–2.
- Linnaeus, C. 1747. *Wästgöta-Resa, på riksens högloflige ständers befallning, förrättad år 1746*, 280 pp. Stockholm: Salvius.
- Löfgren, A. 1978. Arenigian and Llanvirnian conodonts from Jämtland, northern Sweden. *Fossils and Strata* **13**, 1–129.
- Löfgren, A. 1998. Apparatus structure of the Ordovician conodont *Decoriconus peselephantis* (Lindström 1955). *Palaeontologische Zeitschrift* **72**, 337–50.
- Löfgren, A. 1999a. The Ordovician conodont *Semiacontiodus cornuformis* (Sergeeva, 1963) and related species in Baltoscandia. *Geologica et Palaeontologica* **33**, 71–91.
- Löfgren, A. 1999b. A septimembrata apparatus model for the Ordovician conodont genus *Cornuodus* Fähræus, 1966. *Bollettino della Società Paleontologica Italiana* **37** (2–3), 175–86.
- Löfgren, A. 2000. Early to early Middle Ordovician conodont biostratigraphy of the Gillberga quarry, northern Öland, Sweden. *GFF* **122**, 321–38.
- Löfgren, A. 2003. Conodont faunas with *Lenodus variabilis* in the upper Arenigian to lower Llanvirnian of Sweden. *Acta Palaeontologica Polonica* **48** (3), 417–36.
- Löfgren, A. 2004. The conodont fauna in the Middle Ordovician *Eoplacognathus pseudoplanus* Zone of Baltoscandia. *Geological Magazine* **141** (4), 505–24.
- Löfgren, A. 2006. An *Oistodus venustus*-like conodont species from the Middle Ordovician of Baltoscandia. *Palaeontologische Zeitschrift* **80** (1), 12–21.
- Löfgren, A. & Tolmacheva, T. 2008. Morphology, evolution and stratigraphic distribution in the Middle Ordovician conodont genus *Microzarkodina*. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **99**, 27–48.
- Löfgren, A. & Zhang, J. 2003. Element association and morphology in some middle Ordovician platform-equipped conodonts. *Journal of Paleontology* **77** (4), 721–37.
- Nielsen, A. T. 1992. Ecostratigraphy and the recognition of Arenigian (Early Ordovician) sea-level changes. In Webby, B. D. & Laurie, J. R. (eds) *Global perspectives on Ordovician geology*, 355–66. Rotterdam: Balkema.
- Nielsen, A. T. 1995. Trilobite systematics, biostratigraphy and palaeoecology of the Lower Ordovician Komstad Limestone and Huk formations, southern Scandinavia. *Fossils and Strata* **38**, 1–374.
- Nielsen, A. T. 2004. Ordovician sea level changes: a Baltoscandian perspective. In Webby, B. D., Paris, F., Droser, M. L. & Percival, I. G. (eds) *The great Ordovician biodiversification event*, 84–93. New York: Columbia University Press.
- Pander, C. H. 1856. *Monographie der fossilen Fische des Sihirischen Systems der Russisch-Baltischen Gouvernements*. St. Petersburg: Buchdruckerei der Kaiserlichen Akademie der Wissenschaften. 91 pp.
- Pohler, S. M. L. 1994. Conodont biofacies of the Lower to lower Middle Ordovician megaconglomerates, Cow Head Group, western Newfoundland. *Geological Survey of Canada Bulletin* **459**, 1–71.
- Rasmussen, C. M. O., Hansen, J. & Harper, D. A. T. 2007. Baltica: a mid Ordovician diversity hotspot. *Historical Biology* **19** (3), 255–61.
- Rasmussen, J. A. 1991. Conodont stratigraphy of the Lower Huk Formation at Slemmestad, southern Norway. *Norsk Geologisk Tidsskrift* **71**, 265–88.
- Rasmussen, J. A. 2001. Conodont biostratigraphy and taxonomy of the Ordovician shelf margin deposits in the Scandinavian Caledonides. *Fossils and Strata* **48**, 1–180.
- Rasmussen, J. A. & Stouge, S. 1995. Late Arenig–Early Llanvirn conodont biofacies across the Iapetus Ocean. In Cooper, J. D., Droser, M. L. & Finney, S. C. (eds) *Ordovician Odyssey: Short Papers for the Seventh International Symposium on the Ordovician System. SEPM, Pacific Section, Book 77*, 443–47.
- Schmitz, B., Tassinari, M. & Peucker-Ehrenbrink, B. 2001. A rain of ordinary chondritic meteorites in the early Ordovician. *Earth and Planetary Science Letters* **194**, 1–15.
- Schmitz, B., Häggström, T. & Tassinari, M. 2003. Sediment-dispersed extraterrestrial chromite traces a major asteroid disruption event. *Science* **300** (5621), 961–4.
- Schmitz, B., Harper, D. A. T., Peucker-Ehrenbrink, B., Stouge, S., Alwmark, C., Cronholm, A., Bergström, S. M., Tassinari, M. & Wang, X. 2008. Asteroid breakup linked to the Great Ordovician Biodiversification Event. *Nature Geoscience* **1** (1), 49–53.
- Schmitz, B. & Häggström, T. 2006. Extraterrestrial chromite in Middle Ordovician marine limestone at Kinnekulle, southern Sweden – Traces of a major asteroid breakup event. *Meteoritics & Planetary Science* **41** (3), 455–66.
- Sergeeva, S. P. 1963. Conodonts from the Lower Ordovician of the Leningrad Region. *Akademi Nauk SSSR. Paleontologicheskii Zhurnal* **1963** **2**, 93–108. [In Russian.]

- Sergeeva, S. P. 1974. Some new Ordovician conodonts from the Leningrad region. *Paleontologicheskii Sbornik* **11**, 79–84. [In Russian.]
- Stauffer, C. R. 1935. Conodonts of the Glenwood beds. *Geological Society of America Bulletin* **46**, 125–68.
- Stouge, S. 1984. Conodonts of the Middle Ordovician Table Head Formation, western Newfoundland. *Fossils and Strata* **16**, 1–145.
- Stouge, S. 2001. Lower Ordovician stratigraphy from Degerhamn, Grönhögen, and Ottenby of southern Öland, Sweden. In Harper, D. A. T. & Stouge, S. (eds) *WOGOGO-2001 Abstracts*, 42–3. Copenhagen: Geological Museum of Copenhagen and Geological Survey of Denmark and Greenland.
- Stouge, S. & Bagnoli, S. 1990. Lower Ordovician (Volkhovian–Kundan) conodonts from Hagudden, northern Öland, Sweden. *Palaeontographia Italica* **77**, 1–54.
- Stouge, S. & Nielsen, A. T. 2003. An integrated biostratigraphical analysis of the Volkhov-Kunda (Lower Ordovician) succession at Fågelsång, Scania, Sweden. *Bulletin of the Geological Society of Denmark* **50**, 75–94.
- Thorslund, P. & Jaanusson, V. 1960. The Cambrian, Ordovician, and Silurian in Västergötland, Närke, Dalarna and Jämtland, central Sweden. Guide to Excursions Nos. A23 and C18. In Sorgenfrei, T. (ed.) *The Geological Survey of Sweden. International Geological Congress 21 Session, Norden 1960, Sweden, Guide Book e*, 1–51. Copenhagen: Det Berlingske Bogtrykkeri.
- Tinn, O. & Meidla, T. 2001. Middle Ordovician ostracods from the Lanna and Holen Limestones, south-central Sweden. *GFF* **123**, 129–36.
- Tinn, O., Meidla, T. & Ainsaara, L. 2006. Arenig (Middle Ordovician) ostracods from Baltoscandia: Fauna, assemblages and biofacies. *Palaeogeography, Palaeoclimatology, Palaeoecology* **241** (3–4), 492–514.
- Viira, V. 2008. Conodont biostratigraphy in the Middle–Upper Ordovician boundary beds of Estonia. *Estonian Journal of Earth Sciences* **57**, 23–38.
- Viira, V., Löfgren, A., Mägi, S. & Wickström, J. 2001. An Early to Middle Ordovician succession of conodont faunas at Maekalda, northern Estonia. *Geological Magazine* **138** (6), 699–718.
- Villumsen, J. 2001. *Trilobitzoneringen omkring Volkhov/Kunda gränsen, nedre Mellem Ordovicium, i Hällekis stenbrud, Västergötland, Sverige*. Unpublished Bachelor's Thesis, University of Copenhagen, Denmark.
- Zhang, J. 1998a. Middle Ordovician conodonts from the Atlantic Faunal Region and the evolution of key conodont genera. *Meddelanden från Stockholms Universitetets Institution för Geologi och Geokemi* **298**, 5–27.
- Zhang, J. 1998b. Conodonts from the Guniutan Formation (Llanvirnian) in Hubei and Hunan Provinces, south-central China. *Stockholm Contributions in Geology* **46**, 1–161.

MS received 15 May 2009. Accepted for publication 9 February 2010.