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Early–Middle Ordovician biotic and sedimentary dynamics in the Baltoscandian paleobasin

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Lithosphere and Biosphere Science
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Front cover: Artist's impression of an Ordovician ecosystem. Illustration: Iris Lindskog (age four).

Back cover: The author excavating a section through the Lower–Middle Ordovician boundary interval at Kinnekulle, Västergötland, southern Sweden. Photo: Mats Eriksson (age forty-three).

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Abstract

The Baltoscandian region forms part of the paleocontinent Baltica, which was largely covered by a shallow epeiric sea throughout much of the Ordovician (c. 485.5–444 Ma). This ancient sea is today recorded by a thin succession of sedimentary rocks. During the Early–Middle Ordovician (c. 485.5–457.5 Ma), Baltica was situated in mid-latitudes on the southern hemisphere and cool-water carbonates formed across large areas of the Baltoscandian paleobasin. The so-called orthoceratite limestone is the most widely distributed rock type from the Early–Middle Ordovician in Sweden. It developed in a time-transgressive manner geographically, but much of the Lower–Middle Ordovician succession in the mainland of Sweden is typically characterized by this lithology. The depositional environment of the 'orthoceratite limestone' has long remained poorly understood in many respects. This is in large part due to a lack of analogous depositional environments in modern seas, but also due to remaining gaps in our knowledge about the rock type in general. It has generally been agreed upon that the 'orthoceratite limestone' is a cool-water deposit formed in a sediment-starved epeiric sea, but interpretations have differed widely with regards to prevailing water depth.

The eight papers appended to this doctoral dissertation are based on various investigations of the 'orthoceratite limestone' in Sweden and coeval rocks in surrounding countries. Detailed macroscopic and microscopic studies of the biotic and sedimentary characteristics have added information about the Baltoscandian paleobasin and the biotic and paleoenvironmental development during the Early–Middle Ordovician. It is concluded that the depositional environment of the 'orthoceratite limestone' varied considerably through both space and time; it spanned from intertidal areas to settings many tens of meters deep. Variations in the overall characteristics and fossil content of the 'orthoceratite limestone' and coeval regional rocks appear to mainly record variations in (relative) sea level.

The collective results indicate that sea level varied significantly throughout the Early–Middle Ordovician, likely in large part as a response to variations in climate and related changes in global marine water volume. The inferred variations are consistent across multiple different proxies – abiotic and biotic alike – and cyclic patterns occur in the datasets. Geochemical data suggest that the global climate changed considerably during the Early–Middle Ordovician, and that the climate ultimately entered an 'Icehouse'-like state. The onset of the latter phase is recorded as a distinct drop in sea level during the Middle Ordovician. The aforementioned changes reverberated through the marine realm and likely contributed to the rapid diversification that is seen among fossils during the so-called Great Ordovician Biodiversification Event (GOBE). Based on a refined absolute and relative time scale for the Middle Ordovician, the GOBE can be confidently shown to be unrelated to a prolonged meteorite bombardment that occurred during this time interval.

The papers in the dissertation collectively show that a combination of approaches and analytic techniques leads to maximal information output and confidence in interpretations. The use of state-of-the-art analytic and imaging techniques further allows for the discovery of previously undocumented rock characteristics and fossils, and better description and understanding of such documented before.

Key words: Ordovician; 'orthoceratite limestone'; carbonate sedimentology; microfacies; paleoecology; paleoenvironment; paleontology; Baltoscandia

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Contents

List of papers

This dissertation is based on eight appended papers, which are listed below. Paper I has been reproduced with permission from John Wiley and Sons, Inc. Papers II and V have been reproduced with permission from Taylor & Francis Group. Paper III has been reproduced with permission from Elsevier. Papers IV and VI have been reproduced in accordance with the Creative Commons Attribution 4.0 International License (http://creativecommons.org/licenses/by/4.0/). Papers VII and VIII are reproduced with preliminary layout.

Paper I

Lindskog, A., 2014: Palaeoenvironmental significance of cool-water microbialites in the Darriwilian (Middle Ordovician) of Sweden. *Lethaia 47*, 187–204 (doi: 10.1111/let.12050).

Paper II

Lindskog, A., Eriksson, M.E. & Pettersson, A.M.L., 2014: The Volkhov–Kunda transition and the base of the Holen Limestone at Kinnekulle, Västergötland, Sweden. *GFF 136*, 167–171 (doi: 10.1080/11035897.2014.880507).

Paper III

Lindskog, A., Eriksson, M.E., Tell, C., Terfelt, F., Martin, E., Ahlberg, P., Schmitz, B. & Marone, F., 2015: Mollusk maxima and marine events in the Middle Ordovician of Baltoscandia. *Palaeogeography, Palaeoclimatology, Palaeoecology 440*, 53–65 (doi: 10.1016/j.palaeo.2015.08.018).

Paper IV

Rasmussen, C.M.Ø., Ullmann, C.V., Jakobsen, K.G., Lindskog, A., Hansen, J., Hansen, T., Eriksson, M.E., Dronov, A., Frei, R., Korte, C., Nielsen, A.T. & Harper, D.A.T., 2016: Onset of main Phanerozoic marine radiation sparked by emerging Mid Ordovician icehouse. *Scientific Reports 6*, 18884 (doi: 10.1038/srep18884).

Paper V

Eriksson, M.E., Lindskog, A., Servais, T., Hints, O. & Tonarová, P., 2016: Darriwilian (Middle Ordovician) worms of southern Sweden. *GFF 138*, 502–509 (doi: 10.1080/11035897.2016.1181102).

Paper VI

Lindskog, A., Costa, M.M., Rasmussen, C.M.Ø., Connelly, J.N. & Eriksson, M.E., 2017: Refined Ordovician timescale reveals no link between asteroid breakup and biodiversification. *Nature Communications 8*, 14066 (doi: 10.1038/ncomms14066).

Paper VII

Lindskog, A. & Eriksson, M.E., 2017: Megascopic processes reflected in the microscopic realm: sedimentary and biotic dynamics of the Middle Ordovician 'orthoceratite limestone' at Kinnekulle, Sweden. *Accepted for publication in GFF* (doi: 10.1080/11035897.2017.1291538).

Paper VIII

Lindskog, A., Pettersson, A.M.L., Johansson, J.V., Ahlberg, P. & Eriksson, M.E., 2017: The Cambrian–Ordovician succession at Lanna, Närke, Sweden: stratigraphy and depositional environments. *In manuscript*.

1. Introduction

This dissertation is based on eight papers, which are summarized and discussed below. The aim is to present a broad perspective on the geologic evolution of the Baltoscandian paleobasin during the Early to Middle Ordovician (c. 485.5–457.5 Ma; Gradstein et al. 2012; Lindskog et al. 2017a), and to increase our understanding of the biotic and paleoenvironmental development during this time interval. The dissertation is thus based on a multi-proxy approach to the aforementioned theme. Hence, the included papers deal with sedimentology, paleoecology, paleontology, stratigraphy, geochronology and related subdisciplines.

The studies vary in perspective and scale (both literally and figuratively), and a range of methods, spanning from the most basic field studies to state-of-the-art analytic techniques, have been employed in an effort to interpret events and developments during the Early and Middle Ordovician. The dissertation mainly revolves around the Baltoscandian region and particular focus has been put on the so-called orthoceratite limestone (see below), especially that in the Kinnekulle area in the province of Västergötland, southern Sweden. During the course of this project, a number of localities with outcropping Ordovician strata in Sweden (the provinces of Närke, Västergötland, Skåne and the island of Öland), Estonia, Norway and Russia have been visited and several drill cores have been studied.

Both individually and collectively, the papers that form the backbone of this dissertation have added some pieces to the puzzle that is our distant past and hopefully the results and interpretations will withstand the test of time – at least for a while...

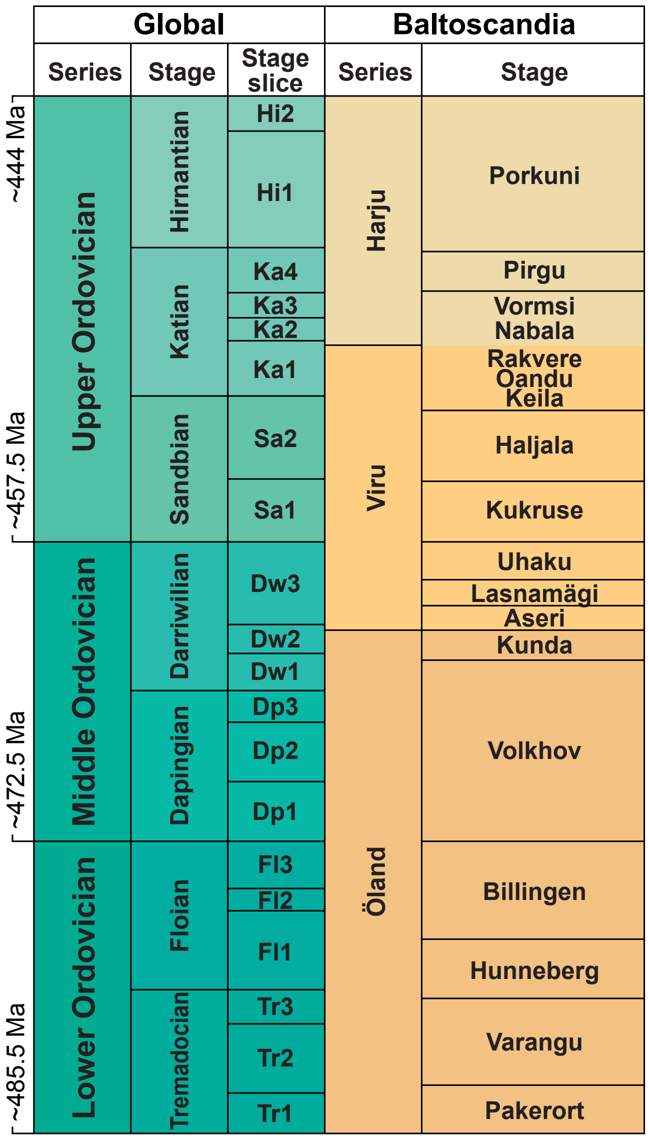

Fig. 1. Global and Baltoscandian stratigraphic subdivision of the Ordovician System (after Bergström et al. 2009; Gradstein et al. 2012; Lindskog et al. 2017a).

2. The Ordovician

The Ordovician Period, which spanned c. 485.5–444 million years ago (Fig. 1; Gradstein et al. 2012; Ogg et al. 2016), was characterized by record-high global sea level and, thus, shallow epeiric seas covered vast areas of the existing continents. Nearly all continents were situated in the southern hemisphere, and the northern hemisphere was mostly one big ocean (Cocks & Torsvik 2006). The vast majority of the multi-cellular organisms were confined to marine environments, although plants begun to colonize land about halfway through the time period (Rubinstein et al. 2010). Hence, marine sedimentary rocks form the main archive from which we extract information about this time.

2.1. The Ordovician of Baltoscandia

The Baltoscandian region, which essentially includes Scandinavia and the East Baltic countries (including westernmost Russia), forms part of Baltica, a paleocontinent that would later become a part of Eurasia (Cocks & Torsvik 2005, 2006). Much of the paleocontinent was covered by marine water, today recorded by a relatively thin succession of sedimentary rocks (Fig. 2). Originally, lower Paleozoic strata formed a broad blanket that covered most of the Baltoscandian region, but later erosion has decreased the geographic distribution. Except for strata in the west that became directly affected by the Caledonian orogeny, the preserved Ordovician succession is largely unmetamorphosed and undisturbed (e.g., Jaanus-

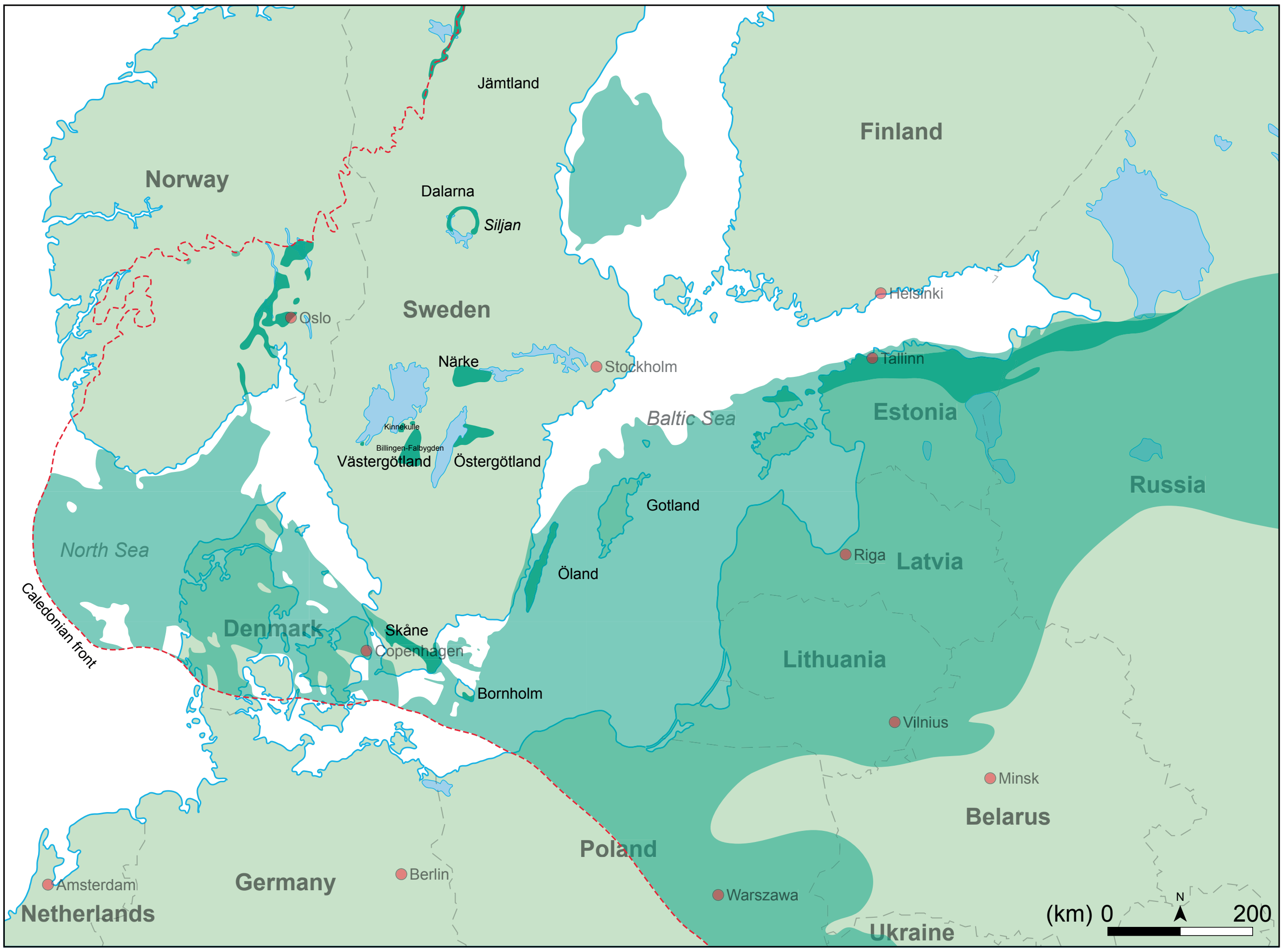

Fig. 2. Map of southern Sweden and the surrounding Baltoscandian region. The distribution of lower Paleozoic rocks is indicated by green shading; areas with significant outcrops of Ordovician strata are indicated by darker shading (modified from Lindskog & Eriksson 2017).

son 1982a).

Throughout the Ordovician, Baltica drifted northwards from high into low southern-hemisphere latitudes (Cocks & Torsvik 2005, 2006). The latitudinal voyage of Baltica is reflected in the development of the regional geologic succession through a gradual change from cool-water to warm-water sedimentary and paleontologic characteristics (e.g., Jaanusson 1973). During the Early–Middle Ordovician, the paleocontinent was situated in mid-latitudes (on the southern hemisphere) and cool-water carbonates formed across large areas of the paleobasin.

2.2. The Great Ordovician Biodiversification Event

The fossil record shows that a remarkable rise in diversity occurred among marine organisms during the Ordovician. This phenomenon has been termed the Great Ordovician Biodiversification Event (GOBE; e.g., Webby et al. 2004; Servais et al. 2009). Starting at the beginning of the Ordovician and taking off in earnest during the Dapingian, the GOBE ultimately resulted in an at least threefold increase in biodiversity globally. Different organisms began to diversify at different times, however, and diversification patterns varied through time. In addition to this increase in diversity, the GOBE was associated with the expansion of marine organisms into new environments, niches and life modes, and the establishment of more complex food webs (e.g., Harper et al. 2015). The cause(s) of the GOBE is still under debate, and suggested drivers include climate change, high global sea level, the presence of numerous separate continents, tectonic and magmatic activity, ecologic interactions, and extraterrestrial influence.

3. The ‘orthoceratite limestone’

The so-called orthoceratite limestone forms a central theme of this dissertation. Hence, the following sections provide some background information about this lithologic unit. Further information can be found in the appended papers and cited literature.

3.1. Characteristics and distribution

The 'orthoceratite limestone', which strictly is an informal geologic unit, encompasses a range of superficially similar carbonate rocks that formed in the Baltoscandian paleobasin during the Early–Middle Ordovician. These rocks are typically grayish and/or reddish in color, with subordinate yellowish and greenish hues (Fig. 3). Lithologically, the 'orthoceratite limestone' consists of a variably muddy matrix strewn with variable amounts of skeletal grains. Some intervals further contain significant amounts of authigenic mineral grains (such as glauconite and limonite). Terrigenous components are overall relatively scarce and net deposition of the 'orthoceratite limestone' was on the order of millimeters per millennia (e.g., Lindström 1971; Jaanusson 1973, 1982a; Lindskog & Eriksson 2017).

The areal distribution of the 'orthoceratite limestone' largely runs meridionally along the mainland of Sweden, where it is the dominant rock type in the Lower–Middle Ordovician succession. The sediments that came to form the 'orthoceratite limestone' were originally deposited across large areas of Sweden, but today only patches occur as erosional remnants. Areas with notable occurrences of 'orthoceratite limestone' include Jämtland, Närke, Västergötland, Öland and Östergötland. Especially the island of Öland in the Baltic Sea has become intimately associated with the rock type, which is thus commonly referred to as 'Ölandskalk' ('Öland limestone') regardless of geographic origin. However, its traditional type area is in the province of Västergötland (Hisinger 1828; Jaanusson 1982b).

From a regional perspective, the 'orthoceratite limestone' was mainly confined to the central parts of the Baltoscandian paleobasin, but its areal distribution varied through time. It appeared in a time-transgressive manner during the Early Ordovician and attained its greatest distribution in the Middle Ordovician (e.g., Jaanusson 1973; Nielsen 2004). At times, superficially similar facies migrated into other parts of Baltoscandia that otherwise host more argillaceous sediment. The Komstad Limestone of Skåne represents a notable example (see Nielsen 1995).

3.2. Depositional environment

In large part due to a lack of recent analogues, the depositional environment of the 'orthoceratite limestone' has been the subject of much scientific debate over the years. While it has generally been agreed upon that the rock represents a cool-water depositional environment in a sediment-starved intracratonic setting, the depth of deposition has remained a particular point of disagreement. Widely different interpretations have been brought forward in the literature, and estimates range from intertidal (fluctuating near zero) to hundreds of meters (com-

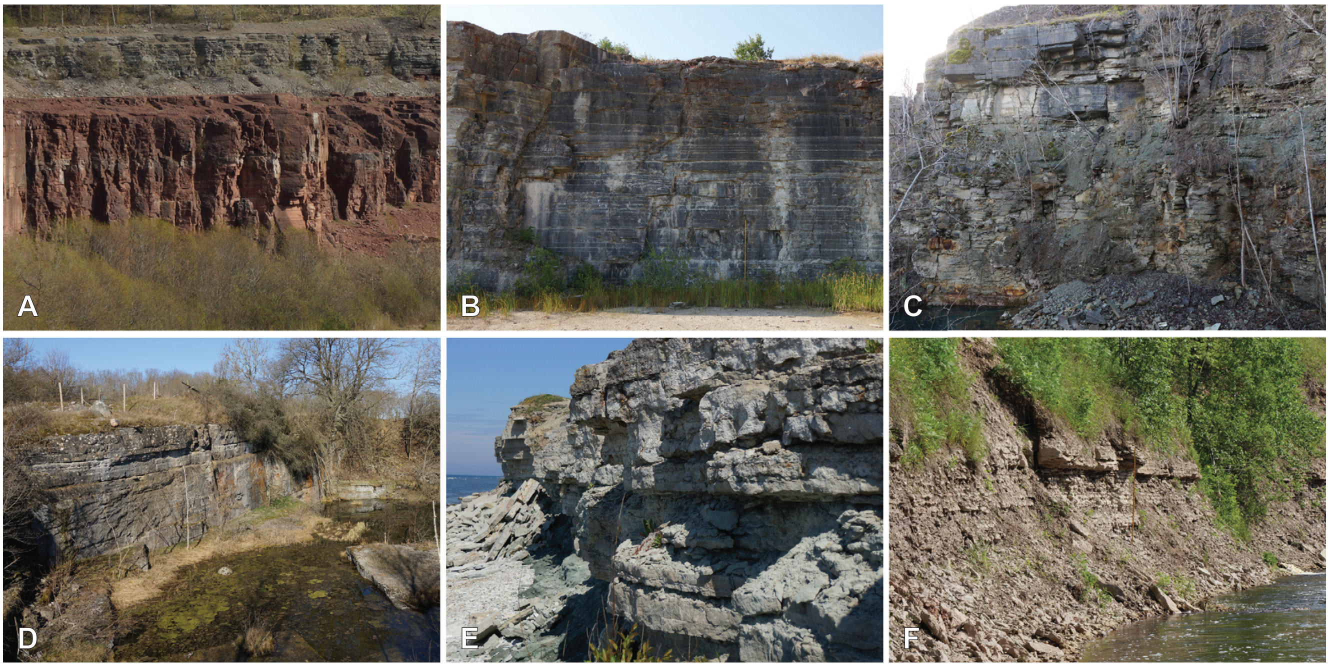

Fig. 3. Field photographs of select localities with Lower–Middle Ordovician rocks exposed. **A.** Middle Ordovician 'orthoceratite limestone' and overlying younger strata at the Hällekis quarry, Västergötland (Kinnekulle), southern Sweden. **B.** Middle Ordovician 'orthoceratite limestone' at the Tomten quarry, Västergötland (Falbygden), southern Sweden. **C.** Cambrian alum shale and Lower–Middle Ordovician 'orthoceratite limestone' at the Lanna quarry, Närke, southern Sweden. **D.** Middle Ordovician 'orthoceratite limestone' at the Killeröd quarry, Skåne, southernmost Sweden. **E.** Lower–Middle Ordovician strata at Uuga Cliff, Pakri Peninsula, northwestern Estonia. **F.** Middle Ordovician strata along the Lynna River, St. Petersburg region, northwestern Russia.

pare, e.g., Jaanusson 1973; Larsson 1973; Holmer 1983; Nordlund 1989; Chen & Lindström 1991; Lindström et al. 1996; Lindskog 2014; Lindskog & Eriksson 2017; Lindskog et al. 2017). Summary accounts of the state of the debate at different points in time can be found in Lindström (1963), Jaanusson (1973), Chen & Lindström (1991) and Lindskog (2014).

4. Summary of papers

The following papers form the basis of this dissertation. They are arranged in order of date of publication and each paper is accompanied by a summary of central results and conclusions.

4.1. Paper I

Lindskog, A., 2014: Palaeoenvironmental significance of cool-water microbialites in the Darriwilian (Middle Ordovician) of Sweden. *Lethaia 47*, 187–204.

Numerous microbial structures (oncoids and stromatolites) in the 'orthoceratite limestone' at Kinnekulle, Västergötland, southern Sweden, are described in detail and interpreted in light of the paleoenvironmental conditions in the study area. Together with associated sedimentologic and ichnologic details, the microbialites indicate that much of the studied succession was formed in rather shallow water. The seafloor was largely within the photic zone and water depth at most a few tens of meters. This interpretation contrasts with some earlier ones wherein a (very) deep setting was envisioned for the 'orthoceratite limestone', with water depth even of some hundreds of meters. A conspicuous acme in microbial structures is seen in the 'Täljsten' interval, which appears to record a significant drop in sea level.

4.2. Paper II

Lindskog, A., Eriksson, M.E. & Pettersson, A.M.L., 2014: The Volkhov–Kunda transition and the base of the Holen Limestone at Kinnekulle, Västergötland, Sweden. *GFF 136*, 167–171.
This paper was awarded for being among the best papers published in GFF during 2014 (see Skovsted 2015).

Field and thin-section observations show that the transition between the Volkhov and Kunda Baltoscandian stages is clearly expressed in the 'orthoceratite limestone' succession at Kinnekulle, Västergötland, Sweden. The boundary between the stages is marked by an abrupt change from dense into marly limestone and a corresponding fining of carbonate textures. Above this transitional fine-textured interval, the Kunda interval (Holen Limestone) is characterized by coarser limestone than the underlying Volkhov interval (Lanna Limestone). Similar lithologic changes occur in large parts of Sweden.

4.3. Paper III

Lindskog, A., Eriksson, M.E., Tell, C., Terfelt, F., Martin, E., Ahlberg, P., Schmitz, B. & Marone, F., 2015: Mollusk maxima and marine events in the Middle Ordovician of Baltoscandia. *Palaeogeography, Palaeoclimatology, Palaeoecology 440*, 53–65.

Mollusk fossils vary distinctly in abundance throughout the 'orthoceratite limestone'. Field observations showed that mollusk fossils are quite common in some intervals, whereas they are largely missing in others. The studied assemblages, which were previously largely undocumented, are relatively diverse. Quantitative analyses of skeletal grains in thin sections from Västergötland (Hällekis, Kinnekulle) and Skåne (Killeröd) in Sweden revealed rhythmic fluctuations in the relative abundance of mollusk fossils (mainly gastropods) in grain assemblages throughout the studied successions. These fluctuations likely reflect changes in relative sea level, with mollusks being most common when water was relatively shallow. Comparison to previously published literature shows similar stratigraphic patterns in the abundance of mollusks across Baltoscandia.

4.4. Paper IV

Rasmussen, C.M.Ø., Ullmann, C.V., Jakobsen, K.G., Lindskog, A., Hansen, J., Hansen, T., Eriksson, M.E., Dronov, A., Frei, R., Korte, C., Nielsen, A.T. & Harper, D.A.T., 2016: Onset of main Phanerozoic marine radiation sparked by emerging Mid Ordovician icehouse. *Scientific Reports 6*, 18884.

Isotope geochemistry (C, O, Sr), together with paleontologic and sedimentologic data, indicates a marked shift in the global climate during the Early and Middle Ordovician time interval. Based on geochemical data from the East Baltic, the temperature dropped considerably throughout the Floian–Dapingian and close to the transition into the Darriwilian the global climate inferably entered 'icehouse' conditions. Through influences on oceanic and biogeochemical cycles, and subsequent feedback processes, climate change may have played a central role in the overall biotic development during the Great Ordovician Biodiversification Event.

4.5. Paper V

Eriksson, M.E., Lindskog, A., Servais, T., Hints, O. & Tonarová, P., 2016: Darriwilian (Middle Ordovician) worms of southern Sweden. *GFF 138*, 502–509.

Acid-insoluble residues from a thin interval in the Middle Ordovician 'orthoceratite limestone' at Kinnekulle (the 'Täljsten') yielded numerous scolecodonts, which represent the jaws of polychaete worms. An assemblage of scolecodonts, partial jaw apparatuses and teeth of putative priapulids is documented. Albeit limited, the assemblage described adds to the global scolecodont record, in which data on Middle Ordovician and older specimens are still rudimentary but of importance for understanding early polychaete phylogeny. The documented specimens form the first and only evidence of this animal group in the studied strata, apart from trace fossils that may have been produced by annelids.

4.6. Paper VI

Lindskog, A., Costa, M.M., Rasmussen, C.M.Ø., Connelly, J.N. & Eriksson, M.E., 2017: Refined Ordovician timescale reveals no link between asteroid breakup and biodiversification. *Nature Communications 8*, 14066.

While searching for microfossils and heavy minerals in acid-insoluble residues from the 'orthoceratite limestone' at Kinnekulle, one sample was found to be extremely rich in euhedral zircon grains. The circumstances indicate that ash clouds generated by distal volcanic activity brought the grains to the Västergötland area. As zircon allows for absolute dating, this provided the opportunity to put a numeric age on meteorite-rich strata at Kinnekulle. Uranium-lead (U-Pb) analyses gave an age of 467.50±0.28 Ma. Coupled with previously published cosmic-ray exposure ages of fossil meteorites in the studied succession, the U-Pb data constrain the breakup of the L chondrite parent body to 468.0±0.3 Ma. Contrary to a previous claim, the results reveal no connection between this breakup event and biodiversification during the Great Ordovician Biodiversification Event. A refined (absolute and relative) time scale for the Middle Ordovician is introduced.

4.7. Paper VII

Lindskog, A. & Eriksson, M.E., 2017: Megascopic processes reflected in the microscopic realm: sedimentary and biotic dynamics of the Middle Ordovician 'orthoceratite limestone' at Kinnekulle, Sweden. *Accepted for publication in GFF.*

The Middle Ordovician 'orthoceratite limestone' was documented in detail in its traditional type area at Kinnekulle in Västergötland, southern Sweden. Field and thin-section observations at high stratigraphic resolution show that the characteristics of the 'orthoceratite limestone' vary considerably throughout the succession. Long-term changes in carbonate textures and fossil grain assemblages, together with recurring cyclic patterns, suggest a strong influence from sea level on microfacies characteristics. The collective results indicate that the cool-water 'orthoceratite limestone' behaved much like 'model' siliciclastic sedimentary systems, in that carbonate texture varied with depositional depth as particle size of siliclastics does. Fossil grain assemblages appear to record high-frequency cycles of changes in both sea level and substrate conditions. A relative sea level curve based on the microfacies data is presented. The most important factor for the long-term establishment and regional dominance of the 'orthoceratite limestone' throughout much of the Early and Middle Ordovician appears to have been a limited terrigenous sediment input to the Baltoscandian paleobasin. Hence, much of the regional facies zonation reflects distance from weathering sources rather than water bathymetric conditions.

4.8. Paper VIII

Lindskog, A., Pettersson, A.M.L., Johansson, J.V., Ahlberg, P. & Eriksson, M.E., 2017: The Cambrian–Ordovician succession at Lanna, Närke, Sweden: stratigraphy and depositional environments. *In manuscript.*

The Cambrian–Ordovician (Furongian–Darriwilian) strata at Lanna, Närke, southern Sweden, were documented in detail. Field and thin-section observations at high stratigraphic resolution show that sea level gradually fell during the late Cambrian, and the Lanna area and much of Sweden eventually became subaerially exposed. Stromatolites occur in the uppermost Cambrian shale-dominated strata. Subaerial conditions appear to have dominated in Närke well into the Early Ordovician (latest Tremadocian), when sedimentation recommenced. The Early–Middle Ordovician 'orthoceratite limestone' shows widely varying microfacies characteristics, indicating that the depositional environment underwent significant changes through time, largely due to changes in sea level. A long-term trend of coarsening carbonate textures and more diverse fossil assemblages is seen upward through the succession. Recurrent cyclic patterns in the microfacies data appear to record high-frequency sea-level changes. Comparisons to other parts of Sweden and Baltoscandia reveal remarkably consistent patterns in the sedimentary development.

5. Discussion

The depositional environments and their biotas in the Baltoscandian paleobasin underwent notable changes during the Early–Middle Ordovician, likely in large part due to changes in sea level (Lindskog 2014; Lindskog et al. 2014, 2015, 2017b; Eriksson et al. 2016; Rasmussen et al. 2016; Lindskog & Eriksson 2017; and references therein). The inferred changes in the paleoenvironment are typically quite consistent between geographic areas and different abiotic and biotic proxies, allowing for relatively precise comparisons between datasets and confident interpretations at the regional scale. Geochemical data suggest that the changes in sea level were strongly influenced by changes in the global climate, which became gradually cooler throughout the studied time interval (see Rasmussen et al. 2016). Several proxies (both abiotic and biotic) appear to record cyclic patterns, with varying amplitudes and frequencies, possibly reflecting Milankovitch cyclicity (see below). Consequently, inferred sea-level curves to a large degree seem to reflect eustasy, but some differences in the sedimentary development at the regional scale suggest tectonic activity in the Baltoscandian paleobasin (see Lindskog & Eriksson 2017). Climate change is likely to have played an important – even crucial – role in the Great Ordovician Biodiversification Event (GOBE), as marine environments and their ecosystems benefited from better circulation of nutrients, oxygen and other essential resources during cooler conditions, and abiotic and biotic feedback processes thereby were accelerated (Rasmussen et al. 2016).

Marked spatiotemporal variations in sedimentary and paleontologic characteristics suggest that the 'orthoceratite limestone' does not represent one single and homogeneous depositional environment, at least not in terms of water depth (e.g., Lindskog 2014; Lindskog et al. 2014, 2015, 2017b; Lindskog & Eriksson 2017). Rather, this rock type represents a range of environments joined together mainly by oligotrophic cool-water conditions and a lack of terrigenous input to the depositional environment. The sediments that would come to form the 'orthoceratite limestone' were thus deposited at different water depths, which varied significantly both through space and time. Much of the earlier debates concerning the depth of deposition may have been misguided and unnecessary, as different workers have concentrated on different geographic areas and rock intervals – one interpretation does not necessarily rule out another, unless the interpretations differ for the same strata at the same locality. In fact, the 'orthoceratite limestone' may very well encompass nearly all depth settings envisioned by different authors (see above), although depths of several hundreds of meters appear exaggerated in light of the intracratonic setting and the reactivity of the sedimentary environments. Many oft-repeated generalizations about the 'orthoceratite limestone' should be avoided in future literature, as its characteristics are more variable than first meets the eye.

Further detailed studies are needed in order to improve our understanding of the paleoenvironmental development during the Ordovician, and to enable more precise correlations at the regional and global scale. Problems persist especially in the detailed correlation between (paleo)continents, entailing difficulties in disentangling isostatic and eustatic signals in the sea-level history (and in extension the climate history). Accurate and precise correlations are key to understanding abiotic and biotic events and processes in any larger perspectives. Geochemical proxies, mainly carbon isotopes, have become important tools for global correlations, but some patterns in the data appear to be significantly different between geographic areas both at the regional and global scales. These differences are typically left unexplained. Hence, large gaps exist in the understanding of what drove geochemical changes in these ancient marine environments. During the course of this doctoral project, isotopic data has been produced for some of the studied sections with the aim to analyze the data in light of paleoenvironmental proxies. These studies remain to be published.

The absolute (numeric) time scale for the Ordovician is still poorly resolved in many respects. This presents problems for the understanding of the timing and tempo of events and processes during the studied time interval, and it directly hinders confident testing of cyclic patterns in light of Milankovitch cyclicity and other processes (see Lindskog & Eriksson 2017). Much remains to be done in the case of the lower Paleozoic time scale overall. As this time interval records some of the arguably most important phases of early evolution of the biosphere, it should be in the interest of all to amend this situation.

In the case of the Baltoscandian sedimentary succession, it has become clear that at least the Swedish stratigraphic framework for the Lower–Middle Ordovician needs to be reviewed (see Kumpulainen 2017; Lindskog & Eriksson 2017; Lindskog et al. 2017b). Large parts of this interval comprise topostratigraphic units (see Jaanusson 1960), which must be substituted by formally ratified lithoformations. However, more work needs to be done in order to solve this situation and enable the introduction of a practically useful framework. This may result in a quite different subdivision of the Lower–Middle Ordovician succession of Sweden than what has been used previously.

6. Acknowledgments

My most sincere thanks are extended to my main supervisor, Mats Eriksson, who has proven – again and again – to be an excellent guide and role model in the (virtual minefield that is called the) academic world, as well as the larger (read: real) one outside it. I am particularly grateful for the confidence and unwavering support Mats has awarded me, whatever the costs and consequences, ever since I was an undergraduate student. A more humble and selfless person is difficult to find. I will bring many nice memories with me into the future. In lack of a sufficient vocabulary to express my gratitude, I resort to an essentially forbidden combination of typographic emphases: ***THANKS, MATS!***

My co-supervisor Per Ahlberg is next in line to be thanked. Per has provided a seemingly never-ending stream of valuable insights into the early Paleozoic world and the classic literature that tells of it. I have enjoyed many nice discussions and moments with Per during my years at the department, both before and during my doctoral studies. The humility and respect Per has always shown is admirable and inspirational. *Thanks, Per!*

Anna Pettersson is thanked for her endless support (and patience) throughout my years as a doctoral student, and for practical help during fieldwork and writing. You are invaluable, Anna!

Iris Lindskog is thanked for providing much inspiration and many good reasons to take my mind off 'work', and for producing the awesome cover art of this dissertation. I look forward to seeing who comes out of mom's belly next – you really set the bar high, Iris!

A number of additional persons among colleagues, friends and family surely deserve my thanks in this section, but I am afraid that I might miss someone and have them forever lost in print if I start listing names (there will be no revised editions of this dissertation!). Hence, I will make sure to express my gratitude in person whenever I get the opportunity. If you feel (and know) that you deserve my thanks and *really* want to see it in print, however, then: Thanks!

Much insight and inspiration has been gained from the works of older generations of geoscientists, among which Gustaf Linnarsson (1841–1881), Gerhard Holm (1853–1926), Anton Westergård (1880–1968), Torsten Tjernvik (1902–1991) and Valdar Jaanusson (1923–1999) deserve special mention and posthumous thanks.

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Svensk sammanfattning

Baltoskandien utgör en del av paleokontinenten Baltica, vilken mestadels var täckt av ett grunt epeiriskt hav under den ordoviciska tidsperioden (ca 485,5–444 Ma). Detta uråldriga hav efterlämnade en tunn lagerföljd av sedimentära bergarter. Under tidig–mellanordovicium (ca 485,5–457,5 Ma) befann sig Baltica vid tempererade breddgrader på södra halvklotet och kallvattenkarbonater bildades över stora områden i den Baltoskandiska paleobassängen. Den så kallade ortoceratitkalkstenen är den mest vittspridda bergartstypen från tidig–mellanordovicium i Sverige. Den spred sig successivt geografiskt och stora delar av under–mellanordovicium på Sveriges fastland karaktäriseras av denna litologi. "Ortoceratitkalkstenens" avsättningsmiljö har länge varit ofullständigt känd. Detta beror till stor del på en avsaknad av motsvarigheter bland nutida avsättningsmiljöer, men också på luckor i vår kunskap om bergarten i allmänhet. Det råder en generell enighet om att "ortoceratitkalkstenen" representerar en kallvattenkarbonat avsatt i ett epeiriskt hav med mycket begränsat sedimentinflöde, men tolkningar angående rådande vattendjup har skiljt sig åt.

De åtta artiklar som utgör grunden till den här doktorsavhandlingen baseras på olika undersökningar av "ortoceratitkalkstenen" i Sverige och likåldriga lager i omgivande länder. Detaljerade makro- och mikroskopiska studier av biotiska och sedimentära egenskaper har gett värdefull information om den Baltoskandiska paleobassängen samt den biotiska och miljömässiga utvecklingen under tidig–mellanordovicium. Resultaten visar att "ortoceratitkalkstenens" avsättningsmiljö varierade avsevärt i både rum och tid; den spände från intertidala områden till miljöer med många tiotals meter djupt vatten. Variationer i övergripande egenskaper och fossilinnehåll i "ortoceratitkalkstenen" samt likåldriga regionala lager tycks främst avspegla variationer i (relativ) havsnivå.

De sammantagna resultaten tyder på att havsnivån varierade kraftigt genom tidig–mellanordovicium, sannolikt som en följd av klimatvariationer och relaterade förändringar i vattenmassorna globalt. De skönjbara variationerna är samstämmiga mellan flera olika proxies – både abiotiska och biotiska – och cykliska mönster förekommer ofta. Geokemiska data indikerar att klimatet förändrades avsevärt genom tidig–mellanordovicium och att det slutligen gick in i en istidsliknande fas. Inträdet i den senare fasen avspeglas i en tydlig sänkning av havsnivån under mellanordovicium. De tidigare nämnda förändringarna påverkade marina miljöer och bidrog sannolikt till den snabba diversifiering som skedde under den så kallade stora ordoviciska biodiversifieringen (fritt översatt från engelskans Great Ordovician Biodiversification Event). Förfinade absoluta och relativa tidsskalor för mellanordovicium visar att biodiversifieringen var oberoende av ett utdraget meteoritbombardemang under detta tidsavsnitt.

Artiklarna i avhandlingen visar tillsammans att en kombination av infallsvinklar och analysmetoder ger maximal information och tolkningsförmåga. Användning av toppmoderna analys- och avbildningstekniker möjliggör nya upptäckter av tidigare okända bergartsegenskaper och fossil, samt bättre beskrivning av och förståelse för sådana som varit kända sedan tidigare.

Appendix A

Publications by the author not included in this dissertation, ordered by category and from newest to oldest.

Articles in peer-reviewed scientific journals

Johansson, S., Sparrenbom, C., Fiandaca, G., Lindskog, A., Olsson, P.-I., Dahlin, T. & Rosqvist, H., 2017: Investigations of a Cretaceous limestone with spectral induced polarization and scanning electron microscopy. *Geophysical Journal International 208*, 954–972 (doi: 10.1093/gji/ggw432).

Lindskog, A., Eriksson, M.E., Bergström, S.M., Terfelt, F. & Marone, F., 2017: Palaeozoic ’conodont pearls’ and other phosphatic micro-spherules. *Lethaia 50*, 26–40 (doi: 10.1111/let.12172).

Ahlberg, P, Eriksson, M.E., Lundberg, F. & Lindskog, A., 2016: Cambrian stratigraphy of the Tomten-1 drill core, Västergötland, Sweden. *GFF 138*, 490–501 (doi: 10.1080/11035897.2016.1190545).

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Eriksson, M.E., Lindskog, A., Calner, M., Mellgren, J.I.S., Bergström, S.M., Terfelt, F. & Schmitz, B., 2012: Biotic dynamics and carbonate microfacies of the conspicuous Darriwilian (Middle Ordovician) ‘Täljsten’ interval, south-central Sweden. *Palaeogeography, Palaeoclimatology, Palaeoecology 367–368*, 89–103 (doi: 10.1016/j.palaeo.2012.02.012).

Book chapters, editorship, etc.

Lindskog, A., Ahlberg, P., Calner, M. & Lehnert, O., 2013: Stop 11. Thorsberg (Österplana) quarry. *In* M. Calner, P. Ahlberg, O. Lehnert & M. Erlström (eds.): *The Lower Palaeozoic of southern Sweden and the Oslo Region, Norway. Field guide for the 3rd annual meeting of the IGCP project 591. Sveriges geologiska undersökning Rapporter och meddelanden 133*, 49–50.

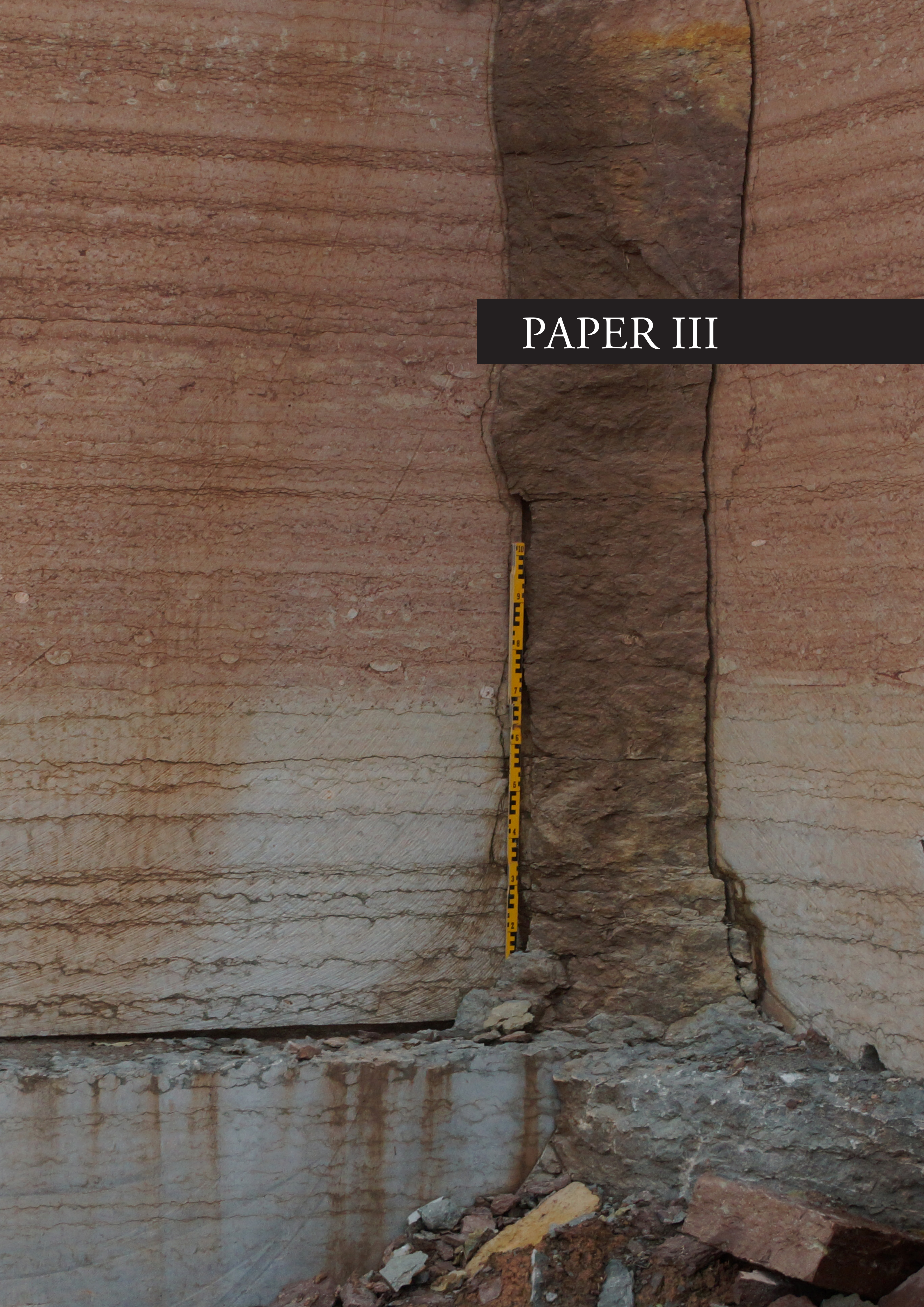
Lindskog, A., Ahlberg, P., Calner, M. & Lehnert, O., 2013: Stop 10. Hällekis. *In* M. Calner, P. Ahlberg, O. Lehnert & M. Erlström (eds.): *The Lower Palaeozoic of southern Sweden and the Oslo Region, Norway. Field guide for the 3rd annual meeting of the IGCP project 591. Sveriges geologiska undersökning Rapporter och meddelanden 133*, 46–49.

Lindskog, A. & Mehlqvist, K. (eds.), 2013: *Proceedings of the 3rd IGCP 591 annual meeting – Lund, Sweden, 9–19 June 2013*. Lund University, Lund. 364 pp. ISBN: 978-91-86746-87-2.

PAPER I

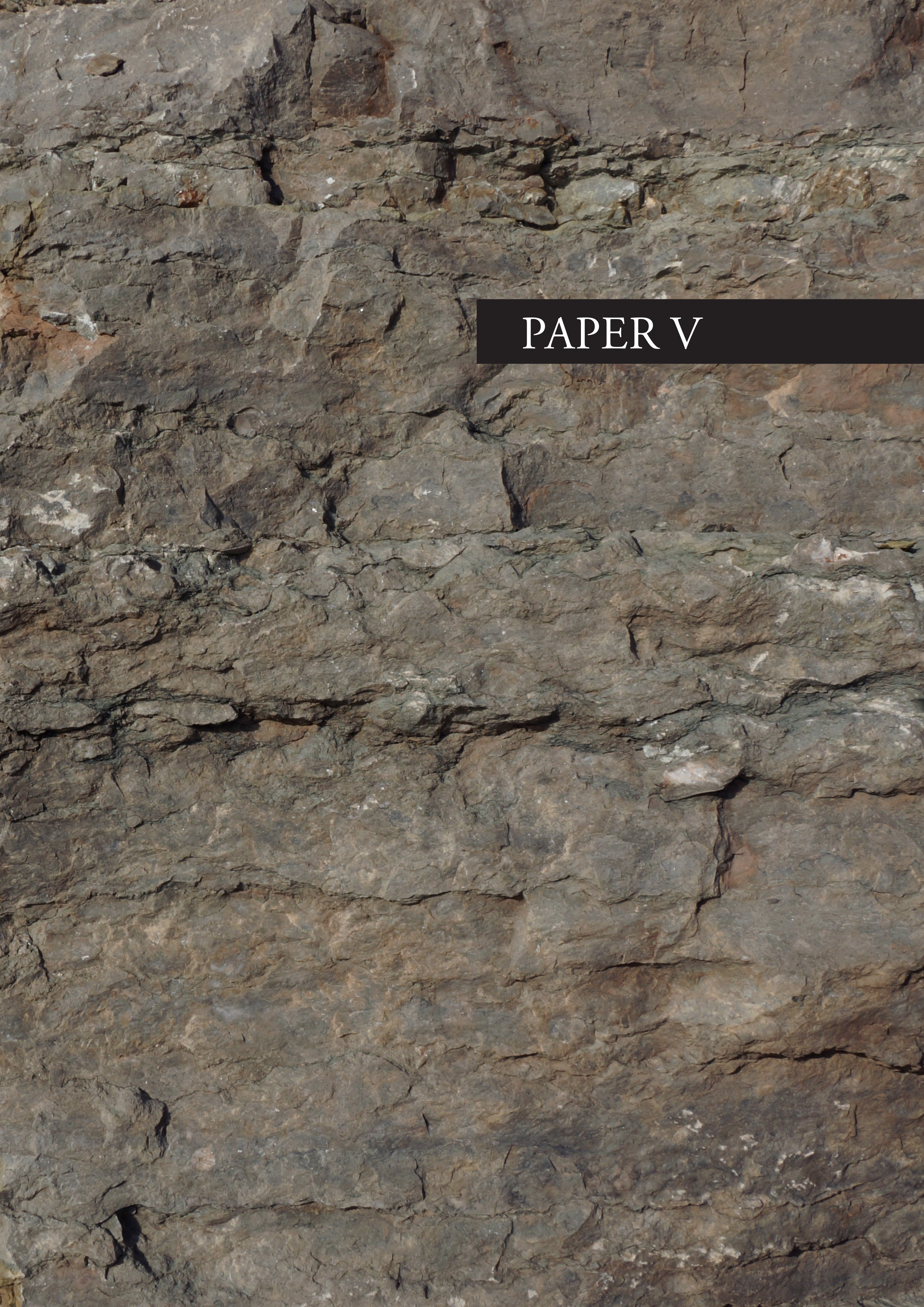
PAPER II

PAPER III

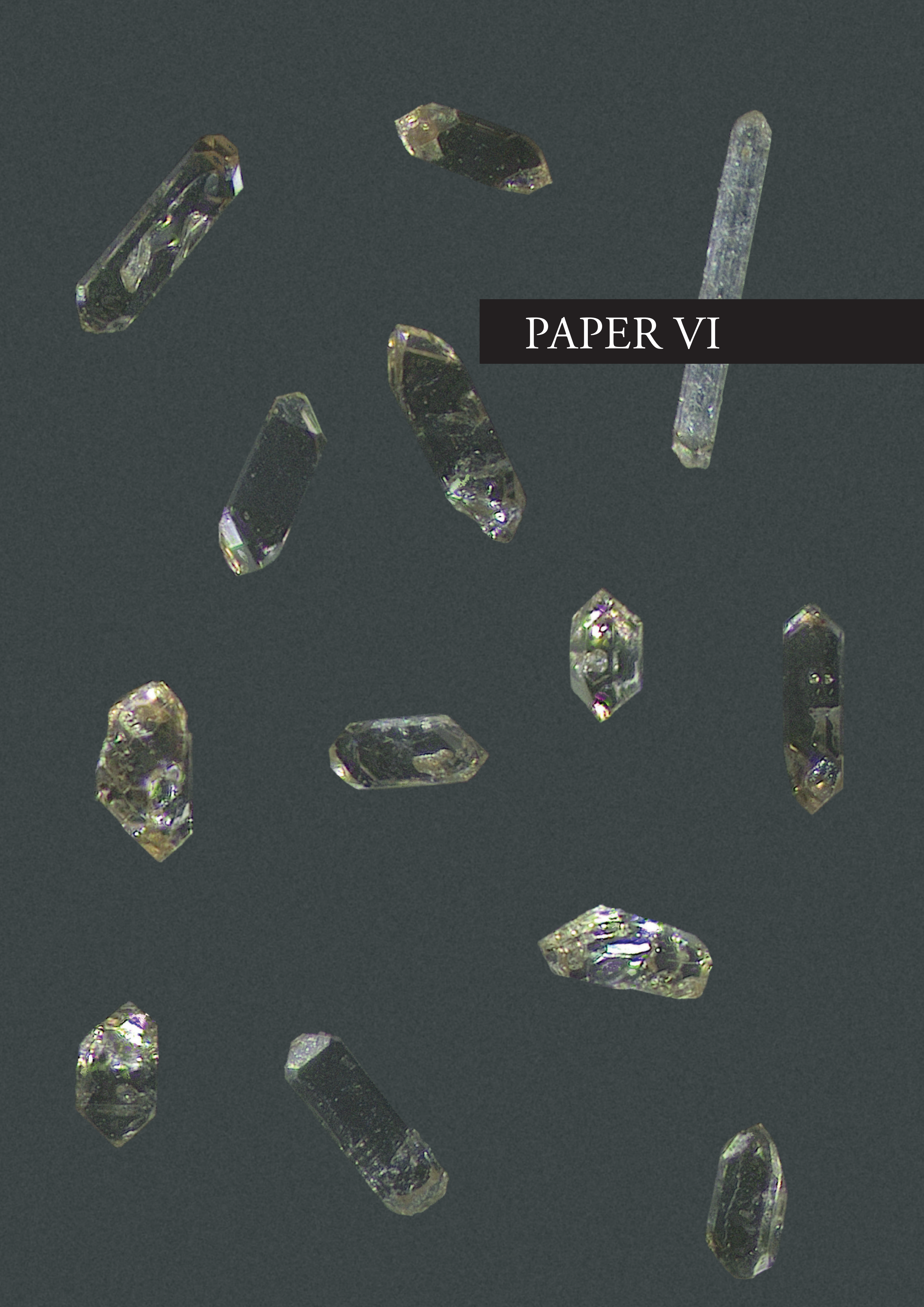


PAPER IV

PAPER V



PAPER VI



PAPER VII

PAPER VIII

Litholund Theses

Dissertations

1. *Emma F. Rehnström, 2003:* Geography and geometry of pre-Caledonian western Baltica : U-Pb geochronology and palaeomagnetism.

2. *Oskar Paulsson, 2003:* U-Pb geochronology of tectonothermal events related to the Rodinia and Gondwana supercontinents : observations from Antarctica and Baltica.

3. *Ingela Olsson-Borell, 2003:* Thermal history of the Phanerozoic sedimentary succession of Skåne, southern Sweden, and implications for applied geology.

4. *Johan Lindgren, 2004:* Early Campanian mosasaurs (Reptilia; Mosasauridae) from the Kristianstad Basin, southern Sweden.

5. *Audrius Cecys, 2004:* Tectonic implications of the ca. 1.45 Ga granitoid magmatism at the southwestern margin of the East European Craton.

6. *Peter Dahlqvist, 2005:* Late Ordovician-Early Silurian facies development and stratigraphy of Jämtland, central Sweden.

7. *Mårten Eriksson, 2005:* Silurian carbonate platform and unconformity development, Gotland, Sweden.

8. *Jane Wigforss-Lange, 2005:* The effects of Late Silurian (mid-Ludfordian) sea-level change : a case study of the Öved-Ramsåsa Group in Skåne, Sweden.

9. *Erik Eneroth, 2006:* Nanomagnetic and micromagnetic properties of rocks, minerals and sulphide-oxidation products.

10. *Niklas Axheimer, 2006:* The lower and middle Cambrian of Sweden : trilobites, biostratigraphy and intercontinental correlation.

11. *Fredrik Terfelt, 2006:* Upper middle Cambrian through Furongian of Scandinavia with focus on trilobites, paleoenvironments and correlations.

12. *Andrius Rimsa, 2007:* Understanding zircon geochronology : constraints from imaging and trace elements.

13. *Mårten Eriksson 2007:* Silurian carbonate platforms of Gotland, Sweden : archives of local, regional and global environmental changes.

14. *Jane Wigforss-Lange, 2007:* Geochemical and sedimentary signatures of Phanerozoic events.

15. *Tobias Hermansson, 2007:* The tectonic evolution of the western part of the Svecofennian orogen, central Sweden : Insight from U/Pb and $^{40}Ar/^{39}Ar$ geochronology at Forsmark.

16. *Pia Söderlund,* 2008: ^{40}Ar-^{39}Ar, AFT and (U-Th)/He thermochronologic implications for the low-temperature geological evolution in SE Sweden.

17. *Anders Cronholm,* 2009: The flux of extraterrestrial matter to Earth as recorded in Paleogene and Middle Ordovician marine sediments.

18. *Carl Alwmark,* 2009: Traces in Earth's geological record of the break-up of the L-chondrite parent body 470 Ma.

19. *Linda Larsson-Lindgren,* 2009: Climate and vegetation during the Miocene : evidence from Danish palynological assemblages.

20. *Ingemar Bergelin,* 2010: $^{40}Ar/^{39}Ar$ whole-rock geochronology of Mesozoic basalts in Scania : evidence for episodic volcanism over an extended period of ca. 80 Myr.

21. *Johanna Mellgren,* 2011: Conodont biostratigraphy, taxonomy and palaeoecology in the Darriwilian (Middle Ordovician) of Baltoscandia : with focus on meteorite and extraterrestrial chromite-rich strata.

22. *Johan Olsson,* 2012: U-Pb baddeleyite geochronology of Precambrian mafic dyke swarms and complexes in southern Africa : regional-scale extensional events and the origin of the Bushveld complex.

23. *Kristina Mehlqvist,* 2013: Early land plant spores from the Paleozoic of Sweden : taxonomy, stratigraphy and paleoenvironments.

24. *Andreas Petersson,* 2015: Evolution of continental crust in the Proterozoic : growth and reworking in orogenic systems.

25. *Karolina Bjärnborg,* 2015: Origin of the Kleva Ni-Cu sulphide mineralisation in Småland, southeast Sweden.

26. *Lorraine Tual,* 2016: P–T evolution and high-temperature deformation of Precambrian eclogite, Sveconorwegian orogen.

27. *Mimmi Nilsson,* 2016: New constraints on paleoreconstructions through geochronology of mafic dyke swarms in North Atlantic Craton.

28. *Sanna Alwmark,* 2016: Terrestrial consequences of hypervelocity impact : shock metamorphism, shock barometry, and newly discovered impact structures.

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This doctoral dissertation is based on eight papers that provide new insights into the vast epeiric sea that covered much of Baltoscandia in the Ordovician Period (c. 485.5–444 million years ago). Together, the studies represent a multi-proxy approach to unraveling the biotic and paleoenvironmental development during the Early–Middle Ordovician (c. 485.5–457.5 million years ago). In the course of the doctoral project, several areas with outcropping Ordovician strata have been visited and the studies span basic field observations to state-of-the-art analytic techniques. Focus has been put on the 'orthoceratite limestone', which is the dominant lithology in Sweden from the studied time interval.

The author, Anders Lindskog, is a geologist trained in the profession at Lund University (and by interested, loving parents). His interest in geology – in particular fossils and paleontology – has been present since childhood. As a young boy, Anders spent many days out on 'scientific expeditions' in the Scanian countryside, looking for fossiliferous rocks that were cracked open with a hammer. The treasures hiding within the rocks were brought home to an ever-growing collection of petrified organisms. Today, the many rocks that remain strewn around his parents' garden remind visitors of the young amateur geologist that once lived there!

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