

Chitinozoan dynamics and biostratigraphy in the Vão Formation (Darriwilian) of the Uuga Cliff, Pakri Peninsula, NW Estonia

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Abstract. The distribution of chitinozoans in the Vão Formation (Lasnamägi and Uhaku regional stages, Darriwilian) of the Uuga Cliff, Pakri Peninsula, NW Estonia, was investigated from 62 samples. Chitinozoans are very common and assemblages are diverse, with a total of 36 species and up to 170 specimens per gram of rock. The assemblage is dominated by *Belonechitina*, *Desmochitina*, *Cyathochitina*, and *Euconochitina*. The relative and absolute frequency of particular taxa displays regular and possibly cyclic patterns, which are not directly reflected in lithology or geochemistry. Abrupt changes in chitinozoan abundance, coinciding with some of the discontinuity surfaces, suggest the presence of stratigraphical gaps. The diversity of chitinozoans is the highest in the lower part of the Vão Formation (Rebala Member), where up to 20 species were identified in one sample and the standing species diversity exceeded 25. Within the studied interval at least 11 biostratigraphical horizons can be distinguished, including the subzonal boundaries within the *Laufeldochitina striata* Zone. The disappearance of abundant *Belonechitina pellifera* can be used for tracing the lower boundary of the Uhaku Stage.

Key words: chitinozoans, frequency patterns, diversity, biostratigraphy, Ordovician, Estonia.

INTRODUCTION

The Middle Ordovician Darriwilian Stage includes the uppermost Volkhov, and the Kunda, Aseri, Lasnamägi, and Uhaku regional stages in the Baltic region. This stage falls within a crucial interval of geological time characterized by rapid diversification of several groups of organisms (see, e.g., Servais et al. 2009 and references therein).

The chitinozoans, most likely representing a reproductive stage of yet unknown marine metazoans (Paris & Nõlvak 1999), originated in the Early Ordovician. However, it was in the Darriwilian when they became a diverse group and common microfossils. Next to graptolites and conodonts, chitinozoans are some of the most useful index fossils for the entire Ordovician (Paris et al. 2004; Webby et al. 2004). Their huge biostratigraphical potential was first suggested by Männil (1969, 1971, 1972), who successfully correlated Ordovician sequences between the East Baltic and Scandinavia. Since then many studies on Ordovician and Silurian chitinozoans of Estonia and neighbouring areas have been published. The Ordovician chitinozoan biozonation of Baltoscandia was formally proposed by Nõlvak & Grahn (1993), and later updated by Nõlvak (1999) and Nõlvak et al. (2006). This biozonal scheme is nowadays widely used for regional and wider correlations (e.g. Webby et al. 2004).

Although the largest chitinozoan collections in the world come from the Baltic area (Paris et al. 2004), our knowledge of their taxonomy and distribution in the Baltic Darriwilian is still unsatisfactory. A number of Darriwilian species are yet to be described and their biostratigraphical potential to be fully utilized.

This study concentrates on the upper Darriwilian Vão Formation and its under- and overlying strata, which represent an interval of rapid increase in chitinozoan abundance and diversity in the Baltic area. Better documentation of this diversification episode and improved biostratigraphical resolution have been the main objectives of this study. With respect to biostratigraphy, finding new criteria for the lower boundary of the Uhaku Stage and correlation between the chitinozoan and conodont biozones have been of particular interest. We also aimed at obtaining abundance and relative frequency data on East Baltic Ordovician chitinozoans. Hitherto such data are practically missing except for the report by Grahn (1984) from Tallinn, northern Estonia. Yet, quantitative microfossil data may contribute to a better understanding of palaeoenvironments and depositional regime, and aid regional biostratigraphy.

The Vão Formation is also of economic interest as it contains the so-called Lasnamägi Building Limestone that has been actively quarried and used in constructions for more than 600 years. Precise dating of these beds may help, for instance, archaeologists and restoration builders in their work.

The studied locality is an easily accessible coastal cliff on the Pakri Peninsula, representing the best Lower Cambrian to Middle Ordovician succession in north-western Estonia. In spite of the fact that several palaeontological studies have been conducted on the Pakri succession in recent decades and the sections are frequently visited by geologists, the Darriwilian biostratigraphy has remained virtually unknown in this locality. The present study aims to fill this gap.

GEOLOGICAL SETTING AND STRATIGRAPHY

During the Darriwilian the Baltica palaeocontinent, with the epicontinental Baltic palaeobasin, was located between 60° and 30° southern latitudes, drifting northwards (Cocks & Torsvik 2005). At that time the Baltic palaeobasin was characterized by carbonate sedimentation in the areas of present-day Sweden, Estonia, Latvia, Lithuania, and NW Russia.

The Uuga coastal cliff (59°21'41"N, 24°2'22"E; outcrop 4a of Orviku 1940) is located on the Pakri Peninsula, NW Estonia, some 50 km west of Tallinn. This area represents shallow-water settings of the Ordovician palaeobasin, traditionally called as the North Estonian Confacies or Estonian Shelf (Fig. 1). Fennoscandian land was located north of it, whilst deeper shelf environments, known as the Central Baltoscandian Confacies or Livonian Basin, were present to the south and to the west (in South Estonia, Latvia, and Sweden). The configuration and development of the Baltic palaeobasin are discussed in detail by, e.g., Männil (1966) and Nestor & Einasto (1997).

The studied 6-m succession is composed of limestones (wacke- to packstones, occasional grainstone interbeds) and secondary dolostones. Above the dolomitic Pae Member, limestones are slightly dolomitized (dolomite reaching to ca 12%). The content of siliciclastic material varies generally between 5% and 15% (average ca 8%) in the Vão Formation, reaching ca 25% in the Aseri Formation (Fig. 2). Siliciclastic material is mostly represented by clay, except in the Aseri Formation, where phosphatic or goethitic oolites and admixture of quartz sand are recorded. Numerous impregnated and commonly bioturbated discontinuity surfaces occur in the studied interval (Fig. 2, see also Orviku 1940). The $\delta^{13}\text{C}$ stable carbon isotope curve only shows small variations, mostly between -1.0‰ and 0.0‰ , with an increasing trend in the Aseri and lower Lasnamägi stages and slightly decreasing values in the Uhaku Stage (Fig. 2). The Vão Formation on the Pakri Peninsula is rich in shelly fauna and various groups of acid-resistant microfossils such as acritarchs, chitinozoans, scolecodonts, and conodonts.

An up-to-date stratigraphical scheme on the studied interval is provided by Nõlvak et al. (2006). Individual rock units of this interval are described in full by, e.g.,

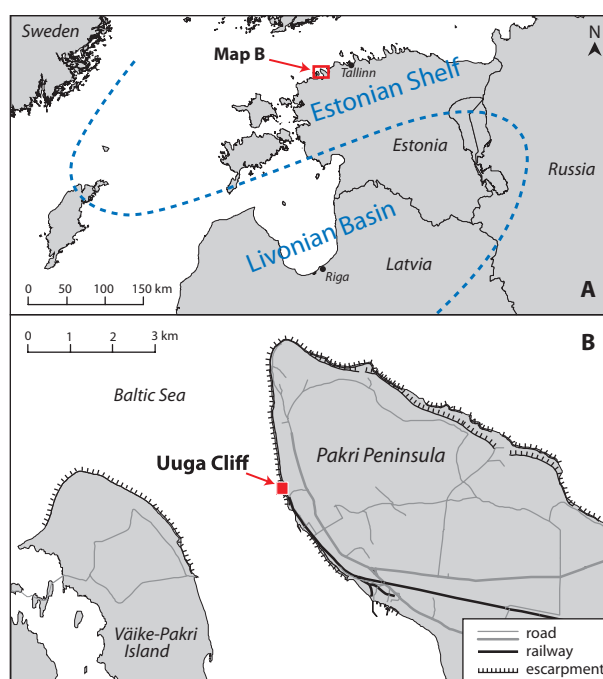


Fig. 1. (A) General map showing the distribution of shallow-water (Estonian Shelf) and deeper-water settings (Livonian Basin) during the Darriwilian. (B) Location of the Uuga Cliff on the Pakri Peninsula.

Orviku (1940), Rõõmusoks (1970), and Hints (1997). The Vão Formation spans the Lasnamägi and Uhaku regional stages and is underlain by the Aseri Formation (Aseri Stage) and overlain by the Kõrgekallas Formation (Uhaku Stage). It is further subdivided into the Rebala, Pae, and Kostivere members. The Pae and Kostivere members and the lower part of the Kõrgekallas Formation make up the so-called Lasnamägi Building Limestone. Local quarrymen have named over 50 individual beds within this unit. Many of these units can be recognized all over northern Estonia (e.g. Einasto & Hints 2004), denoting a very flat sea-floor and uniform depositional conditions as suggested also by, e.g., Jaanusson (1976). The succession of the Building Limestone on the Pakri Peninsula is discussed and illustrated by Einasto & Rähni (2005; based on the Paldiski 5 drill core).

The boundary between the Lasnamägi and Uhaku stages falls within the Vão Formation and is approximated by the first appearance datums (FADs) of the graptolite *Gymnograptus linnarssoni* and conodont *Eoplacognathus robustus* (e.g. Männil 1986). In the type section in Tallinn this boundary is drawn at the level of a marked discontinuity surface within the bed named 'Raudsüda', above which *G. linnarssoni* appears. In the Uuga section the same discontinuity surface is recognized at 2.45 m above the base of the Vão Formation. According to V. Viira (pers. comm. 2009), *E. robustus* appears ca 0.25 m below that level. A single find of *G. linnarssoni* comes from

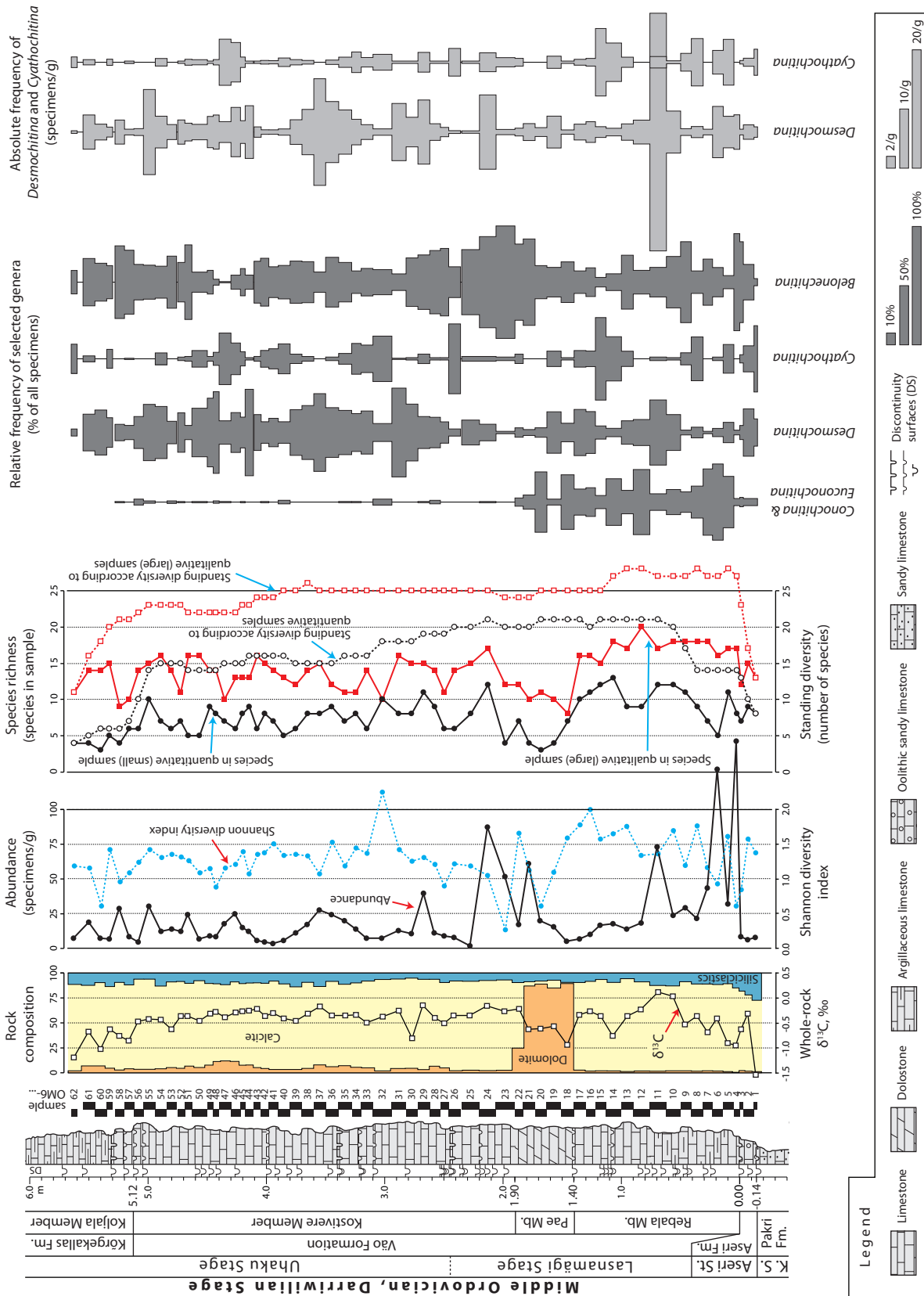


Fig. 2. Stratigraphy, composition of rocks, $\delta^{13}\text{C}$ curve, and the abundance, diversity, and relative frequency of the most common chitinozoan genera in the Uuga Cliff. St., stage; Fm., formation; K.S., Kunda Stage; DS, discontinuity surface.

slightly younger strata (ca 3.2 m from the base of the Vão Formation), which probably indicates unfavourable environment rather than the true FAD of this species.

MATERIAL AND METHODS

The study is based on 62 bed-by-bed samples collected in 2006 for integrated geochemical and micropalaeontological analysis from the Aseri, Lasnamägi, and Uhaku stages of the Uuga Cliff. The sampling depths are measured from the base of the Vão Formation. The samples are numbered consecutively from OM6-1 (lowermost) to OM6-62 (uppermost); for brevity they are referred to as samples 1 to 62 in this paper.

All bulk rock samples were split into three parts before processing. In order to obtain abundance and relative frequency data on chitinozoans, 1–40 g (on average 10 g) of each initial sample was digested using diluted hydrochloric acid. From these ‘portions’, referred to as quantitative samples below, all chitinozoans were picked and counted. In order to reveal large and rare species, assess variability of chitinozoans, and study conodonts and scolecodonts, another 250–1100 g (on average 700 g) of each bulk sample was treated with diluted acetic acid. From these ‘portions’, referred to as qualitative samples, only a selection of chitinozoans were picked. The remaining parts of the bulk samples were used for geochemical and lithological analyses, and kept for future reference. Two of the bulk rock samples (24 and 25) were further split into nine stratigraphically successive ‘spot samples’, 1–15 g each, for detailed abundance analysis. The acid preparation residues were sieved through a 20 or 45 µm mesh; chitinozoans were hand-picked and stored in glycerin.

The term *abundance* used in this paper means the number of chitinozoan specimens per gram of rock;

relative frequency denotes the percentage of a taxon in a sample. Diversity indices were calculated and some statistical analyses performed with the PAST software (Hammer et al. 2001). Chitinozoan classification in this study follows Paris et al. (1999).

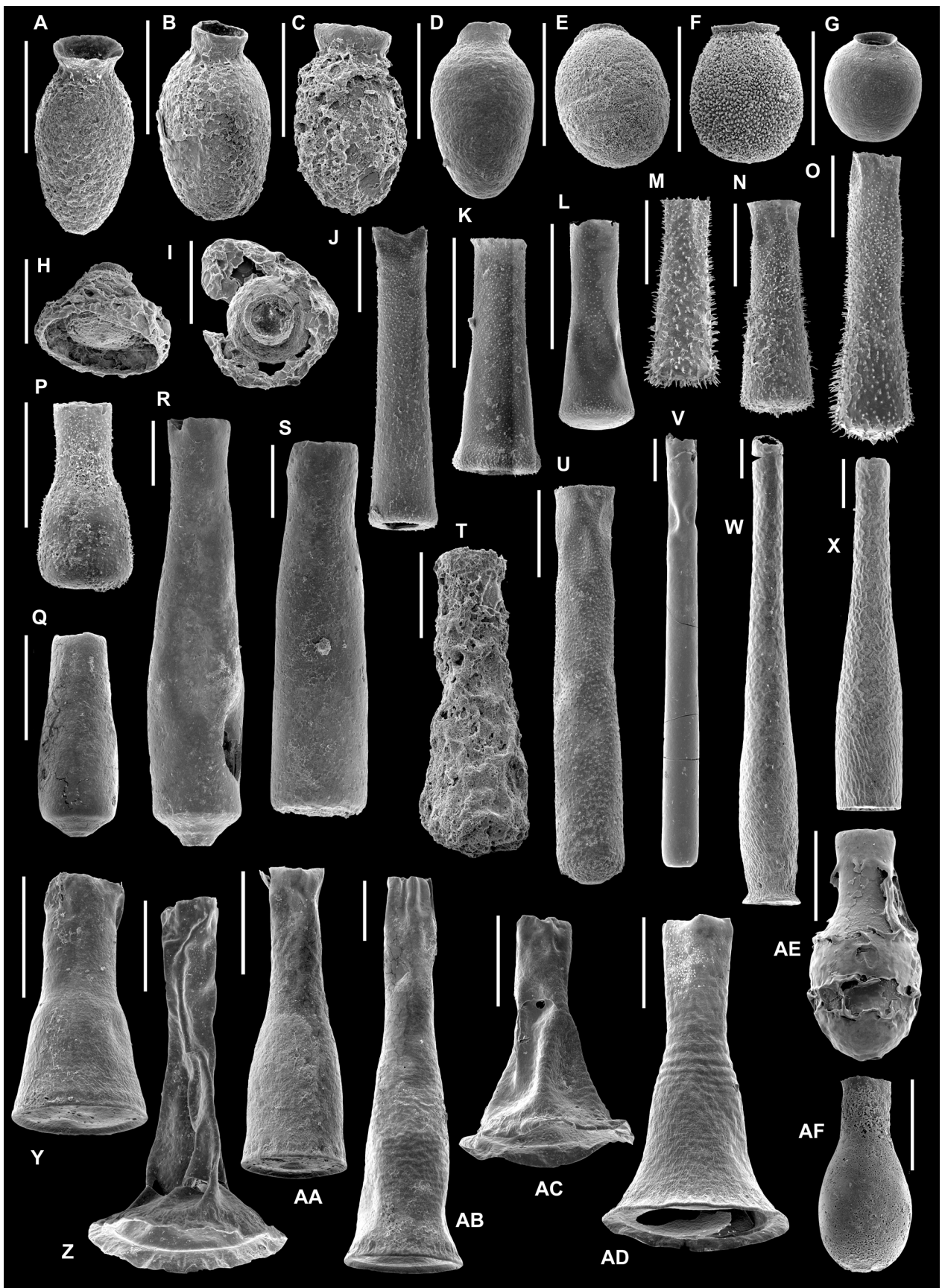
Background information on rock composition was obtained from polished and thin sections, and from XRF chemical analysis of 11 major elements (Mg, Al, Si, P, S, K, Ca, Ti, Mn, Fe, Ba). Additionally, whole-rock $\delta^{13}\text{C}$ was measured from all samples. The research was conducted at the Institute of Geology at Tallinn University of Technology (GIT), where also the samples, residues, and all recovered specimens are deposited. For figured specimens the collection number 590 is allocated. More information on individual samples and specimens can be obtained from the on-line catalogue at <http://sarv.gi.ee>.

RESULTS AND DISCUSSION

The chitinozoan fauna

Chitinozoans are very common in all samples studied. Approximately 10 600 specimens were picked, identified, and counted from the quantitative samples. In the set of large (qualitative) samples the total yield was roughly 100 times larger, but not all specimens were picked and none were counted. Altogether 36 different species have been identified, including a few morphologically distinct and stratigraphically constrained species which are referred to under open nomenclature. The preservation of organic-walled microfossils is mostly good to excellent in the sampled section, but poor in dolostone of the Pae Member and partly in dolomitized and/or weathered limestones of the Kostivere Member and Kõrgekallas Formation. Selected characteristic chitinozoans are illustrated in Fig. 3.

Fig. 3. Scanning electron micrographs of selected Darriwilian chitinozoans from the Uuga Cliff, Pakri Peninsula. Scale bar corresponds to 100 µm. All specimens from the Vão Formation, except Y and Z, which come from the Aseri Formation. **A**, *Desmochitina elongata* Eisenack, GIT 590-1, sample OM6-23. **B**, *Desmochitina ovulum* Eisenack, GIT 590-2, sample OM6-13. **C**, *Desmochitina rugosa* Eisenack, GIT 590-3, sample OM6-13. **D**, *Desmochitina piriformis* Laufeld, GIT 590-4, sample OM6-23. **E**, *Desmochitina minor* s.l. Eisenack, GIT 590-5, sample OM6-13. **F**, *Desmochitina erinacea* Eisenack, GIT 590-6, sample OM6-13. **G**, *Desmochitina cocca* (Eisenack), GIT 590-7, sample OM6-13. **H**, *Pterochitina retracta* (Eisenack), GIT 590-8, sample OM6-6. **I**, *Pterochitina retracta* (Eisenack), GIT 590-9, sample OM6-23. **J**, *Belonechitina micracantha* (Eisenack), GIT 590-10, sample OM6-4. **K**, *Belonechitina micracantha* (Eisenack), GIT 590-11, sample OM6-22. **L**, *Belonechitina micracantha* (Eisenack), GIT 590-12, sample OM6-22. **M**, *Belonechitina crinita* (Grahn), GIT 590-13, sample OM6-13. **N**, *Belonechitina pellifera* (Eisenack), GIT 590-14, sample OM6-17. **O**, *Belonechitina pellifera* (Eisenack), GIT 590-15, sample OM6-17. **P**, *Belonechitina cactacea* (Eisenack), GIT 590-16, sample OM6-22. **Q**, *Conochitina* sp., without covering, GIT 590-17, sample OM6-16. **R**, *Conochitina clavaherculi* Eisenack, GIT 590-18, sample OM6-12. **S**, *Conochitina clavaherculi* Eisenack, GIT 590-19, sample OM6-12. **T**, *Conochitina* sp., with covering, GIT 590-20, sample OM6-16. **U**, *Conochitina tuberculata* (Eisenack), GIT 590-21, sample OM6-56. **V**, *Rhabdochitina magna* (Eisenack), GIT 590-22, sample OM6-56. **W**, *Laufeldochitina striata* (Eisenack), GIT 590-23, sample OM6-12. **X**, *Laufeldochitina striata* (Eisenack), GIT 590-24, sample OM6-12. **Y**, *Cyathochitina campanulaeformis* (Eisenack), GIT 590-25, sample OM6-1. **Z**, *Cyathochitina sebyensis* Grahn, GIT 590-26, sample OM6-3. **AA**, *Cyathochitina calix* (Eisenack), GIT 590-27, sample OM6-47. **AB**, *Cyathochitina calix* (Eisenack), GIT 590-28, sample OM6-9. **AC**, *Cyathochitina kuckersiana* (Eisenack), GIT 590-29, sample OM6-12. **AD**, *Cyathochitina* cf. *sebyensis* Grahn, GIT 590-30, sample OM6-13. **AE**, *Lagenochitina tumida* Umnova, with partly detached covering, GIT 590-31, sample OM6-12. **AF**, *Lagenochitina tumida* Umnova, GIT 590-32, sample OM6-12.



Abundance

The abundance of chitinozoans in the studied interval extends from ca 1.5 to 170 specimens per gram of rock, with an average of 22 specimens per gram (Figs 2 and 4). It is rather low in the Aseri Stage (6–8 vesicles per gram), highly variable in the Lasnamägi Stage (1.5–170), and less fluctuating in most part of the Uhaku Stage (5–30).

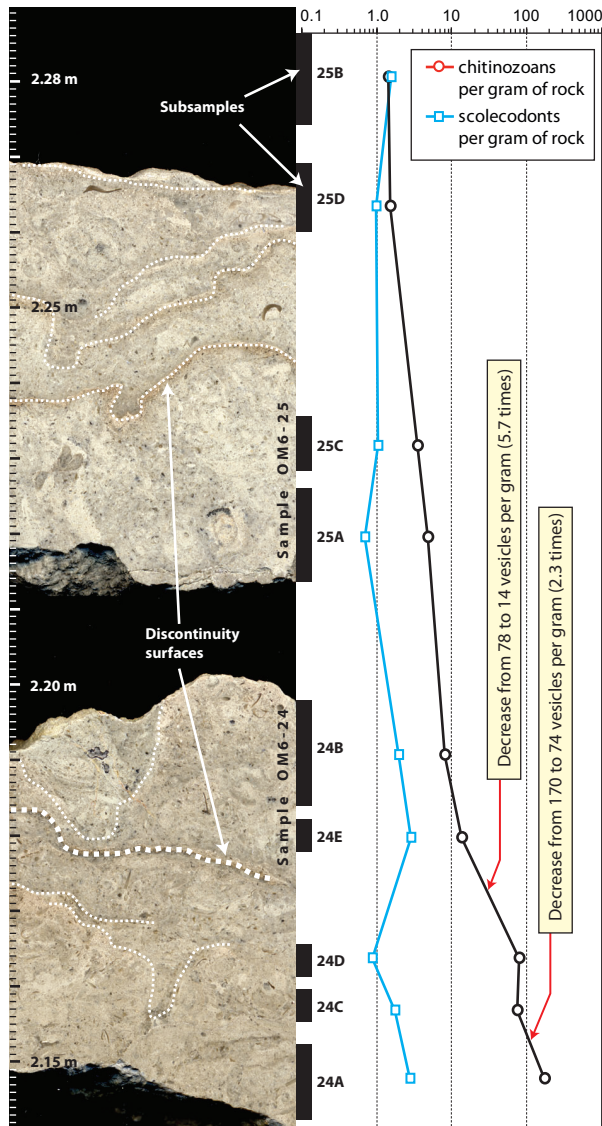


Fig. 4. Detailed abundance curves of chitinozoans and scolecodonts in samples OM6-24 and OM6-25, based on nine successive ‘subsamples’ to achieve higher temporal resolution. For general abundance curve see Fig. 2. The top of sample OM6-25 was on a separate small rock slab that could not be polished and scanned. The ca 1.5 cm gap between samples OM6-24 and OM6-25 is due to difficulties in taking monolithic samples from a vertical cliff wall. Note that the graph is drawn in the logarithmic scale.

The maximum abundance values were recorded in the basal beds of the Rebala Member and in the lowermost part of the Kostivere Member. Minimum abundance was observed in sample 25 close to the Lasnamägi–Uhaku boundary.

Grahn (1984) studied chitinozoans of the same interval from Tallinn, some 50 km to the east of the Uuga Cliff (Fig. 1A). Both localities belong to the shallow-water Estonian shelf and the environmental gradients between the two localities were supposedly subtle. Grahn (1984) reported somewhat smaller abundance values in the Aseri (2–6 specimens per gram) and Uhaku stages (5–10, occasionally 21 specimens per gram). The difference is more pronounced in the Lasnamägi Stage, where Grahn (1984) found generally less than 2 specimens per gram in the lower part of the stage, and 7–15 specimens per gram in the upper part of the stage, with a maximum of 7 and 48 specimens, respectively. This discrepancy may partly be a result of different sediment accumulation rates that have ‘diluted’ microfossils in the matrix in the Tallinn area, where the entire Vao Formation is 1.5–2 times thicker than on the Pakri Peninsula. However, this alone is not sufficient to explain 10-fold differences in chitinozoan abundance. As far as a methodological off-set cannot be ruled out, the question awaits resampling of the Tallinn section in order to test if such a difference truly exists and is statistically significant. Only then possible factors responsible for notable areal as well as stratigraphical variations in abundance can be discussed and perhaps explained. A similar, likely methodological difference between data of different chitinozoan students has previously been reported by Vandembroucke (2004) from the Fågelsång section, Sweden.

The question about possible causes of abundance variations rises also in case of a single section. Studying lower Silurian microfossils, Hints et al. (2006) noted that chitinozoans often display highly variable abundance patterns not matching the lithological change. Grahn (1982) also reported that fluctuations in chitinozoan abundance could not be correlated with lithology. The same is true of the Uuga section, where notable changes in chitinozoan abundance occur in lithologically rather monotonous intervals. For instance, the interval at ca 3–4.5 m displays two gentle peaks in the abundance curve, which are traced on the basis of nearly 20 samples (Fig. 2) and thus unlikely occasional. Similar trends in rock composition could not be detected.

A considerable drop in abundance occurs between samples 24 and 25, where the number of vesicles decreases from ca 90 to 2 per gram of rock. Both samples contain several discontinuity surfaces (DS), but otherwise the lithology is very similar and no clear indications for, e.g., a transgressive event or major change in the

deposition rate can be detected (Fig. 2). In order to obtain more information about this particular change, a separate set of centimetre-scale samples was studied. The results illustrated in Fig. 4 show that the number of vesicles first decreases sharply from ca 170 to 70 within sample 24, and then drops further to ca 14 vesicles per gram at the level of a pyritized DS. Possibly the actual sharp change coincides with the DS and the strata 2–3 cm below it contain a time-averaged assemblage. Hence the DS most likely marks a stratigraphical gap, which is also supported by the appearance of the zonal conodont *Eoplacognathus robustus* in sample 25. Above this DS a smooth decrease in abundance continues, achieving the minimum value of 1.4 vesicles per gram in the upper part of sample 25. In that sample several phosphatic DSs occur (Fig. 4), but they seem to lack clear relationship with chitinozoan abundance. In contrast to chitinozoans, the abundance of polychaete jaws shows only slight variations in the same interval (ca 1–3 maxillae per gram of rock; Fig. 4). Therefore, the decreasing chitinozoan abundance cannot be explained by general depositional processes that would affect all microfossils with a similar size and composition.

Grahn (1982) suggested that several physical factors such as temperature, salinity, and nutrient input may have been responsible for variations in chitinozoan abundance, leaving no obvious traces in lithology. The same explanation may perhaps apply to the Vão Formation of the Uuga Cliff section. However, other localities need to be studied in order to exclude the possible effects of, e.g., local currents and hydrodynamic concentration.

Genus- and species-level frequency patterns

The most common genera that dominate the chitinozoan faunas in the Uuga section are *Belonechitina* and *Desmochitina*. The maximum relative frequency of these genera is 95% and 75%, respectively. Throughout the section species of *Cyathochitina* display several stratigraphically restricted pulses of higher frequency, accounting occasionally for nearly 70% of recovered vesicles (Fig. 2). In the Rebala Member also *Euconochitina* often predominates in the assemblage, with a maximum of 65% of specimens. All other genera, including *Conochitina*, *Pterochitina*, *Rhabdochitina*, and *Laufeldochitina*, may be common, but their relative frequency typically remains well below that of the aforementioned taxa.

The dominant species make up 20–90% and on average 40% of the assemblage. The most common chitinozoan in the Uuga Cliff is *Belonechitina micracantha* s.l., whose relative frequency peaks in the basal part of the Rebala Member and basal part of the Kostivere Member (note the frequency charts in Fig. 2).

Other species that may account for more than half of specimens in a sample are *Euconochitina primitiva*, *Cyathochitina calix*, *Cyathochitina campanulaeformis*, and *Desmochitina minor* s.l.

Relative frequency, expressed as percentage, is dependent on other taxa found in a sample. Thus the absolute frequency (i.e. abundance, specimens per gram of rock) of a particular taxon may be rather different from its relative frequency curve. To illustrate this feature, absolute frequency curves of *Desmochitina* and *Cyathochitina* are shown in Fig. 2 (a selection was made since all other genera could not be fitted into the same scale). One can see that in case of *Cyathochitina* the two curves are relatively similar, but notably different for *Desmochitina*. For instance, continuous increase was detected in relative frequency of *Desmochitina* in samples 26–31 but not in absolute frequency. Samples 24 and 25 were rather similar in relative frequency but very different with respect to absolute frequency.

The frequency curves of particular genera or species seem not to be occasional but represent a rather regular pattern. This is best illustrated by the fluctuating frequency of *Desmochitina* (Fig. 2; note that *Desmochitina* accounts largely also for the above-discussed abundance fluctuations).

Grahn (1982) was able to distinguish three groups of Middle Ordovician chitinozoan taxa, each with different environmental preferences: (1) high water energy (shallow-water) taxa, (2) low water energy taxa, and (3) ‘facies-independent’ taxa. For instance, *Desmochitina* was reported to reach its maximum frequency in skeletal sand bottoms with relatively high water energy in Sweden (Grahn 1981, 1982). When applying the same concept to interpret frequency patterns in the Uuga section, one might expect that *Desmochitina*-dominated intervals (for instance sample 37) represent shallower-water conditions than intervals with a smaller proportion of the same genus (sample 40). However, only slight variations in skeletal sand content and composition, and bulk-rock geochemistry were detected between these samples. The frequency curves of other taxa show no better correlation with lithological or geochemical data. This supports the opinion of Vandembroucke et al. (2009) that chitinozoans (and most likely their parent organisms) were epi-planktonic and water-mass-specific rather than facies-specific.

On a larger scale, however, there seems to be a certain correspondence to Grahn’s data. In the Gullhøgen Formation (lower Uhaku Stage in Västergötland, Sweden), which represents more offshore environments than in northern Estonia, the average proportion of *Desmochitina* is much lower than in the Uuga Cliff, remaining mostly below 10% and only occasionally reaching 20% (Grahn 1981). At the same time, *Laufeldochitina striata*, a ‘low

water energy species', reached well over 50% in the Gullhøgen Formation (Grahm 1981). In the Uuga section, the latter species accounts only for a few per cent of the assemblage.

Diversity

The diversity of an assemblage can be estimated by species richness or various diversity indices. The former may be expressed by the number of species actually recorded in a sample. When studying the succession of samples (or time slices), diversity curves can take into account also range-through taxa.

In the Uuga Cliff 8–20 (on average 14) species were recorded in qualitative (large; see methods above) samples, the highest values occurring in the Rebala Member. In quantitative (small) samples only 3–13, and on average 7.5 species were identified (Fig. 2). The total diversity curves including range-through species also show notable difference between small and large samples, suggesting that less than 50 g samples are clearly inadequate for documenting taxonomic diversity in the studied section and similar limestone successions. The total diversity based on large samples reaches 28 in the Rebala Member, 25 up to ca 3.7 m level, and displays a decreasing trend upwards.

According to Hints et al. (2009) and Paris et al. (2004), the total diversity of chitinozoans in the Aseri–Lasnamägi–Uhaku interval of the entire Baltoscandian area is some 45 species, whilst the estimated mean standing diversity is only about 30. This is very close to what is observed in the Uuga section. It may be argued that this single section is taxonomically very diverse and complete, but more likely the hitherto provided assessments of the mean standing diversity underestimate the actual taxonomic richness of late Darriwilian chitinozoan faunas of Baltica.

The diversity indices, such as the widely used Shannon index (see Hammer et al. 2001), take into account both the number of taxa as well as the number of individuals. The more taxa are present and the more evenly they are represented, the higher is the index. Generally higher values indicate smaller environmental stress. In the Uuga section the index is highly variable, fluctuating between 0.5 and 2. It is somewhat higher in the Rebala Member, roughly showing an increasing trend. Low values are encountered within the Pae Member, but these likely result from poor preservation of chitinozoans. In the Kostivere and Koljala members the Shannon diversity stays mostly between 1.0 and 1.5, with a probably random peak in sample 32. No clear trend can be seen in this interval. It should be noted that the Shannon index correlates rather well with the observed species richness. On the other hand, there is no obvious

relationship between the diversity and abundance, except that the highest abundances are recorded in relatively low diversity samples (Fig. 2).

Both the species richness and diversity index calculations show that generally the Rebala Member is characterized by somewhat higher diversity of chitinozoans than the overlying Pae, Kostivere, and Koljala members (but note that the data from the Pae Member may be biased due to poor preservation). Additionally certain small-scale diversity fluctuations can be observed, but not fully interpreted as of now. Compared to Grahm's (1984) data from Tallinn, northern Estonia, chitinozoan diversity is somewhat higher in the Uuga Cliff, but this may well be attributed to methodological differences and recent advancements in taxonomy.

Biostratigraphy

The general (qualitative) picture of chitinozoan distribution in the Vão Formation is relatively invariable, which probably indicates rather uniform sedimentological conditions as well as a short period of geological time. Many species, particularly of *Desmochitina* and *Belonechitina*, range throughout the sampled interval, being of limited use for biostratigraphy (Fig. 5). Others, however, can be useful for dating and subdividing the rocks of the Vão Formation.

The Vão Formation corresponds to the *Laufeldochitina striata* chitinozoan total range zone (Nölvak & Grahm 1993). In the Uuga section *L. striata* was recovered in most of the qualitative samples (Fig. 5). In smaller quantitative samples, however, only rare specimens were found, indicating that at least ca 300 g samples are needed to establish accurate biostratigraphy. The *L. striata* Zone is further subdivided into three subzones (*Cyathochitina sebyensis*, *Conochitina clavaherculi*, and Lower *Conochitina tuberculata*) that can also be recognized in the Uuga Cliff (Fig. 5).

A new species of *Baltochitina* was found in the lower part of the Aseri Formation. The same form has previously been recorded in the Kunda Aru quarry, NE Estonia, in the lower or middle part of the Aseri Formation. *Desmochitina grandicolla* is also typical of the Aseri Formation, with only a single specimen recorded in the basal Vão Formation.

The Aseri–Vão boundary is marked by the appearance of *Belonechitina pelifera* and *Conochitina* sp. n. 1. *Cyathochitina sebyensis*, *Belonechitina crinita*, *Pterochitina retracta*, and *Tanuchitina tallinnensis* also appear approximately at the same level. The basal part of the Vão Formation corresponds to the *C. sebyensis* Subzone. *Tanuchitina tallinnensis* and *Conochitina* sp. n. 1 disappear and the first specimens of *Conochitina clavaherculi* appear some 0.4 m above the base of

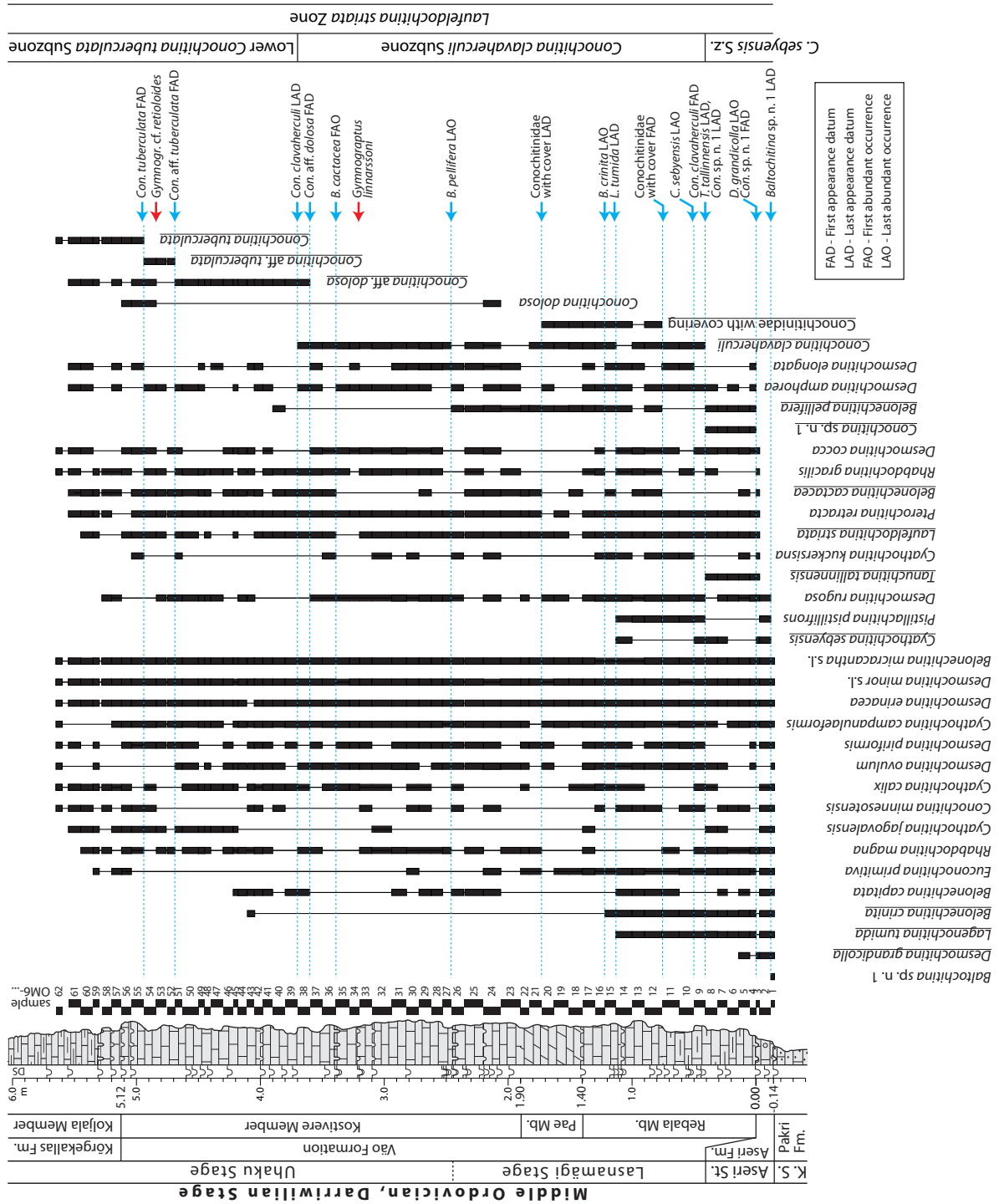


Fig. 5. Distribution of chitinozoans and biostratigraphical importance of the Uga Cliff. Taxa of biostratigraphical importance are underlined. For lithological legend and abbreviations see Fig. 2.

the formation, marking already the base of the *Con. clavaherculi* Subzone.

The interval between 0.8 and 1.7 m contains conochitinids with peculiar light-brownish soft covering (Fig. 3T). Although these forms may include different species, the temporal distribution of this structure seems to be restricted and may be of regional stratigraphical utility. The level of ca 1.2 m corresponds to the last appearance datum (LAD) of *Lagenochitina tumida* and the end of continuous and abundant occurrence of *B. crinita*. Only two specimens of the latter species are found higher up in the section in sample 43 (4.1 m from the base of the formation). A similar distribution pattern was observed also in the case of *B. pellifera*, whose continuous range ends at ca 2.4 m, at the lower boundary of the Uhaku Stage. Rare specimens are found ca 1.5 m above that level in sample 40. For regional biostratigraphy continuous ranges are indeed more useful.

Almost continuous and abundant occurrence of *Belonechitina cactacea* begins at 3.4 m, coinciding with a lithological marker horizon known as the ‘double discontinuity surface’. *Conochitina* aff. *dolosa* appears and *Con. clavaherculi* disappears at 3.6–3.7 m, marking the base of the Lower *Con. tuberculata* Subzone. Note that Nölvak et al. (2006) proposed defining the base of the Lower *Con. tuberculata* Subzone as the appearance of the nominal species. It seems, however, to be more practical to follow the original definition for the base of the *Con. tuberculata* Subzone provided by Nölvak & Grahn (1993). Thus, in this paper the base of the Lower *Con. tuberculata* Subzone is drawn at the top of the last occurrence of *Con. clavaherculi*. The actual appearance of the *Conochitina tuberculata* group, containing also *Con. aff. tuberculata* (*Con. subtuberculata* nom. nud. of Männil 1986, fig. 2.1.1), begins at 4.7 m in the uppermost Vão Formation. The first specimens of *Con. tuberculata* are recorded just below the lower boundary of the Kõrgekallas Formation at a depth of 4.9 m.

The above-described pattern conforms generally well with earlier data (e.g. Grahn 1984; Männil 1986, fig. 2.1.1; Nölvak 1999). In few cases, however, the ranges recorded in the Uuga section are slightly different. For instance, *L. tumida* seems to disappear earlier in the Uuga Cliff than in the Lasnamägi section discussed by Männil (1986). Biostratigraphically significant *Cyathochitina regnelli* and *Baltochitina nolvaki* (‘*Sagenachitina*’ in Männil 1986) were not recovered from the Uuga section.

Männil & Rubel (1969) and Nölvak (1972) applied recurrent abundance zones of *Cyathochitina campanulaeformis*, *C. kuckersiana*, and *C. calix*, and barren intervals in between them, to subdivide and

correlate early Late Ordovician (Uhaku to Haljala stages) in northeastern Estonia. Männil (1986, fig. 2.1.1), using the term ‘zonule’ for this kind of units, extended the concept also to the Lasnamägi Stage of the Tallinn area. In the Uuga section species of *Cyathochitina* are common, but the recurrent ‘zonules’ of Männil (1986) cannot be unambiguously followed. Further data from between Pakri and Tallinn are needed to resolve this question. The range of *C. sebyensis* fits, however, well with previous data. The abundant occurrence of *C. calix*, which begins at the level of the Lasnamägi–Uhaku boundary in the Lasnamägi section (Männil 1986), is observed in slightly younger strata in the Uuga Cliff (sample 32, ca 0.5 m above the boundary).

Apart from chitinozoan distribution, it is interesting to note that graptoloids were very rare in the Uuga section. Only a single specimen of *Gymnograptus linnarssoni* was found in sample 34 and *G. cf. retiolooides* occurred in sample 54.

CONCLUDING REMARKS

Chitinozoans are common and diverse microfossils in the Vão Formation and its under- and overlying strata, with at least 36 species recorded, and up to 170 specimens per gram of rock. Their abundance and relative frequency show rather regular and possibly cyclic fluctuations, which are not correlated with lithological or geochemical data. Whilst some chitinozoan species seem to display environmental preferences on a larger scale, some other explanation is needed for successive frequency fluctuations within the Uuga section. Possibly these are related to changes in, e.g., temperature, currents, or nutrient supply that are not directly reflected in lithology.

Numerous discontinuity surfaces that are common in the Vão Formation represent different events or processes. Only some of them coincide with notable changes in chitinozoan abundance and relative frequency, probably marking stratigraphical gaps. Hence quantitative data on chitinozoans may turn useful for interpreting sedimentary successions and possibly for stratigraphy.

Chitinozoan biodiversity, which shows a marked peak in the late Darriwilian of Baltica, is complemented by the data from the Uuga Cliff. The highest chitinozoan diversities within the studied interval were recorded in the Rebala Member of the Vão Formation, where the standing species diversity exceeds 25. From the methodological point of view, it turned out that 5–20 g samples yielding many hundreds of vesicles are still too small for adequate diversity estimations as well as for detailed biostratigraphy.

At least 11 biostratigraphical horizons, including the subzonal boundaries of the *Laufeldochitina striata* Zone, can be distinguished within the studied interval. The disappearance of abundant *Belonechitina pelfifera* seems to serve as a good proxy for tracing the lower boundary of the Uhaku Stage, which is otherwise identified by graptolites and conodonts. These levels could be useful for regional refinement of biostratigraphical subdivision of the Vão Formation and dating parts of the Lasnamägi Building Limestone. In order to test if the observed chitinozoan ranges and frequency patterns are primarily time-controlled, environmentally caused, or simply represent changes in the hydrodynamic regime and local currents, data from other sections are needed.

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Väo kihistu (Darriwili lade) kitiinikute dünaamika ja biostratigraafia Uuga pangal Pakri poolsaarel

Mairy Tammekänd, Olle Hints ja Jaak Nõlvak

On uuritud kitiinikute levikut Väo kihistu kivimites (Lasnamäe ja Uhaku lade) Uuga pangal Pakri poolsaarel. Kitiinikute arvukas ja mitmekesine fauna sisaldab 36 liiki ning kuni 170 eksemplari grammi kivimi kohta. Kooslustes domineerivad perekondade *Belonechitina*, *Desmochitina*, *Cyathochitina* ja *Euconochitina* esindajad. Üksikute taksonite suhtelist ja absoluutset arvukust iseloomustavad regulaarsed ning võimalik, et tsüklilised muutused, mis ei korreleeru otseselt litoloogia ja geokeemiaga. Järsud arvukuse muutused, mis langevad kokku katkestuspindadega, viitavad tõenäoliselt settelüngale. Kitiinikute suurim mitmekesisus tehti kindlaks Väo kihistu alaosas (Rebala kihistikus), kus ühes proovis esineb kuni 20 liiki ja summaarne mitmekesisus ulatub üle 25. Uuritud intervallis määrati 11 biostratigraafiliselt olulist taset, sh *Laufeldochitina striata* biotsooni alamsoonide piirid, mida on võimalik kasutada Lasnamäe ehituslubjakivi liigestamisel. Uhaku lademe alumise piiri korreleerimiseks sobib enim *Belonechitina pellifera* pideva ja arvuka esinemisintervalli ülemine piir.