DISSERTATIONES GEOLOGICAE UNIVERSITATIS TARTUENSIS
17

SILURIAN (LLANDOVERY-WENLOCK) TABULATE CORALS OF BALTOSCANDIA: TAXONOMY, PALAEOECOLOGY, DISTRIBUTION

MARI-ANN MÕTUS

TARTU UNIVERSITY
PRESS

Institute of Geology, Faculty of Biology and Geography, University of Tartu, Tartu, Estonia.

This dissertation is accepted for the commencement of the degree of Doctor of Philosophy (in Geology) on November, 30, 2004 by the Council of the Faculty of Biology and Geography, University of Tartu.

Opponent: Dr. Bernhard Hubmann, the Graz Karl-Franzens-University, Austria.

The thesis will be defended at the University of Tartu, Vanemuise 46, room 246, on February, 18, 2005 at 13.15.

Publication of this thesis is granted by the University of Tartu.

Taxonomic disclaimer: This doctoral thesis and included unpublished articles are not a publication in sense of International Code of Zooloogical Nomenclature.

ISBN 9949–11–010–6 (trükis)
ISBN 9949–11–011–4 (PDF)

Tartu Ülikooli Kirjastus
www.tyk.ut.ee
Tellimus nr. 687

CONTENTS

LIST OF ORIGINAL PUBLICATIONS

I Mõtus, M.-A. and Klaamann, E. 1999. The halysitid coral genera *Halysites* and *Cystihalysites* from Gotland, Sweden. GFF 121, pp. 81–90.

II Mõtus, M.-A. 2001. Environment related morphological variation in Early Silurian tabulate corals from the Baltic area. *In*: Y. Ezaki, K. Mori, T. Sugiyama and J. E. Sorauf (eds). Bulletins of Tohoku University Museum (1). Proceedings of the 8th International Symposium on Fossil Cnidaria and Porifera, Sendai, Japan, 62–69.

III Mõtus, M.-A,. 2004 Tabulate corals from the Lower Silurian of Jämtland (Sweden). GFF 126, pp. 339–352.

IV Calner, M., Sandström, O. and Mõtus, M.-A. 2000. Significance of a halysitid-heliolitid mud-facies autobiostrome from the middle Silurian of Gotland, Sweden. PALAIOS 5, pp. 511–523.

V Mõtus, M.-A. 1997. Tabulate corals. In: A. Raukas and A. Teedumäe, (eds). Geology and Mineral resources of Estonia, Tallinn, pp. 219–223.

VI Mõtus, M.-A. And Sandström, O. (submitted). *Cystihalysites* sp. and its significance in biostratigraphy and event stratigraphy in the Ludlow of Gotland, Sweden. GFF.

THE AUTHOR'S RESPONSIBILITY

Paper I. The paper is based on species sampling and on an unfinished descriptive draft by E. Klaamann (from the 1980s, in Russian). The lead author re-selected the species for the description (some were excluded, others synonymised), re-described the material, revised discussions, provided supplementary graphics, maps and digital photographs and is fully responsible for the geological aspects of the manuscript.

Paper II. The author is fully responsible for all aspects of the paper (field-work, lab work, data processing, analytical work and writing the paper).

Paper III. The author is fully responsible for all aspects of the paper (field-work, lab work, data processing and writing the paper).

Paper IV. The third author is responsible for identification of reef-building tabulate species, for the descriptive measurements of *Stelliporella* cf. *parvistella* and for palaeontological photography.

Paper V. The author is fully responsible for all aspects of the paper.

Paper VI. The first author performed a part of field work for primary data collecting, is responsible for lab preparation, wrote a part of the text and is responsible for tabulate taxonomy in the manuscript.

Mõtus, M.-A. 2005. Silurian (Llandovery-Wenlock) tabulate corals of Baltoscandia: taxonomy, palaeoecology, distribution. Dissertationes Geologicae Universitatis Tartuensis, 17, Tartu University Press, 167 pp.

ABSTRACT

High diversity and a cosmopolitan nature characterize the early Silurian tabulates in Baltoscandia. The intraspecific variability of tabulate corals is great, a reflection of their colonial nature. The taxonomy of tabulate corals in Baltoscandia is based generally on the concept of typological species. Diagnostic features of species commonly overlap and therefore species are often difficult to distinguish. Due to this overlap of features, several species may be synonymous to each other.

This research is an attempt to revise the complicated taxonomy of early Silurian tabulates, concentrating also on the nature of the intraspecific variability. For this purpose, the ecophenotypic response of tabulates has been studied. It is shown that the upward growth of columnar and branching tabulates is characteristic of environments of moderate to high sedimentation rates, whereas tabular coralla are indicative of high-energy environments. Some species (e.g. *Paleofavosites asper*) are characterised by much higher intraspecific variability than others (e.g. *Halysites catenularius*). Taxonomic changes resulted from biometric description of the diagnostic characters of tabulates and analysis of intraspecific variability. Several species have been synonymised and the validity of some genera is questionable.

The diversity and abundance of tabulate corals changed significantly throughout the Silurian. These changes may be related to global events occurring at the Rhuddanian-Aeronian boundary and the Llandovery-Wenlock boundary. The appearance of peculiar biostromes in Gotland follows the middle Homerian event. It is also suggested that particular changes in the tabulate composition (disappearance of heliolitids and halysitids in Wenlock of Estonia) are due to facies changes.

The biostratigraphy of tabulate corals is quite regional due to the strong facies control over the distribution of taxa. Tabulates may be valuable in cases lacking stratigraphically important taxa. A case study demonstrates close affinities between the tabulate faunas from Estonia and Jämtland, suggesting the Aeronian age of the Berge Formation.

INTRODUCTION

Tabulate corals emerged first in the Middle Ordovician and became extinct in the Upper Permian. The oldest tabulates in Baltoscandia are known from the Viru Series, Oandu Stage of Estonia. These tabulates had already achieved high diversity in the area by the end of the Ordovician.

There were no significant extinctions among tabulate corals in the Late Ordovician and many tabulate taxa continued into the Silurian. During the Llandovery the generic diversity of tabulates remained generally the same as in the Late Ordovician, but the role of cosmopolitan taxa increased in the early Silurian (PAPER V, Kaljo and Klaamann 1973). During the Llandovery Epoch, the species diversity was greatest within the order Favositida, which comprises tabulates with extremely large intraspecific variability. The diversity of tabulates was also great during the Wenlock Epoch.

The species and generic diversity of tabulate corals depends largely on the quality of taxonomic examination. We need to consider that several established species and genera in Baltoscandia might be synonymous, primarily because intraspecific variability has rarely been considered. The diagnostic characters among species often overlap due to an inadequate definition of metric characters. Species diagnoses also contain some non-diagnostic characters. The appearance of cosmopolitan species in the Silurian introduces new taxonomical problems, because widespread species are often divided into many species in different regions. That many difficulties in tabulate taxonomy persist makes a taxonomic revision of this group relevant.

The taxonomy of tabulate corals in Baltoscandia is largely based on the species that have been defined according to diagnostic characters of a single type specimen. In the tabulate literature, the term “typological approach” or “typological species concept” is used to consider the problems in tabulate taxonomy (Lee and Noble 1988, Scrutton 1989, Tesakov 1978). Only in studies involving many specimens of a particular species can the true nature of such poorly defined taxa be established.

The contemporaneous species concept takes into account intraspecific variability of the taxa. Due to their colonial nature, different kinds of variation can be observed in tabulates. Scrutton (1989) distinguished ontogenetic (visible development of corallite), astogenetic (apparent development of corallum), cyclomorphic (cycling of growth bands) and topomorphic (caused by environmental impacts) variation. The specifics of variation can easily be characterised biometrically.

Tabulates are adapted to many environments and is expressed in various corallum shapes even within a particular species (PAPER II).

The different aspects of intraspecific variability must be considered in species discrimination. Because intraspecific variability is genetically determined and ecophenotypically controlled, it is characteristic to some extent to every tabulate species.

Biostratigraphic application of tabulates is fairly limited and mainly regional, because of the confinement of corals to restricted shallow water environments. However, tabulate corals may be useful in cases of limited stratigraphical evidence. The successful application of tabulate corals for the correlation of local units is demonstrated in PAPER III and this case study also demonstrates the need for revised and accurate taxonomy.

The revision of formerly established taxa tends to reduce the number of species but also supports the validity of the revised taxa. Revision that leads to a lower number of genera or species also reduces the earlier measure of diversity. Similarly, paleobiogeographical aspects may also require re-evaluation. These relationships corroborate the value of taxonomic studies of widely distributed fossils like the tabulate corals.

The main aim of this thesis is to revise the taxonomy of the tabulates in Baltoscandia by introducing the emended species concept and to describe the tabulate distribution in the upper Ordovician-lower Silurian strata.

SHORT SUMMARIES OF PAPERS

PAPER I. The halysitid taxa from different localities in Gotland are revised and their stratigraphical distribution in the subunits of the formal beds is shown. *Catenipora crassa* Stasinska, 1967 and *Halysites crassus* Stasinska, 1974, are synonymised with *Halysites senior* Klaamann, 1961. It is shown that the occurrence of specimens morphologically identical to *Halysites catenularius* (Linnaeus, 1767) is restricted only to the Llandovery (Lower Visby Formation) of Gotland. The occurrence of *Cystihalysites blakewayensis* Sutton, 1964 in Gotland is documented for the first time.

PAPER II. The intraspecific variation of *Halysites catenularius* (Linnaeus, 1767) and *Paleofavosites asper* (d'Orbigny, 1850) is analysed based on numerous specimens from Gotland. The correlation is calculated between corallite size and corallum shape in favositids. *P. asper* from the Slite Group shows great variation in corallite size and in corallum shape, both within and between localities. The corallum form varies between the different facies, the coralla are tabular in coarse-grained crinodal limestones and nodular-domical to bulbous in marly limestones. The species are highly variable and widespread, and therefore difficult to identify. Specimens of *H. catenularius*, collected from the biostrome at Ireviken 3, Gotland, are less variable than specimens of *P. asper* from the same locality.

PAPER III. Lower Silurian tabulate coral species of the genera *Paleofavosites*, *Favosites*, *Parastriatopora*, *Propora*, *Aulopora* and *Catenipora* were recorded in Jämtland, Sweden, Scandinavian Caledonides, and biometrically revised. The species composition shows the closest affinity to contemporaneous Estonian fauna. The type specimens from the collection of the Institute of Geology at Tallinn University of Technology were used to examine the intraspecific variability of the typological species. The age of the Berge Limestone at Ede, Verkön and Norderön localities of Jämtland is discussed. Tabulate corals prove an Aeronian age for the unit, judging from the affinities with Estonian faunas.

PAPER IV. The occurrence of a low-diversity halysitid-heliolitid autobiostrome in the Late Wenlock Halla Formation at Blåhäll 1, Gotland is indicative of specific environmental conditions during a short period after the global Mulde event. The dominating coral species building this particular mud-facies biostrome are tabulates *Stelliporella* cf. *parvistella* and *Halysites laticatenatus*. Growth forms of the tabulate corals indicate a high background sedimentation rate during the growth of the biostrome. The appearance of the biostrome is temporally very close to the onset of widespread reef formation in the basin suggesting that the reef growth was controlled by the basin-regional factors. The specific features of the Gotland material assigned to *Stelliporella parvistella* (Roemer, 1861) is discussed.

PAPER V. The development of tabulate coral genera throughout the Estonian Ordovician and Silurian successions is analysed. The first appearance of the Ordovician tabulates in the Oandu Stage, the renewal of tabulate fauna in Llandovery, high diversity in Wenlock and the gradual decrease in Ludlow are clearly demonstrated.

PAPER VI. The occurrence of the youngest halysitid *Cystihalysites* sp. is reported from the Eke Formation (Ludfordian) in Gotland, Sweden. Halysitids were considered absent at this particular level but the new data show that at least the one halysitid species survived the early stage of the Lau extinction event.

MATERIAL AND METHODS

This research is based on both museum collections and newly collected material.

The new specimens were collected from outcrops on Gotland Island (Sweden), Saaremaa Island (Estonia) and at Jämtland (Sweden) (Fig. 1). The collection of halysitids (87 specimens) analysed in PAPER I comes from the Swedish Museum of Natural History, Stockholm (on loan to the late Einar Klaamann). The specimens in this collection, like many other old collections, comprise fragments of halysitid coralla and their thin sections. Such old museum collections provide substantial information about the taxa occurring in a particular area but are largely unsuitable for variability studies because of the limited number of specimens and lack of proper field documentation. To relieve this limitation, a special variability study involving extensive fieldwork was carried out (PAPER II). The localities were selected from the same stratigraphic interval (Slite Group) in Gotland (Asfaltverket 1, Hide 1, Stora Myre 1, Alnäse 1, Klintsbrovik 1, Simunds 1 and Tjäldersholm 1) and representatives of one order (Favositida) were selectively sampled. The Halysitida material was collected from the biostrome at Ireviken 1, Gotland. Altogether 26 favositid specimens and 28 halysitids specimens were used to investigate intraspecific variability. Five additional favositid specimens from the Sepise locality of Saaremaa Island were added to the set.

Figure 1. Map of localities of collected material: Jämtland, Saaremaa and Gotland.

The structure of tabulate corals can be investigated only through thin sections in transmitting light. The identification of the specimens even in generic level may prove impossible by observing them from the surface only, because of poor visibility of the important characters. Therefore, it is important to obtain reasonably large collections that are representative of the species. The palaeoecological studies consist of documentation of the position and orientation of coralla, and of the sedimentological background data. When fragments of large coralla embedded in the sediment are collected, the whole coralla must be measured and sketched in the field.

PAPER III deals with localities in Jämtland, Sweden. Most tabulates in Verkön Island occurred in thick limestone beds, which complicated sampling. Some specimens recorded were also fragmentary. In contrast, material was easy to collect at Ede locality and on Norderön Island. The material is referred to biostromes at both localities, but the biostrome with tabulates could not be documented at the localities during this visit. The biostrome in Norderön was possibly below sea level. Some material from Michael Bassett and Lesley Cherns collected about twenty years ago was added to the Jämtland collection.

Thin sections and photographs of tabulate specimens from the Blåhäll 1 on Gotland Island were used to identify tabulate corals and to describe *Stelliporella* cf. *parvistella* in PAPER IV.

Two halysitid specimens recently collected by Olof Sandström and Lennart Jeppsson from Botvide 1 on Gotland Island, and three other halysitid specimens collected by the author were specially considered in PAPER VI.

Some other field studies substantially complemented my general knowledge of tabulate faunas of the Baltoscandian area. Fieldwork in Norway in 1997 complemented the general overview on Ordovician and Silurian localities (Mjøsa, Oslo Region) and provided a few specimens of tabulates from the Oslo Region (*Favosites kalevi, Paleofavosites dualis, Paleofavosites major, Paleofavosites asper, Heliolites interstinctus, Acidolites* sp., *Riphaeolites lamelliformis, Catenipora quadrata, Catenipora maxima, Angopora hisingeri, Thecia swiderniana*). These personal observations are included in the section on geological setting in this thesis. During the fieldwork in Gotland for PAPER II, almost 100 specimens (favositids, heliolitids, halysitids) were collected (including Ireviken 3, Asfaltverket 1, Tjautet 1, Ygne 1, Ygne 1), but the most of the material remains unpublished. Fieldwork was also carried out in Estonia; the collections were partly incorporated in PAPER II. Altogether 160 tabulate specimens were collected from localities in West Estonia (Saaremaa, Liiva Cliff; Hiiumaa, Hilliste Quarry, Sarve; Päri, Rakvere Quarry). The material from Liiva, 67 specimens (6 species) is mentioned in conference proceedings (Mõtus 2003). A collection of tabulate corals was also assembled during a visit in 1994 to the Dnestr River Basin in Podolia.

Museum visits allowed investigation of the Linnaeus collection (Linnaeus 1767, considered in PAPER I) at the Palaeontological Museum of Uppsala University. Stasinka's collection (Stasinska 1967, considered in PAPER I) was examined at the Paleontological Museum of the University of Oslo. Sokolov

(1951b) described a number of new species making reference to type specimens from Estonia (discussed in PAPER III) but the type material was not found in the museums of St. Petersburg. Therefore the relevant materials from Estonia collected by Klaamann (1964, 1966) were considered. Lindström's collection (Lindström 1899, used for PAPER III) was examined at the Swedish Museum of Natural History.

Several other museum visits complemented to my general knowledge although the observations serve only as supplementary information. The tabulate collections from the Ordovician and Silurian successions of Kazakhstan, Tadzhikistan, Tajmyr and Severnaya Zemlya were examined in VSEGEI, the Russian Institute of Geology, St. Petersburg. The collections at the British Museum of Natural History were also examined for general knowledge. The University of Bergen was visited in order to examine additional Norwegian tabulate material used in BSc theses. The collections from the arctic Urals at the Institute of Geology of the Komi Science Centre in Syktyvkar were examined recently. The laboratory of the Swedish Museum of Natural History was visited to learn the peel method, an alternative to thin-section study. The laboratory of the University of Bergen was visited to observe their method of making serial sections, useful for investigation of the development of corallum.

The examination of the originals and types of the Silurian Baltoscandian tabulate corals indicate that species classification is based on typological concept, like the majority of the Silurian species in Baltoscandia. The earliest taxonomical studies of Lower Silurian tabulates in Baltoscandia started in the 18th century with Linnaeus (1767) on Gotland material and were continued by Schmidt (1858) and Eichwald (1829, 1860) on Estonian material and Lindström (1899) on Gotland material. Lindström also sketched and discussed Estonian specimens. Later taxonomical studies in Baltoscandia were carried out by Klaamann (1959, 1961, 1962a, b, 1964, 1966, 1983) and Sokolov (1951a,b, 1952, 1955) in Estonia and by Stasinska (1967) in Norway. Few of these studies considered intraspecific variability.

There are few studies concerning palaeobiological and palaeoecological aspects of tabulates in Baltoscandia. Several palaeoecological and palaeobiological studies on Gotland tabulates were carried out by Stel (1976, 1978a, b, c, 1979). The growth form of tabulate species from Gotland and the taxonomic value of this feature are discussed by Young and Scrutton (1991). Some halysitid species from Jämtland were analysed by Dahlqvist (1999) with respect to their growth form and environment. These results are complemented by investigations in areas near Baltoscandia. Taxonomy, ecology and biology of early Silurian tabulates of Podolia were investigated by Sokolov & Tesakov (1984) and Tesakov (1971, 1974). Zotov (1986) and Pushkin (1991) compiled lists of Silurian tabulate taxa from the Podljassk-Brest area. Bondarenko (1992) revised all heliolitid taxa from Baltoscandia and Podolian. The species composition of lower Silurian tabulates in these areas is similar to that of Baltoscandia, but the collections themselves have not been examined by the author.

GEOLOGICAL SETTING

The modern views of the margins of the Baltica palaeocontinent in the early Palaeozoic have recently been discussed by Fortey and Cocks (2002, Fig. 2). The northwest margin of Baltica comprises the Scandinavian Caledonides, which were formed during the collision of Baltica and Laurentia. The northern margin extended to the islands of Pai-Khoi and Novaya Zemlya. The eastern margin is drawn through the Novaya Zemlya and further southwards along the Urals to Kazakhstan. The position of the southern margin between west Kazakhstan and Romania is uncertain, but Podolia with Baltic faunas lies some distance of the margin (Cocks and Fortey 1998). The south-western margin of Baltica comprises some parts of the Tornquist-Teysseire Zone in northern Germany and south of Denmark. The suture between Avalonia and Baltica lies eastward of the Ordovician arc-related volcanic rocks found in the western North Sea and in eastern Britain (Pharaoh et al. 1991, Cocks and Fortey 1998).

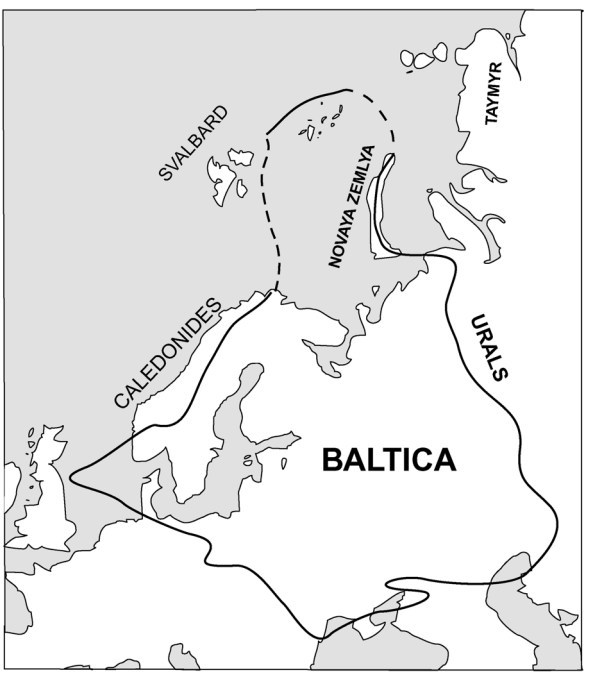

Figure 2. Boundaries of the Lower Paleozoic Baltica paleoplate (thick line) after Fortey and Cocks (2002).

The closing of the Tornquist Sea between the Baltica and Avalonia towards the end of the Ordovician was followed by the collision of Eastern Avalonia and Baltica (Torsvik 1998). This collision is revealed in the palaeomagnetic, tectonic and isotope record and confirmed by the progressive faunal integration of Avalonia and Baltica during the Ashgill (Cocks and Torsvik 2002). The collison of Avalonia and Baltica with Laurentia took place in the middle Silurian (Cocks 2001). The development of the Caledonides, which resulted from collisions among paleoplates, caused rapid accumulation of the silty Bruflat Formation in the Oslo region during the early Silurian (Johnson et al. 1991).

Palaeozoic tabulate corals occupied a large variety of facies. These corals typically occur in carbonate facies, being particularly abundant in reef facies (Hill 1981). Some tabulates also occur in argillaceous-arenaceous, volcanic, sedimentary or terrigenous facies, e.g. Devonian tabulates in Kazakhstan, Russia's Far East, Kuznetsk basin or Holy Cross Mountains (Stasinska 1954; Sokolov 1962).

Silurian fauna can be distinguished around the Baltica Palaeocontinent in five major basins: Central Scandinavian, East Baltic, Timan-Pechora, Dniester and Peri-Caspian (Baarli et al. 2003). The tabulate distribution in these areas is rather uneven, for example, no tabulates have been recorded from the Peri-Caspian Depression. Additionally, some tabulates have been located in platformal settings: two species of tabulate corals have been recorded from dolomites of the vicinity of Moscow, between Yaroslavl' and Vologda (Resheniya 1987).

The tabulate-rich Silurian successions are well exposed in a belt extending from Central-Scandinavia to Dniestr depression (Fig. 3). The Central Scandinavian Basin was most affected by the development of the Caledonides at the western margin of the Baltica and only Llandovery and Wenlock deposits have been preserved in this region. Tabulate corals of Llandovery have been recorded from Jämtland, close to the Caledonides (PAPER III). These corals occur in the Ede Formation, which comprises interbedded quartzites and limestones with bioherms, and in the Berge Formation, which consists of limestones. Although Jämtland has suffered the most intensive post-depositional folding and metamorphism in Scandinavia (Baarli et. al. 2003), the internal structure of most tabulates is sufficiently well preserved. The Oslo Region complements the Central Scandinavian Silurian succession with tabulate occurrences in Wenlock. Slightly different intervals of the Silurian succession are exposed in three areas near Oslo — Malmøya, Asker and Ringerike (Fig. 4). The tabulates occur in limestone facies, represented by the Solvik, Rytteråker, Vik, Skinnerbukta, Brakøya and Steinsfjorden Formations.

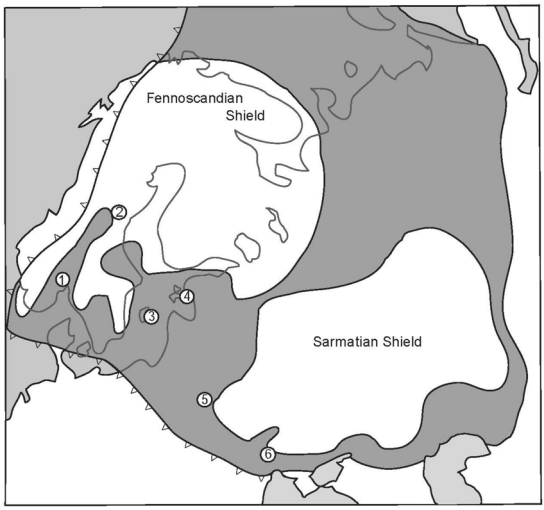

Figure 3. Silurian Baltica showing land and sea areas and active margins (after Baarli et al. 2003). Locality areas of tabulate corals are following: 1, Oslo Region; 2, Jämtland; 3, Gotland; 4, Estonia; 5, Podljassk-Brest and 6, Dniestr River Basin.

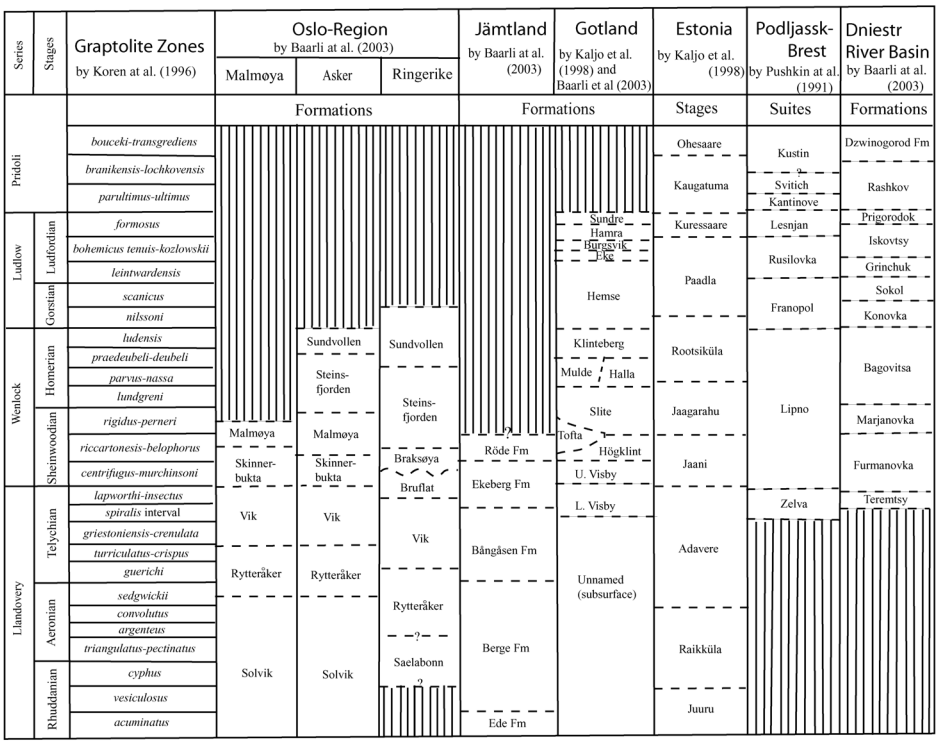

Figure 4. Stratigraphy of the Silurian strata from Oslo-Region, Jämtland, Gotland, Estonia, Podljassjk-Brest and Dniestr River Basin in correlation with the graptolite zonation.

The Silurian of the eastern Baltic area is rich in tabulates. The Silurian succession in Gotland is exposed from the upper Llandovery (Lower Visby Formation) to the upper Ludlow (Sundre Formation). The lower Llandovery sediments are not exposed but can be examined in the File Haidar drillcore, in which tabulate corals have been recorded (Klaamann 1971). Tabulate corals occur in all formations. However, there are some gaps in the Wenlock and Ludlow succession and some units (the Rootsiküla Stage and most of the Ludlow) are poor in tabulates. The Gotland succession fills the gaps of Estonian succession (northern Saaremaa) with the tabulate-bearing Slite, Halla, Mulde and Hemse formations and also the Ludfordian (Jeppsson et. al. 1994). The lowermost and topmost Silurian successions are represented in Estonia but not in Gotland. However, the Wenlock and Ludlow tabulates are more diverse in Gotland, due to the particular facies conditions.

Silurian tabulates are also present throughout the Silurian in the Podljassk-Brest and Dniestr areas. The transition to the Tornquist-Teysseire Zone was steeper in this region than in the Baltic area. In the Podljassk-Brest area tabulates have been described from the Wenlock and Ludlow. The Silurian succession in the Dniestr River Basin is analogous to Podljassk-Brest, being richer in corals in Ludlow. This indicates more favourable conditions for tabulate corals in the Dniestr River Basin during the period when the sea was gradually tapering. Large bioherms occur in the Konovka Formation (Ludlow) and also in older formations. The stratigraphy in the Dniestr River Basin has long been controversial and some outstanding issues remain. Nevertheless, the correlation is this thesis is based on Baarli et al. (2003). The tabulate corals are present throughout the Silurian Teremtsy, Furmanovka, Maryanovka, Bagovitsa, Konovka, Sokol, Grinchuk, Rashkov and Dzwinogorod Formations, being absent only in the Iskovtsy and Prigorodok Formations (Gritsenko pers. comm. 2004, Fig. 4.).

The East Baltic and Dniestr River basins are the areas of the Baltica plate where the tabulate corals have been studied most thoroughly. The material in these areas is well preserved and the localities are well exposed and easily accessible. Estonia and Gotland together comprise the most complete section with diverse tabulate fauna known throughout the Silurian. The individual sections in this area are well studied and therefore suitable for detailed tabulate research. This area is also the focus of this thesis.

The Estonian and Gotland successions constitute the East Baltic Basin. The six major marine facies belts of this basin are listed as follows (by Bassett et al. 1989; Fig. 5): 1 – low energy, fine-grained dolomites and dolomitic marls, interpreted as inshore lagoonal and tidal flat sediments; 2 – high energy, shoal – bar belt with organic buildups and banks; 3 – the open shelf (Nestor and Einasto 1997) belt, predominantly biodetritial calcareous mud or finer grain sediments deposited under lower energy than the shoals, typically forming nodular limestones; 4 – lower energy sediments passing in transition to more open water, which comprise grey calcareous-argillaceous muds, changing offshore into green and red mudstones, forming marls and muddy nodular limestones; 5 –

gray to brownish muds and silty muds with little carbonate content, formed within a depression represented by various monotonous mudrocks; 6 – the outermost facies comprising dark-grey to black muds preserved as graptolitic argillites of the outermost platform beyond increasingly deep zones of central European ocean (Bassett et al. 1989).

Tabulate corals are distributed predominantly in the shallow part of the basin and occur mainly in the high-energy, shoal facies, although they also occur less frequently in all other facies belts except the depression. The corals are rare in tidal flats and transition facies belts and achieve maximum diversity in the belts of shoal to open platform (Klaamann et al. 1980; Fig. 5.).

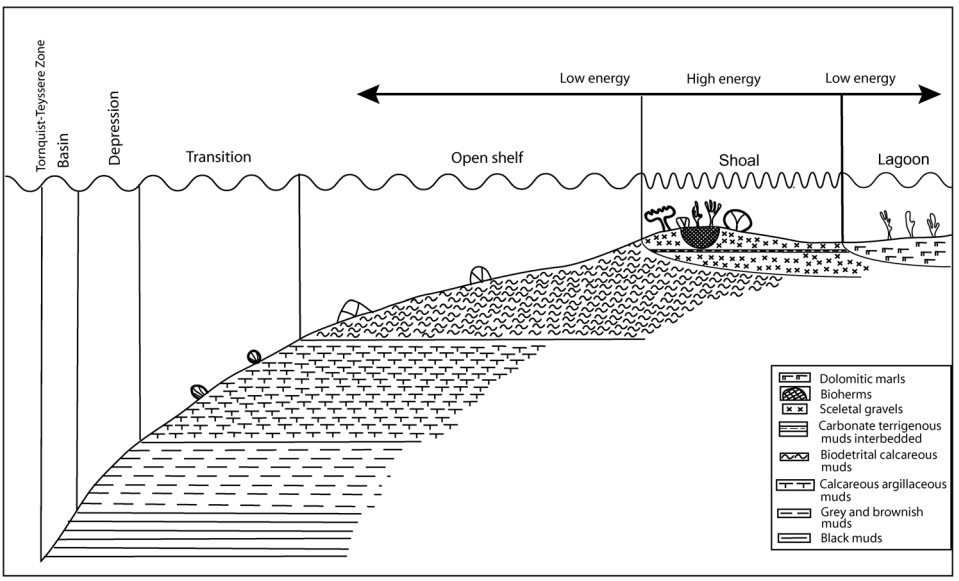

Figure 5. Profile of the Silurian East Baltic Basin (Estonia and Gotland) with the facies from Bassett at al. (1989) showing the position of tabulate corals (figured shapes).

TAXONOMY OF TABULATE CORALS

Biology of tabulate corals, increase and form of coralla

"The tabulata are extinct, almost entirely Paleozoic order of corals characterized by their exclusively colonial mode of growth and by secretion of a calcareous exoskeleton of slender tubes crossed by many fragile transverse partitions called tabulae..." (Hill 1981, p. 340). The corallum (colonial skeleton) is built by individual polyps connected to each other in different ways (Clarkson 1986). The biology of tabulate corals is considered analogous to modern scleractinians (Hill 1981).

Most scleractinians are colonial corals secreting a carbonate skeleton. The skeletal structure of Tabulata features many similarities with the modern Scleractinia. The colonies of both consist of corallites surrounded by walls and with internal septa and tabulae, but the scleractinian skeleton consists of aragonite whereas tabulate coralla were originally composed of calcite (Hill 1981).

Both the sexual and asexual reproduction of tabulate corals is believed to be similar to that of scleractinians. The earliest stage in the ontogeny of scleractinians is the planula stage, which settles on a hard substrate, metamorphoses into a coral polyp and starts to build a calcareous skeleton. The earliest stage of a tabulate coral is the development of a protocorallite (the first coral polyp of a colony), upon which a new offset forms (similar to budding in scleractinians) giving rise to a new corallite.

The process of offsetting, increase, may have different characteristics. Scrutton (1987) provides examples of lateral increase in favositids and intramural increase in sclerosponges. The first case describes a situation when a daughter corallite (offset) arises from the parent corallite. In sclerosponges the offset appears between the calicles unconnected to the parent calicles.

The coenenhymate tabulate corals are characterised by coenenhymal increase, where a new offset arises from a reorganized area in coenenchyme (Srutton 1998). Corallum growth is regulated by the area and density of offsetting and the orientation of offsets causes the variety of corallum shapes (Fig. 6).

Coralla with non-separated polyps are called massive, those with straight or curved and not laterally contiguous corallites are designated as fasciculate. Massive coralla in which the corallites are contiguously prismatic and have their axes normal to the surface (such as favositids) are classified as cerioid. The shape of massive coralla depends on spreading offsets: when regularly produced, massive coralla are domed or hemispherical (Fig. 6A). Massive coralla can be also branching (Fig. 6E), those with cylindrical branches are referred to as ramose; flattened coralla are called foliose, netlike taxa are called anastomosing (e.g. *Aulopora*). Massive coralla with vaulted surfaces, when the axes of corallites are declined, form alveolitoid coralla. Massive coralla with individual tabularia separated by common skeletal tissue are coenenchymal (heliolitids). Massive coralla that are also branching and in which each corallite develops a marginarium of thickened skeletal tissue distally comprise the

Pachyporinae and some Alveolitina. Cateniform coralla have corallites united laterally in palisades forming a network (Hill 1981, Figs. 7J,K).

Although the corresponding terminology is elaborated in great detail, the form of corallum has only limited taxonomical value. For example, some tabulate corals always branch (e.g. *Parastriatopora*, Fig. 6E) but some favositids feature many different forms (PAPER II, Fig. 6A, B, C, D, F). This is due to the large ecophenotypic plasticity of this particular feature. Therefore the study of species/environment interaction is particularly important. In the typological species descriptions the corresponding information is brief, containing usually only general shape features (as massive, spherical or branching), although the variability of shapes is much larger in reality.

Morphology of skeletal structure

Corallites are slender tubes of different shape and size that contain a polyp. The terminology of tabulate corals here follows that by Hill (1981).

The shape of corallites varies from prismatic (favositids; Fig. 7A, C) to oval (halysitids; Fig. 7K), cerioid (heliolitids see Fig. 7H, auloporids see Fig. 7I and syringoporids) and alveolitoid (alveolitids). Prismatic corallites feature various numbers of sides, ranging from 3 to 12. The number of sides increases with the maturity of a corallite, being 3–5 in juveniles and 6 or more in adults (Lee and Noble 1988; PAPER III). The sides of corallites are always counted, but this feature has no high taxonomic value. Corallite size has an important taxonomic value at the species level, but unless biometry is applied correctly its significance is limited.

The distal surface of each corallite forms a **calicle**, with a narrow border, steeply sloping sides and flat or concave base. The calicles are not always preserved and are not measured for taxonomic purposes.

Corallites in most fasciculate and cerioid coralla are enclosed laterally in a carbonate sheath called **epitheca**. In thin sections it is denser and darker in transmitted light, and is recognisable by wrinkles and grooves on the outer side of corallites. Inside the epitheca, the corallite consists of a **wall** (peripheral stereozone), septal elements and tabulae. The corallite wall (Fig. 7E), externally sheated by epitheca, varies in thickness and its original structure is affected differently by diagenesis (Hill 1981). Therefore its microstructure depends on the degree of preservation. Walls contain septal elements such as the bases of septal spines, and pores. The wall thickness and shape are sometimes important in taxonomy. Wall shape can be straight, wavy or corrugated (strongly wavy) in transverse section (see *Paleofavosites hystrix* and *Paleofavsites dualis* in PAPER III).

Septal elements of corallites are radially and longitudinally arranged in the outer parts of the tabularium. The length and number of septa varies with individual taxa. Twelve septa are characteristic only for Heliolitina and Halysitina, whereas others have a variable number of septa. Septal spines (Fig. 7E, F), originally monoacanthine trabeculae (Hill 1981), are long and tiny

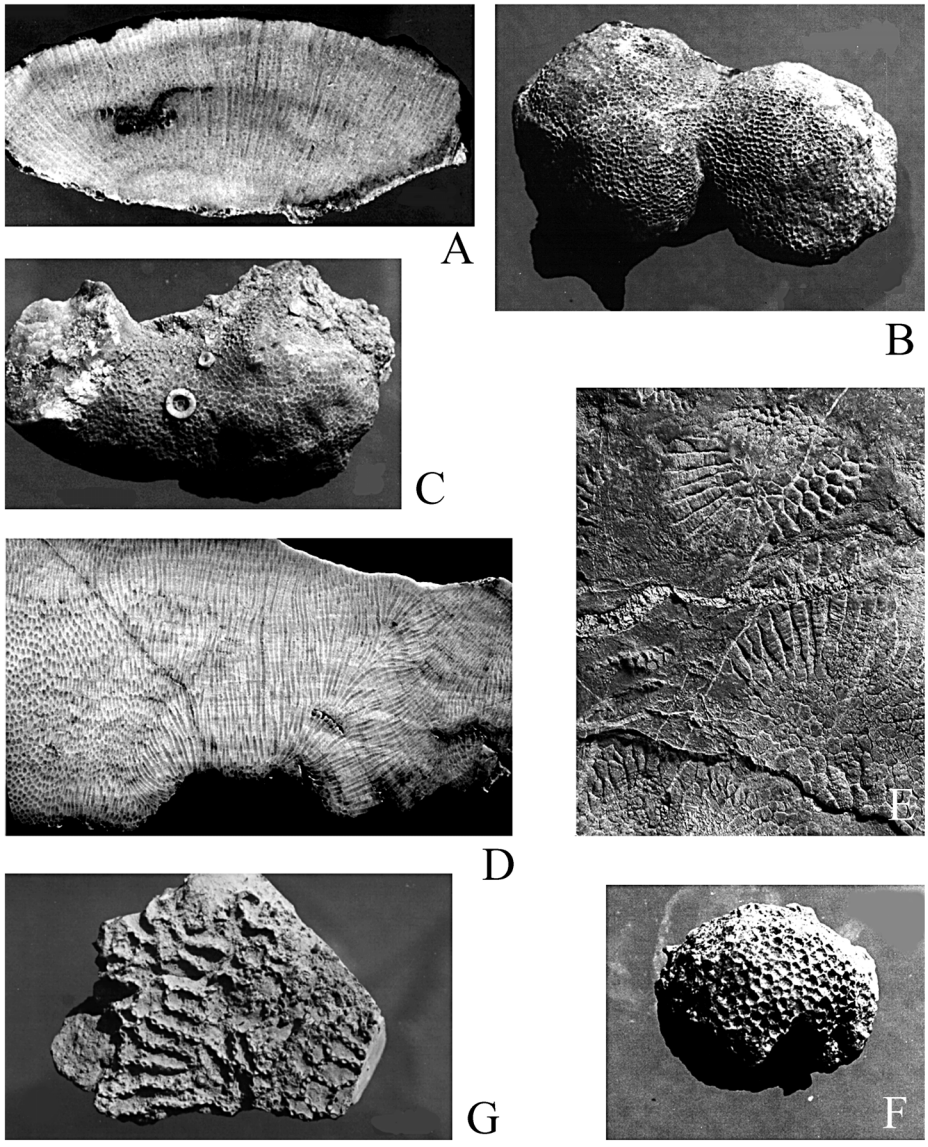

Figure 6. Shapes of massive coralla. **A**. Domal (0.78 x). **B**. Bulbous (0.74 x). **C**. Columnar (0.88 x). **D**. Tabular (0.58 x). **E**. Branching (1.5 x). **F**. Spherical (1 x). **G**. Cateniform corallum (0.57 x).

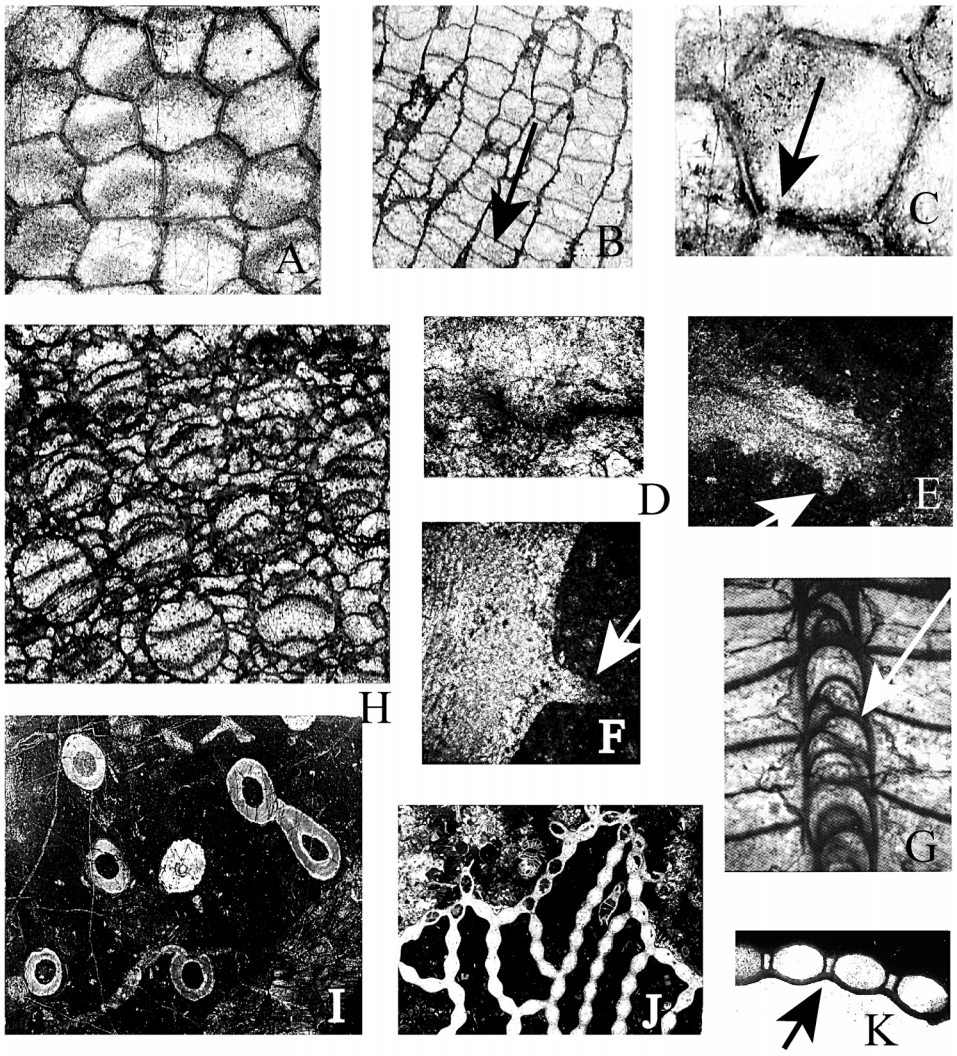

Figure 7. Structure of coralla. Photographs of thin sections. **A**. Transverse section of massive corallum (cerioid), consisting of tightly packed corallites (3.8 x). **B**. Vertical section of corallites with tabulae and septal spines. An arrow pointing on tabulae (4 x). **C**. Transverse section through corallite, an arrow pointing on pore (8.5 x). **D**. Pore plate with an arrow pointing on it (27 x). **E**. Corallite wall with septal spines and an arrow pointing on septal spine (21 x). **F**. Septal spine of *Aulopora* with a sharp tip (70 x). **G**. Vertical section of tubule (mesocorallite) in *Cystihalysites*, an arrow pointing on diessepiment (30 x). **H**. Coenenhymal form of *Propora*, transverse section showing corallites being surrounded with coenenhyme (5 x). **I**. Transverse section of network forming, anastomosing *Aulopora* (3.5 x). **J**. Transverse section of *Halysites*, showing corallites in ranks forming elongated lacunae (1.7 x). **K**. Transverse section through corallites of *Halysites*, an arrow pointing on tubule (mesocorallite), (4 x).

elements, located in rows that are usually oriented upwards, although occasionally horizontally or downwards, and their bases are positioned inside the peripheral stereozone. The development of septal spines, as well as their size, shape and abundance, play an important role in distinguishing the species. There are several species of the same genus that have no septa, such as *Halysites junior* (PAPER I). Some species have variably developed septal spines, such as *Paleofavosites hystrix* (PAPER III).

Tabularium is the inner cavity of a corallite between the wall and septa. Its diameter is measured in heliolitids, auloporids and halysitids (PAPER III).

The tabularia of neighbouring corallites are connected by **pores** (openings through walls, Fig. 7C), which differ in shape and size. In favositids the pores are located in the corners of the corallites or in mid-walls. Syringoporids have connecting tubuli, which are the pores between the widely spaced corallites. A pore may be closed with a pore-plate.

In favositids and syingoporids the polyps are joined through pores. The position of the pores in the corallite walls and also the size and shape of the pores are important in taxonomy. The pore position in walls or at corallite corners is diagnostic for the favositid genera. *Paleofavosites* has the pores in corners and *Favosites* in mid-walls. The genus *Mesofavosites* was founded on the basis of pores located both in corners and mid-walls, but the genus is synonymised with *Paleofavosites* (PAPER III) because the mid-wall pores may sometimes occur in the species of this genus. Even in the type species, *Paleofavosites asper,* the pores are located both in mid-walls and in the corner position (Powell and Scrutton 1978). Some species may have large and abundant pores. Particularly large pores are characteristic of *Multisolenia.*

Tabulae are horizontal skeletal elements attached to the inner surface of the wall (Fig. 7B). Tabulae differ in shape (flat, wavy, concave or convex). Tabulae are commonly thin, but may show growth lamellae and fibres when thick (Hill 1981). Each tabula froms a temporary base for a polyp. The density of tabulae is always recorded in descriptions of tabulates but this feature is not diagnostic due to fenotypic (environmentally dependent) variation. The density of growth banding is also influenced by environmental conditions (Scrutton and Powell 1980). Therefore the interval between tabulae may be considered a non-diagnostic characteristic.

Coenenchyme is the common skeletal tissue between the neighbouring tabularia in Heliolitina (*Propora*, *Heliolites*) and Halysitina (*Halysites*, *Cystihalysites*), It is also characteristic of some *Sarcinula* and some Syringoporicae. Coenenchyme in *Propora* (Fig. 7H) and in *Cystihalysites* (Fig. 7G) is dissepimentate but in *Heliolites* it consists of tubuli (slender tiny tubes). **Dissepiments** are small plates developed as a part of coenenchyme outside the tabularium. They can vary in shape. Similarly to *Heliolites,* the tubuli (mesocorallites) are present in *Halysites*, but they are found at the junctions of a corallite chain (Fig. 7K). Coenenchyme probably fulfilled the same function as the coenosarc in modern Scleractinia, representing a common tissue for coral polyps (Preobrazhenskij 1974).

Microstructure

The crystallites of the corallite in the Scleractinian corals, as seen under the scanning electron microscope, are oriented perpendicular to the secreting ectodermal surface and are grouped in microtufts. Under the optical microscope, the groups of microtufts continue in the same general direction from one growth lamellae to another, appearing as single fibres grouped in tufts of fascicles (Hill 1981). Growth lamellae crossing these fibres are recognised by tonal changes or breaks in the continuity of fibres at the surface of lamellae. It is assumed that the components of microstructure in the tabulate coral wall consist of the similar growth lamellae, but differ in location of the composite spherulitic crystallization.

Three main types of microstructure are lamellar, fibrous and paratrabecular. Lamellar structure is clearly visible in *Aulopora assueta* (PAPER III, Fig. 8E). Heliolitids such as *Propora speciosa*, *Propora tubulata* and *Propora conferta* (PAPER III, Fig. 8C,D) are characterised by the trabecular microstructure of the wall. Sometimes three layers of the wall can be recognised in Halysitids. They differ in colour and structure. The outer layer has transverse fibrous structure, the intermediate layer is lighter and has a lamellar microstructure and the inner layer is dark-grey and contains the bases of septal spines (PAPER I, Fig. 8A,B). In most cases dolomitisation destroys the microstructure. The specimens from Jämtland show no microstructure, except for some specimens of *Propora* and *Aulopora* (PAPER III).

Diagrams from Dubatolov (1971) give a good overview of types and subtypes of the microstructure in the walls of the upper Silurian and Devonian tabulate corals (Fig. 9); only examples of Silurian genera are referred to in parentheses. The sub-types of lamellae are concentric, with outer ephiteca (*Syringopora*), coarse concentric (*Pachipora*), fine concentric (*Striatopora*, *Cladopora*) and plicate concentric (*Plicatomurus*). The fibrous structure is divided into radially fibrous with traces of growth lamellae (*Thamnopora*), radially fibrous with marked growth lamellae, radially fibrous with no trace of growth lamellae (*Favosites*), cryptoradially fibrous with no trace of growth lamellae (*Favosites*) and pinnately (clinogonally) fibrous with growth lamellae. The wall microstructure with clinogonally fibrous septal trabeculae such as *Echyropora* (Hill 1981) is classfied paratrabeculate by Dubatolov (1971) and is illustrated in Fig. 9.

Much has been discussed with respect to original and secondary microstructures. It is assumed that the biomineral of modern Scleractinia is aragonitic and the primary mineral of Tabulata was calcitic (Sorauf 1996). It is still unclear weather the skeleton of tabulate corals was originally built of fibrous biocrystals, as is the case with scleractinians, or if some tabulates had a lamellar skeletal microstructure (Sorauf 1996).

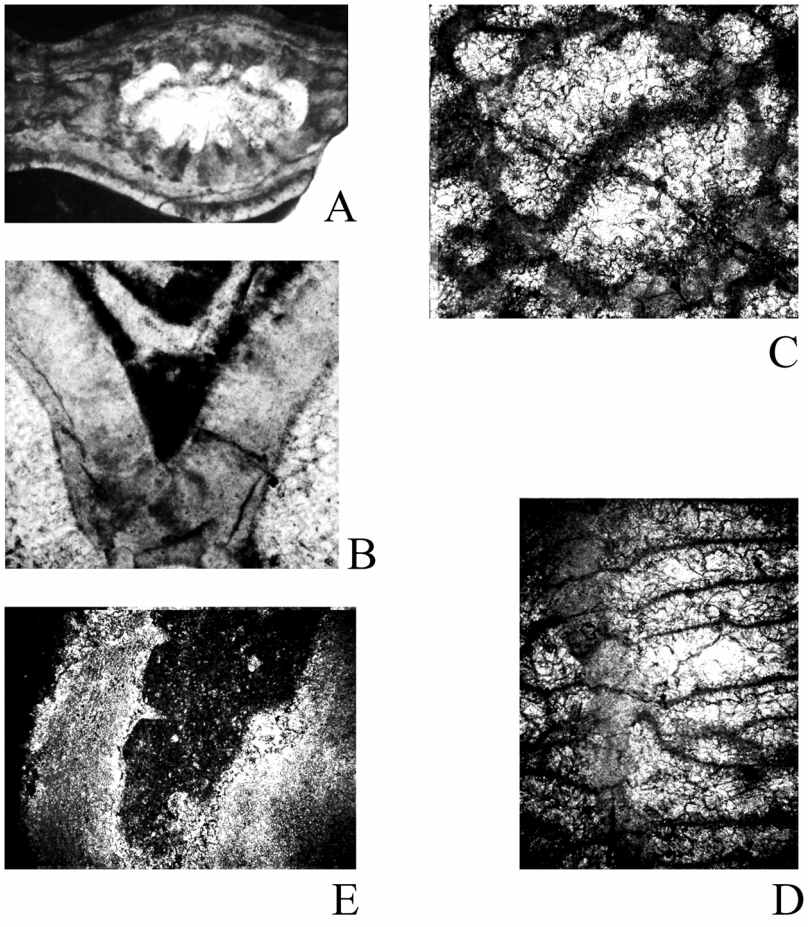

Figure 8. Microstructure of the corallite wall. **A**. Transverse section of corallite in *Halysites*. Outer layer consists of transverse fibrous structure, intermediate layer is lighter with lamellar structure and inner layer consists the bases of septal spines (x 20). **B**. The same as in A, but the third, inner layer is absent (x 40). **C**. Transverse section. Trabecular microstructure of corallite wall in *Propora* (20 x). **D**. Vertical section through corallite wall in Propora, showing the trabecular structure of corallite wall (17 x). **E**. The section through *Aulopora*, showing light homogenous lamellar structure of corallite wall (35 x).

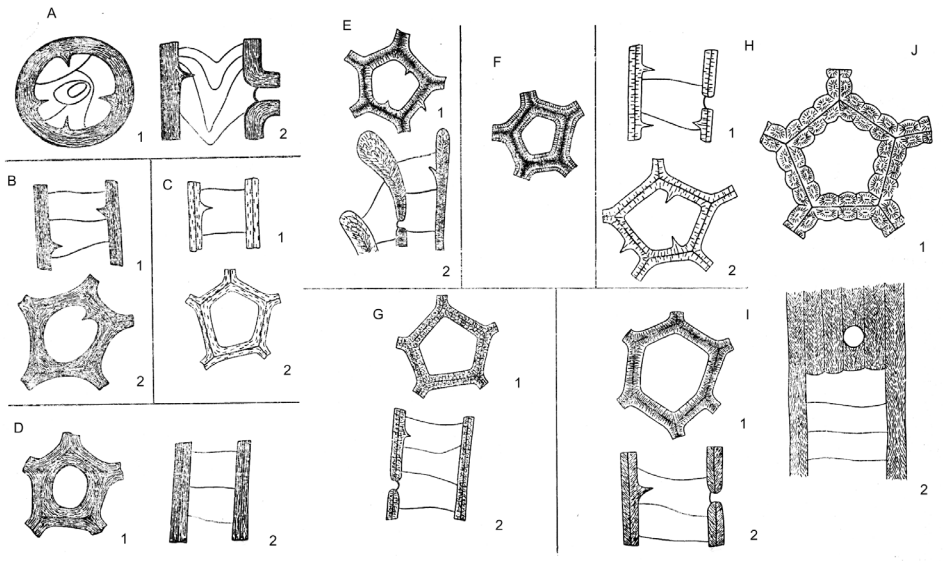

Figure 9. Types of microstructures of the corallite wall. **A**–**D**. Lamellar type after Dubatolov (1971). **A**. Concentric with outer ephiteca, 1, transverse section, 2 vertical section. **B**. Coarse concentric, 1, vertical section, 2, transverse section. **C**. Fine concentric, 1, vertical section, 2, transverse section. **D**. Plicate concentric, 1, transverse section, 2 vertical section. **E**–**I**. Fibrous type after Dubatolov with some completions of growth lamellae from Hill (1981). **E**. Radially fibrous with traces of growth lamellae,1, transverse section, 2 vertical section. **F**. Radially fibrous with marked growth lamellae. **G**. Radially fibrous without trace of growth lamellae, 1, transverse section, 2 vertical section. **H**. Cryptoradially fibrous without trace of growth lamellae, 1, vertical section, 2, transverse section. **I**. Pinnately (clinogonally) fibrous of the growth lamellae, 1, transverse section, 2 vertical section. **J**. Paratrabeculate by Dubatolov (1971) and the wall microstructure of clinogonally fibrous septal trabeculae by (Hill, 1981), 1, transverse section, 2 vertical section.

Lamellar structure is called “secondary lamellation” by Hill (1981) and “micro-lamellar” and “undulating lamellar” by Lafuste and Tourneur (1987), to distinguish it from biogenic growth lamellae. Oekentorp (2001) called the lamellar structure “pseudolamellar” emphasising its abiogenic nature. He also indicates that the zigzag pattern (such as in *Aulopora* and *Syringopora)* depends on the orientation of the thin section, as the orientation and distinctness of the cleavage in different planar sections through the rhombohedra may create different patterns. The fibrous and paratrabecular types of microstructure by Dubatolov (1971) are classified by Hill (1981, p. 452) as traces of primary structure. Hill (1981) also proposes that the septal spines of Tabulata are fine trabeculae with an axis of calcification, such as in Ordovician *Lyopora* and Silurian *Thecia* and *Coccoseris*. There are also different opinions on trabecular

structure. Schouppe and Oekentorp (1974) suggest that no real trabecular structure exists in tabulate corals as they do not possess centres of crystallization.

However, Nothdurft and Webb (2003) compared the microstructure of extant *Acropora* (Scleractinia) and *Michelinia* (Tabulata) in ultra-thin sections. They found that there could be a biological basis for microlamellae and some tabulates could originally have microlamellar structure, or microlamellar structure with some diagenetic overprint (Webby pers. comm. 2004).

It is clear that microstructure holds some importance in tabulate taxonomy. Hill (1981) assigns heliolitid corals to the subclass Tabulata in a typical microstructural pattern. The character of microstructure could be distinct in some taxa of a family group (e.g. Coccosseriididae), but the same feature might be less important on the genus or species level.

The microstructural pattern of different taxa is recognised here and described in the taxonomical section and used as supplementary information.

Retrospective of tabulate studies

The tabulate taxonomy in Baltoscandia has been based so far on the typological concept with little revision until now. A large number of species has been described by many authors starting from the 18th century (see "Material and methods"). The state-of-art in taxonomy of tabulates of Baltica is based on these studies.

Genetic theories of the early 20th century have also influenced the species concept in palaeontology (Simpson 1944, 1953; Carter 1954). Tripp (1933) analysed the variation in favositids from Gotland and modified the "meaning" of a tabulate species. The variability study of favositids carried out by Jones (1936) considers the taxonomical problems and contains an attempt to revise favositids in an environmental context. The intraspecific variability in tabulate corals was considered also by Klaamann (1964), who synonymised several species founded by Sokolov (1952a) due to overlapping diagnostic characters. Tesakov (1971) improved the concept of a species. The smallest taxonomical unit according to his concept is the corallum, whereas the coralla are joined hierarhically into a populational generation, a population, a popularia and a subspecies. All these categories, established with respect to biological, palaeoecological, stratigraphical and geographical aspects, illustrate the complicated structure of a tabulate species by Tesakov (1978).

Many studies continue to be carried out on tabulate biology. The biological aspects of tabulate (favositid, halysitid) growth and reproduction were studied by Lee and Noble (1990) and Noble and Lee (1991) and the species/environment interaction by Young and Scrutton (1991), Young and Elias (1997, 1999). The aspects of species/environment interaction in Silurian favositids from Gotland and Saaremaa have been considered in PAPER II. The studies by Lee and Noble (1988) and Sutton (1966) focused on the details of species discrimination as the importance of corallite size and their measurement technique.

Typological species

In a typological species, the intraspecific variation is not sufficiently considered. Species of tabulate corals are established often on the basis of a single specimen or on a fragment of a specimen. Therefore some characters may remain neither observed nor described. As a rule, the metrical values of diagnostic characters are not analysed statistically, and therefore the intraspecific variability is inadequately described.

The major problem is the overlap of metric characters. This problem is addressed in papers I and III. Because of the overlap of diagnostic characters, *Halysites crassus* is considered a junior synonym of *H. senior* (PAPER I). Similarly, *Favosites subfavosus* and *F. favosiformis* are synonymised with *Favosites favosus* (PAPER III). Additionally several species are tentatively synonymised in paper III. The holotype of *Paleofavosites juuru* is poorly described and the holotype itself is a small corallum, being fairly similar in diagnostic characters to *P. hystrix*. *P. fleximurinus* is tentatively synonymised with *P. dualis* due to the large intraspecific variability of both species, but more specimens are required to resolve this problem completely.

Stelliporella parvistella Roemer was described originally from the Upper Ordovician in Estonia, but the same species is reported to be diverse in Wenlock and Ludlow successions in Gotland. The specimens described from Gotland differ substantially from the holotype (PAPER IV), but more specimens are needed to reveal distinct differences between the Ordovician and Silurian populations.

In addition, the authenticity of some genera has been questioned during revision. *Solenihalysites* Statsinska (1967) was distinguished on the basis of filled tubules, but this was based on a mistaken interpretation of skeletal structure (PAPER I). The same approach has been criticised by Laub (1979) and Young and Elias (1995), based on an example of *Schedohalysites* Hamada and *Acanthohalysites* Hamada, as discussed in PAPER I.

Biometry

The characters are not explained and defined properly in older taxonomic papers, yet one problem is the confusing terminology of massive corallum shapes. The main forms of massive coralla are discoidal, hemispherical or spherical. The varieties of these forms are defined as being cookie-like, crust-like, platy, puffy or flat (Klaamann 1964; Sokolov 1951a,b, 1952). The characters of skeletal elements are based mainly on corallite size, which is expressed as the most common interval of the corallite diameter and the prevailing size of some other skeletal elements (pores in favositids, shape and thickness of corallite wall or septal elements in most tabulates). Many species are also compared on the basis of the interval between tabulae, although this characteristic is considered nowadays to be highly variable ecophenotypically.

Biometry is important for proper defining of taxonomic characters. The measurement methods used in this thesis are explained thoroughly and all the measured metric characters have been statistically analysed.

Coralla have basic shapes described as tabular, domical, bulbous, ceroid, columnar and branching (Fig. 10). The width and height of the coralla are measured externally for each complete corallum. The shape of coralla is calculated as the width (W) and height (H) ratio of a corallum (PAPER III) and, when necessary the corallum height to the midpoint (M) is measured as well (Fig. 11). The shape categories, distinguished according to the ratio of height, width and height to the midpoint of a corallum follow those by Young and Elias (1995):

- tabular (W:H >=3:1, base and upper surface subparallel),
- domical (W:H >= 1:1 but < 3:1, M < 0,5H),
- bulbous (W:H >= 1:1 but < 3:1, M >= 0.5H),
- columnar (W:H < 1:1, sides subparallel).

Low and high bulbous, low and high domal shapes are also used (Young and Scrutton, 1991).

Twenty measurements of a particular characteristic for one corallum is calculated to be sufficient to represent a species (Dixon 1974, PAPER III). The measurement methods below largely follow those by Young and Elias (1995).

For corallites the minimum and maximum and the mean measurement values have been calculated for each specimen and the range of means for a species is shown. The average transverse axis method (Sutton 1966) was used for favositids. Only one diameter was measured for a tabularium in heliolitids (internally from wall to wall) as the corallites are circular in cross section. For auloporids, both the diametre of tabularia (internal) and the diameter of a corallite (external) were measured in transverse section. For halysitids both the longest and shortest axes of the tabularia were measured.

The diameters of all pores (corner and wall pores) were measured. The length of septa was measured as the distance between the outer side of the wall and the end of a septum. The wall thickness was measured between the septa. The microstructure of the corallite wall was described when the preservation was sufficient; the possible primary and secondary structures were not distinguished. The recorded types of the wall structure are fibrous, lamellar and trabecular. The number of tabulae was counted along a 5 mm interval without the starting tabula.

An example of how much the original diagnosis and a biometrically justified description of a particular species may differ is illustrated below, on the example of *Paleofavosites hystrix*.

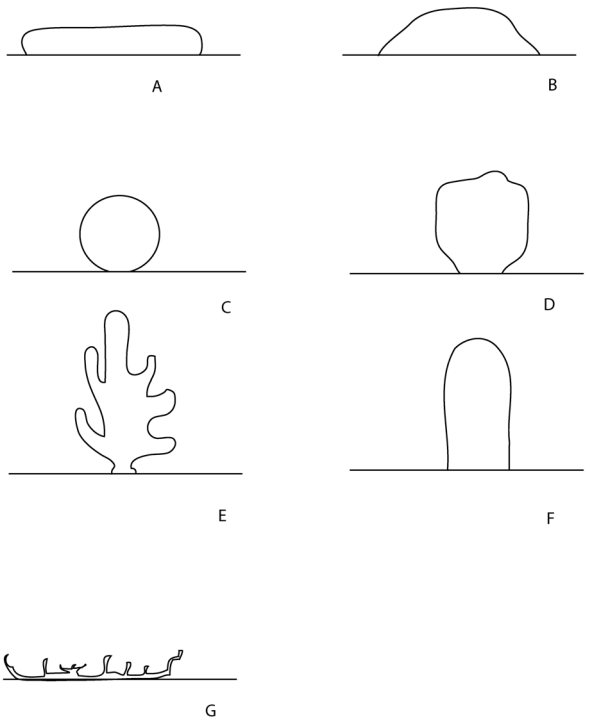

Figure 10. Various corallum shapes: A, tabular; B, domical; C, spherical; D, bulbous; E, branching; F, columnar.

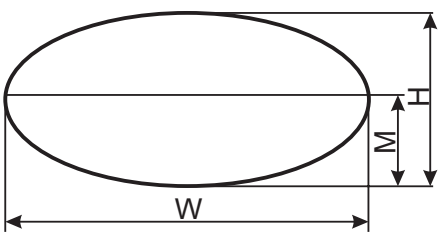

Figure 11. Measurings of corallum; W – width, H – height, M – height to the widest midpoint.

Paleofavosites hystrix Sokolov, 1951 (p. 36)

Diagnosis. Corallum is flat and medium-sized. Corallites are straight and have a slightly corrugated wall with a diameter of 1.2–1.4 mm. The common interval between tabulae is 0.25–0.6 mm, tabulae are wavy. Septal spines are numerous, reaching the centre of corallite and are developed zonally. The zonal development of septal spines is in correlation with the zonal thickening of tabulae.

[The original diagnosis by Sokolov contains some nondiagnostic characters. The shape and size of a corallum and the interval between the tabulae are not diagnostic for a species, because of ecophenotypical variation. The nature of the given interval of corallite diameters is not explained; it could easily be an average or typical diameter, but most possibly it is just a rough estimate in this case).]

Description. Corallum is medium-sized, crust-like, slightly concave in shape. The diameter of the whole corallum was over 150 mm and the height 30–50 mm.
[The corallum shape is not clearly defined and can easily be misinterpreted, i.e. considered a discoidal or a platy form. The height of a corallum is given as an interval of uncertain origin.]

The partly preserved epitheca depicts vertically grown and parallel corallites. Corallites are of a uniform type, mostly 6 sided and prismatic.

The corallite wall is slightly but clearly corrugated, with the prominent mid-line. The zonation is characteristic and resembles the stromatoporoid structure. Dark zones are characterised by thickening and dominating skeletal structures as thick walls, densely spaced tabulae and abundant and long septal spines, whereas the light zones illustrate thinner walls, broadly spaced tabulae and rare and smaller septal spines. The corallite wall is 0.03 mm thick in the light zone and 0.15 mm in the dark zone. Tabulae are thin, wavy and generally densely spaced in an interval of 0.25–0.6 mm, 0.4 mm predominantly in the light zones and 0.15–0.2 mm in the dark zones, with 0.2 as the largest interval. Pores are small and quite rare with a large "circle", are found only at corners and have a diameter of 0.15–0.17 mm.

[The term "circle" is translated here from the Russian "obodok", which has an obscure meaning. The presence of wall-pores was not noted in the original descriptions, which were based on only two thin sections of the species.]

This species typically features long and well-developed septal spines that are oriented upwards. The tip of septal spine is numb. The number of septal spines in vertical section is typically 12. Septal spines are rare or sometimes missing in light zones located at the top parts of the wall's corrugation. As the zones are closely spaced (7 pares of zones is within 2 cm) and slightly declined, both zones are represented in the plane of a transverse cut. There are zones with abundant septal spines and missing septal spines in a transverse section.

Paleofavosites hystrix Sokolov, 1951: PAPER III

Diagnosis. Corallites of variable size with mean diameters of 1.03–1.76 mm. Corallites have from 3 to 8 sides. Corallite wall straight to corrugated and varies in thickness. Corner pores common, mid-wall pores rare. Septa densely spaced

in zones of thickened walls, but are rare or missing elsewhere. Septa of variable length. Tabulae flat, concave, convex or slightly wavy.

[Only taxonomically valuable characters are shown in the diagnosis. The variation of corallite diameters is estimated statistically.]

Description. Coralla are domical in shape. Corallites are irregularly spaced; their orientation has changed during growth, as noted in vertical sections. The corallites are variable in size and shape, having 3 to 7, rarely 8 sides. The number of corallites with less than 6 sides in transverse sections is relatively small. The sizes of 6–8-sided corallites differ largely. The mean diameter of corallites ranges from 1.03 to 1.76 mm. The mean corallite areas are 0.57–1.81 mm^2; in 6–8 sided corallites 0.57–2.46 mm^2.

[Whenever possible, information is given with intervals of statistically estimated metric values.]

Corner pores dominate; 5 of the 28 pores recorded in thin sections are mid-wall pores. The diameter of corner pores is 0.05–0.25 mm and that of wall pores 0.05–0.13 mm. The end of wall adjacent to a pore is square.

[The number of mid-wall pores is given to show that they exist in this species. The interval of pore diameters need not be explained as precisely as that for corallites. The statistical values of all metric characters are shown in special tables added to the description.]

In transverse section, walls are straight and thin in areas without septa, but corrugated and thick in areas with abundant septa. Walls are slightly wavy in vertical section. Septa generally short or absent with a minimum length of 0.08 mm. Septal spines are pointed upwards with sharp tips and reach up to 0.25 mm in length.

Tabulae are flat, concave, convex or slightly wavy, and curved downwards close to the corallite wall. The number of tabulae in 5 mm varies between 4 and 14.

[*The number of tabulae is given as an interval of the number of tabulae counted in a 5 mm interval.*]

The original description is difficult to use for identification of the species. Because of large overlap in diagnostic characters and unclear meaning of the variation intervals, the species can be easily misidentified. Application of biometry and strictly formalised description methods (PAPER III) adds confidence to the identification procedure.

Distribution of tabulate taxa and its influence on taxonomy

The cosmopolitan tabulate species and genera were characteristic of the Silurian Period. *Paleofavosites* became very abundant and diverse in the Llandovery. Forty-two species of *Paleofavosites* have been identified from the west and south of the Baltica paleoplate (Scandinavia, East-Baltic, Podljassk-Brest and Dniestr), but only 16 species occur in Wenlock (Table 1–3). *Catenipora* was also more diverse (18 species) in Llandovery than in Wenlock (only 7 species). The generic diversity was relatively high (19 genera) in Llandovery (Rytteråker, Vik, Lower Visby and Teremtsy formations, Adavere Stage and Zelva Suite) where 8 new genera were identified, but Wenlock is characterised by the highest generic diversity in the Silurian. Thirty-seven genera are known from Wenlock in the western and southern parts of the Baltica paleoplate (Table 1–3.).

Several species considered in papers I, II, III are recorded from the seas of different palaeoplates. *Halysites catenularius* has been recorded, in addition to the Baltica, also in China, Japan and New South Wales; *Favosites favosus* occurs in Laurentia (in modern British Columbia, Niagaran and Anticosti Island) and Kazakhstan (Zeravshan-Gissar mountain region); *Paleofavosites alveolaris* is found in Kazakhstan, *P. dualis* in Siberia (Moyero River), *Propora conferta* in Siberia (Podkamennaya Tunguzka), *Catenipora distans* possibly in Laurentia (Quinn Point, New Brunswik, Gaspé) and *Cystihalysites blakewayensis* and *P. asper* in Avalonia (Fig. 12).

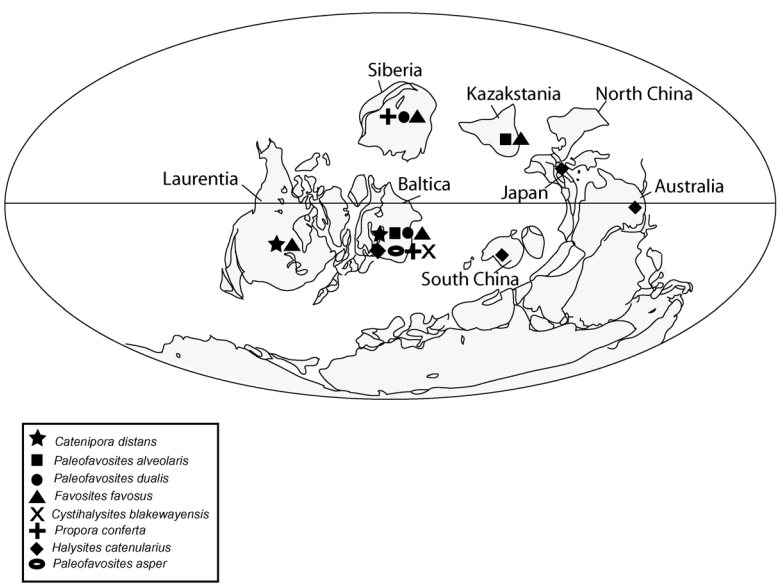

Figure 12. Palaeogeographical distribution of wide-spread tabulate coral species in the Middle Silurian. Paleomap is modified from Scotese (2003).

Table 1. Distribution of all tabulate coral species in the Lower Silurian successions of Oslo Region, Jämtland, Estonia and Gotland. Stratigraphical units are abbreviated as follows: undiff. – undifferentiated, Ordov. – Ordovician, Lland. – Llandovery, Wenl. – Wenlock, L. Visby – Lower Visby, U. Visby – Upper Visby, Mul./Hal. – Mulde/Halla, Skinnebr. – Skinnebrukta.

	Oslo Region									**Jämt-land**		**Estonia**								**Gotland**									
	Silurian	Lland.	Llando-very			Wenl.	Wenlock			Lland.		Ordov.	Llando-very			Wenlock			Ludlow	Silurian	Lland.	Wenl.	Wenlock						Ludlow
	Undiff.	Undiff.	Solvik	Rytteråker	Vik	Undiff.	Skinnebr.	Braksøya	Steinsfjor.	Ede	Berge		Juuru	Raik küla	Adavere	Jaani	Jaagarahu	Rootsiküla		Undiff.	L. Visby	Undiff.	U. Visby	Högklint	Tofta	Slite	Mul./ Hal.	Klinteberg	
Paleofavosites kalvensis			+																										
Paleofavosites spiroddensis			+																										
Paleofavosites abstrusus			+									+																	
Paleofavosites haapsaluensis			+									+									+								
Paleofavosites dualis			+								+	+	+	+							+								
Paleofavosites oelaensis			+										+																
Paleofavosites silicificatus			+										+																
Paleofavosites balticus			+										+								+								
Paleofavosites raikuelaensis			+											+															
Paleofavosites schmidti			+										+		+														
Paleofavosites alveolaris			+								+		+	+	+														
Paleofavosites hystrix					+					+			+																
Paleofavosites validus							+								+														
Paleofavosites major				+												+													
Paleofavosites imbellis		+														+							+			+	+		
Paleofavosites collatatus				+													+									+	+		

	Oslo Region									Jämt-land	Estonia										Gotland									
	Silurian		Llandovery			Wenl.	Wenlock				Ordov.	Llandovery			Wenlock				Ludlow	Silurian		Llandovery		Wenlock					Ludlow
	Undiff.	Undiff.	Solvik	Ryttaråker	Vik	Undiff.	Skinnebr.	Braksøya	Steinsfjor.	Ede	Berge	Ordov.	Juuru	Raik küla	Adavere	Jaani	Jaagarahu	Rootsiküla	Ludlow	Undiff.	L. Visby	Undiff.	U. Visby	Högklint	Tofta	Slite	Mul./ Hal.	Klinteberg	Ludlow
Paleofavosites asper																													
Favosites gothlandicus				+										+	+								+			+		
Favosites kjerulfi		+																											
Favosites norvegicus																													
Favosites favosus				+	+		+				+				+														
Favosites ingens				+											+														
Favosites kalevi					+										+														
Favosites stroemeri					+											+													
Kiaerites norvegicus					+																								
Angopora hisingeri					+										+								+						
Angopora parva					+										+	+							+						
Sparsisolenia kiaeri		+																											
Multisolenia tortuosaeformis		+											+																
Riphaeolites lamelliformis								+									+		+								+		
Parastriatopora sp.											+																		
Coenites juniperius						+											+												
Multithecopora norvegica				+																									
Syringopora multifaria								+																					
Multithecopora norvegica				+																									
Aulopora assueta											+				+														

	Oslo Region									Jämt-land	Estonia										Gotland									
	Silurian		Llandovery			Wenlock					Ordov.	Llandovery				Wenlock				Ludlow	Silurian		Wenl.	Wenlock						
	Undiff.	Lland.	Solvik	Rytteråker	Vik	Undiff.	Wenl.	Skinnebr.	Braksøya	Steinsfjor.	Berge	Ede	Lland.	Jusru	Raik küla	Adavere	Jaani	Jaagarahu	Rootsiküla	Ludlow	Undiff.	L. Visby	Undiff.	U. Visby	Högklint	Tofta	Slite	Mul./ Hal.	Klinteberg	Ludlow
Catenipora minuta		+																												
Catenipora spiroddensis			+																											
Catenipora quadrataeformis			+	+																										
Catenipora malmoeyensis				+																										
Catenipora norvegica				+																										
Catenipora ringerikensis				+						+																				
Catenipora distans						+					+					+														
Catenipora maxima				+											+	+	+				+									
Catenipora oriens				+													+													
Catenipora quadrata				+												+	+							+						
Catenipora exilis					+										+															
Catenipora vespertina						+											+				+									
Catenipora heintzi									+																					
Halysites norvegicus						+																								
Acidolites sp.			+																											
Propora conferta											+			+								+								
Heliolites interstinctus									+																					+

Table 2. Distribution of all tabulate coral species in the Lower Silurian successions of Estonia and Gotland. Question mark is added in case of uncertainty about the formation where species is found. Stratigraphical units are abbreviated as follows: undiff. – undifferentiated, Silur. – Silurian, Lland. – Llandovery, Wenl. – Wenlock, L. Visby – Lower Visby, U. Visby – Upper Visby, Mul./Hal. – Mulde/Halla.

	Estonia							**Gotland**										
		Llandovery			Wenlock					Lland.		Wenlock						
	Ordovician	Juuru	Raikküla	Adavere	Jaani	Jaagarahu	Rootsiküla	Ludlow	Undiff. Silur.	L. Visby	Wenl. Undiff.	U. Visby	Hög-klint	Tofta	Slite	Mul./ Hal.	Klinteberg	Ludlow
Paleofavosites abstrusus	+																	
Paleofavosites haapsaluensis	+									+								
Paleofavosites dualis	+	+	+							+								
Paleofavosites oelaensis		+																
Paleofavosites silicificatus		+																
Paleofavosites balticus		+								+								
Paleofavosites raikuelaensis			+															
Paleofavosites schmidti		+		+														
Paleofavosites alveolaris		+	+	+														
Paleofavosites hystrix		+																
Paleofavosites porosus		+																
Paleofavosites hirtus		+																
Paleofavosites ignotus		+																
Paleofavosites mysticus		+																
Paleofavosites felix		+																
Paleofavosites aaloei		+																

	Estonia							Gotland										
	Ordovician	Llandovery			Wenlock			Ludlow	Undiff. Silur.	Llandovery		Wenl. Undiff.	Wenlock					Ludlow
		Juuru	Raikküla	Adavere	Jaani	Jaagarahu	Rootsiküla			L. Visby	Lland.		U. Visby	Högklint	Tofta	Slite	Mul./ Hal.	Klinteberg	
Paleofavosites rudis		+																	
Paleofavosites paulus		+																	
Paleofavosites vexatus		+																	
Paleofavosites optatus		+																	
Paleofavosites limbergensis		+	+	+															
Paleofavosites aliquantulus			+	+									+	+					
Paleofavosites mirus		+	+																
Paleofavosites similis		+																	
Paleofavosites kiltsiensis		+																	
Paleofavosites inferior		+																	
Paleofavosites multiporus		+	+																
Paleofavosites fortis		+																	
Paleofavosites jaaniensis				+															
Paleofavosites luxuriosus				+															
Paleofavosites septosus				+															
Paleofavosites luhai				+															
Paleofavosites validus				+															
Paleofavosites alveolitoides				+															
Paleofavosites obliquus				+							+								
Paleofavosites forbesiformis					+								+	+					

	Estonia							Gotland											
	Ordovician	Llandovery			Wenlock			Ludlow	Undiff. Silur.	Llandovery		Wenl. Undiff.	Wenlock						Ludlow
		Juuru	Raikküla	Adavere	Jaani	Jaagarahu	Rootsiküla			L. Visby	Undiff.		U. Visby	Hõg-klint	Tofta	Slite	Mul./ Hal.	Klinteberg	
Paleofavosites saaremicus					+														
Paleofavosites tenuis					+														
Paleofavosites suurikuensis					+									+					
Paleofavosites major					+														
Paleofavosites bonus					+														
Paleofavosites secundus					+														
Paleofavosites imbellis					+								+			+	+		
Paleofavosites frivolus						+									+	+	+	+	
Paleofavosites asper						+										+	+		
Paleofavosites collatatus						+										+	+		
Paleofavosites parilis						+										+			
Paleofavosites tersus						+	+									+		+	
Paleofavosites pauculus						+												+	
Favosites antiquus		+																	
Favosites gothlandicus			+	+									+	+			+		
Favosites privatus			+																
Favosites praemaximus			+																
Favosites favosus				+															
Favosites ingens				+															
Favosites kalevi				+															

	Estonia						Gotland											
	Ordovician	Llandovery			Wenlock		Ludlow	Undiff. Silur.	Llandovery	Wenl. Undiff.	Wenlock							Ludlow
		Juuru	Raikküla	Adaverе	Jaani	Jaagarahu	Rootsiküla					U. Visby	Hõg-klint	Tofta	Slite	Mul./ Hal.	Klinteberg	
Favosites hisingeri				+								+	+				+	+
Favosites fallax				+	+							+	+					
Favosites adaverensis				+				+										
Favosites abnormis				+														
Favosites jaaniensis					+							+	+		+			
Favosites subforbesi					+							+	+					
Favosites desolatus					+							+	+					
Favosites exilis					+?								+					
Favosites lichenarioides					+								+					
Favosites serratus					+													
Favosites multicarinatus					**+?**				+						**+?**			
Favosites oculiporoides					**+?**													
Favosites mirandus						+								+				
Favosites subfavosus							+											
Favosites opinabilis																		
Favosites caelestis																		
Favosites similis																		
Favosites forbesi																+		+
Favosites pseudoforbesi																	+	+
Angopora hisingeri				+								+	+				+	

	Estonia						Gotland											
	Ordovician	Llandovery			Wenlock		Ludlow	Undiff. Silur.	Llland.	Wenl. Undiff.	Wenlock							Ludlow
		Juuru	Raikküla	Adavere	Jaani	Jaagarahu	Rootsiküla			L. Visby		U. Visby	Högklint	Tofta	Slite	Mul./ Hal.	Klinteberg	
Angopora parva				+	+							+	+		+			
Angopora tenuicula					+													+
Multisolenia tortuosaeformis		+																
Multisolenia tortuosa		+																
Multisolenia temperans			+															
Multisolenia excelsa					+	+									+			
Syringolites kunthianus					+								+					+
Riphaeolites lamelliformis						+	+										+	
Thecia saaremica						+												
Thecia podolica					+			+										
Thecia tenuicula					+													
Thecia confluens						+									+			
Parastriatopora calyculata										+								
Parastriatopora celebrata			+															
Parastriatopora mirifica			+															
Parastriatopora priva						+												
Parastriatopora commutabilis							+											
Thamnopora ? undvaensis					+								+					
Cladopora ? perrara						+												
Planalveolites fougti												+						

	Estonia						Gotland											
	Ordovician	Llandovery			Wenlock			Ludlow	Undiff. Silur.	Llandovery		Wenl. Undiff.	Wenlock					
		Juuru	Raikküla	Adaverе	Jaani	Jaagarahu	Rootsiküla			L. Visby	Llandovery		U. Visby	Högklint	Tofta	Slite	Mul./ Hal.	Klinteberg	Ludlow
Subalveolites eichwaldi				+															
Subalveolites panderi				+	+								+						
Subalveolites sokolovi					+								+	+					
Subalveolites callosus						+		+				+							
Subalveolitella majuscula				+					+										
Subalveolitella minuscula				+															
Placocoenites pellicula				+															
Coenites juniperius						+													
Syringopora novella					+	+							+	+					
Pachypora lamellicornis													+	+					
Striatopora coenitoides						+													
Striatopora calyculata														+					
Striatopora flexuosa														+					
Nodulipora accuminata												+							
Sinopora operta			+																
Sinopora callosa				+															
Adaverina adaverensis				+															
Adaverina acclinis				+															
Romingeria nana				+															
Aulopora assueta				+															

	Estonia							Gotland										
	Ordovician	Llandovery			Wenlock			Ludlow	Undiff. Silur.	Llandovery		Wenl. Undiff.	Wenlock					Ludlow
		Juuru	Raikküla	Adavere	Jaani	Jaagarahu	Rootsiküla			L. Visby	U. Visby		U. Visby	Högklint	Tofta	Slite	Mul./ Hal.	Klinteberg	
Aulopora celsa				+															
Aulopora enodis					+														
Mastopora incrustata					+?														
Mastopora foederata						+													
Fletcheria tubifera																+			
Favosipora clausa																+			
Catenipora martinssoni		+								+									
Catenipora arctica		+																	
Catenipora gotlandica		+								+									
Catenipora septosa		+																	
Catenipora approximata		+																	
Catenipora copulata			+																
Catenipora elegans				+															
Catenipora distans				+															
Catenipora maxima				+					+										
Catenipora oriens					+														
Catenipora quadrata				+	+						+			+					
Catenipora exilis				+															
Catenipora vespertina					+					+									
Catenipora spirodensiformis									+										

	Estonia							Gotland											
	Ordovician	Llandovery			Wenlock			Ludlow	Undiff. Silur.	Lland.	Wenl. Undiff.	Wenlock							Ludlow
		Juuru	Raikküla	Adavere	Jaani	Jaagarahu	Rootsiküla			L. Visby		U. Visby	Hõg-klint	Tofta	Slite	Mul./ Hal.	Klinteberg		
Catenipora escharoides										+		+							
Catenipora jarviki												+							
Halysites catenularius		+								+									
Halysites regularis				+															
Halysites senior					+							+	+		+	+			+
Halysites junior						+									+				
Halysites klintebergensis																	+		
Halysites laticatenatus															+	+			+
Cystihalysites blakewayensis															+				
Cystihalysites cavernosus															+				
Cystihalysites magnitubus															+	+			+
Pseudocosmiolithus varians									+										
Pycnolithus bifidus									+										
Acidolites lateseptatus		+								+									
Acidolites asteriscus										+									
Cosmiolithus halysitoides												+							
Cosmiolithus ornatus												+							
Diploepora grayi															+				
Propora conferta	+									+									
Propora bacillifera	+	+							+										

	Estonia							Gotland									
	Ordovician	Llandovery			Wenlock			Ludlow	Undiff. Silur.	Llandovery		Wenl. Undiff.	Wenlock				
		Juuru	Raikküla	Adavere	Jaani	Jaagarahu	Rootsiküla			L. Visby	Lland.		U. Visby	Högklint	Tofta	Slite	Mul./ Hal.	Klinteberg	Ludlow
Propora ? ambigua										+									
Propora exigua				+						+									
Propora tubulata					+								+	+			+		
Propora raricellata					+														
Propora speciosa																+			
Propora euryacantha																+			
Mcleodea minima									+										
Mcleodea sp.		+																	
Plasmopora scala										+									
Plasmopora stella		+		+	+					+									
Plasmopora petaliformis					+								+			+			
Plasmopora foroensis																+			
Plasmopora calyculata																+	+		
Plasmopora scita																+			
Plasmopora rudis																+			+
Stelliporella fasciatus										+									
Stelliporella liljevalli										+									
Stelliporella repletus													+						
Stelliporella cf. parvistella																	+		
Stelliporella parvistellus																+			+

	Estonia								Gotland									
	Ordovician		Llandovery				Wenlock		Ludlow	Undiff. Silur.	L. Visby	Lland.	Wenl. Undiff.	Wenlock				
			Juuru	Raikküla	Adavere	Jaani	Jaagarahu	Rootsiküla						U. Visby	Högklint	Tofta	Slite	Mul./ Hal.	Klinteberg	Ludlow
Heliolites interstinctus														+	+		+		+	+
Heliolites barrandei																	+		+	+
Saaremolites inversus							+													
Barrandeolites lichenaroides							+							+	+		+			

Table 3. Distribution of all tabulate coral species in the Lower Silurian successions of Podljassk-Brest, Dniestr River Basin, Estonia and Gotland. Question mark is added in case of uncertainty about the formation where species is found. Stratigraphical units are abbreviated as follows: undiff. – undifferentiated, Ordov. – Ordovician, Lland. – Llandovery, Wenl. – Wenlock, L. Visby – Lower Visby, U. Visby – Upper Visby, Mul./Hal. – Mulde/Halla, Mar'yanov. – Mar'yanovka, Cherchen. – Cherchenka.

	Podljassk-Brest		**Dniestr River Basin**									**Estonia**								**Gotland**										
	Lland.	Wenl.	Lland.	**Wenlock**							Ludlow	Ordov.	Llando-very			Wenlock			Ludlow	Silurian	Lland.	Wenl.	Wenlock							Ludlow
		Strigovo	Teremtsov	Restev	Demshin	Mar'yanov	Cherchen.	Mukshin	Ust'ev				Juuru	Raikküla	Adavere	Jaani	Jaagarahu	Rootsiküla		Undiff.	L. Visby	Undiff.	U. Visby	Högklint	Tofta	Slite	Mul./Hal.	Klinteberg	
Paleofavosites tersus										+																				
Favosites ? multiporus								+																						
Multisolenia tortuosa							+						+																	
Thecia saaremica								+		+							+													
Thecia minor		+			+																									
Thecia podolica						+										+				+										
Thecia confluens								+									+													
Subalveolites panderi						+									+	+							+							
Subalveolitella rependina								+	+	+																				
Tuvaelites hemisphaericus						+	+			+																				
Syringopora fascicularis						+	+			+																				
Syringopora affabilis							+																							
Striatopora flexuosa								+	+	+														+						
Desmidopora alveolaris								+																						

	Podljassk-Brest		Dniestr River Basin												Estonia									Gotland									
	Lland.		Wenl.	Strigovo	Lland.	Teremtsov	Wenlock							Ludlow	Ordov.	Llando-very			Wenlock				Ludlow	Undiff.	Silurian	L. Visby	Lland.	Undiff.	Wenl.	U. Visby	Wenlock					Ludlow
							Restev	Demshin	Maryanov	Chercheh.	Mukshin	Ustev				Juuru	Raikkula	Adavere	Jaani	Jaagarahu	Rootsikula									Högklint	Tofta	Slite	Mul./Hal.	Klinteberg	
Taxopora xenia				+							+	+																					
Favosipora clausa														+																			
Halysites catenularius				+		+			+	+						+									+							
Cystihalysites mirabilis										+			+																			
Pseudocosmiolithus varians		+?																						+								
Cosmiolithus ornatus				+																						+							
Propora exigua									+									+														
Propora tubulata									+										+										+				
Propora parvituba									+																								
Plasmopora calyculata									+																					+		+	
Plasmopora scita									+																					+			
Stelliporella podolica									+																								
Stelliporella caespitosa									+																								
Derivatolites parvistellus									+																								
Heliolites irregularus									+																								
Heliolites barrandei				+																										+			+
Laminoplasma pseudocalyculatum									+																								
Podollites diseptatus										+																							
Gritsnkolites vladimiri											+																						

The definitions of *P. conferta*, *P. dualis*, *C. distans* and *H. catenularius* have been confusing (PAPER I, II, III). *P. conferta* is in process of revision. *C. distans* is tentatively synonymised with *C. simplex* from North America because of the great similarity, although they occur in distant localities. Widespread species often "produce" synonyms in distant areas, particularly when they are identifiable on the basis of only a few characters (typological concept). During the past decades many regional species have been established that appear to be synonymous with each other or with particular widespread species.

The poor definition of species is artificially increasing the number of recorded taxa and influencing the measures of species and generic diversity, particularly at the high diversity periods. The large number of paleofavositids in the Llandovery could be the result of artificial "splitting" of species. Thirty-two new paleofavositid species in Estonia were described by Sokolov (1951a, b) from the early Silurian and 17 were added by Klaamann (1961, 1962b, 1964). More than half of these occurred in the Llandovery. During the revision (PAPER I, III) several species and some genera were synonymised. Only revised taxa are presented (Table 1–3) and tentative and synonymised taxa are not shown in this list.

In addition to already synonymised genera, there are other genera of questionable validity. *Mastopora* is at least partly synonymous with *Aulopora* (Mistiaen 1988). *Barrandeolites*, which is tentatively included to Tabulata (Hill 1981), might actually be a bryozoan.

TABULATE CORALS AND (ENVIRONMENT) PALAEOECOLOGY

Tabulate morphology and environment

Tabulate corals were benthic organisms associated with particular environments. The environmental factors influencing distribution of the Palaeozoic corals are substrate and turbidity, water energy, depth, light, temperature, salinity and oxygenation (Scrutton 1998). The morphology of tabulate corals was environmentally controlled. The intraspecific variability of tabulates also depended on environmental factors.

There are few studies dealing with the relations of the species morphology and its environment in the Silurian of Baltoscandia. Stel (1978b) analysed the intraspecific variability of several species in an environmental context. He concentrated mainly on the variability of corallite size and concluded that this characteristic depended on the environment, but to different extents. Young and Scrutton (1991), comparing *Stelliporella parvistella* and *Propora tubulata*, found that the former had much larger genetic plasticity than the latter. This was expressed in an environmentally controlled variation in shape, which was more prevalent than in the other species.

Similar evidence is discussed in regard to *Paleofavosites asper* from Gotland (PAPER II). The diameter of corallites in the holotype is relatively small (not exceeding 1.5 mm and being 1.1 in average) and septal spines are present in this species. The comparison of specimens from different localities from the same stratigraphical interval shows that several similar species of the genus may represent one species. The holotype of *Paleofavosites asper* has been described by Oekentorp (1976) and Powell and Scrutton (1978). The latter study describes the holotype of *P. asper* together with the additional topotype material (Ludlow Series, Aymestry limestone, Leinthall Earls) and with additional material from other localities from the Wenlock of Great Britain. Powell and Scrutton concluded that this species has a large variation in development of septal spines, in thickness of the wall and also a considerable variation in pore diameter, but the average size of the corallites is constantly small and the shape of coralla varies from lamellar to broadly domed. However, this study does not address the environmental aspects and facies control.

The investigations demonstrate that the upward-growing coralla have smaller corallites and the spherical coralla have larger corallites (PAPER II). Corallites are less tightly packed in spherical coralla and have more space to grow compared to those in the columnar ones. Therefore, corallite size may vary remarkably in coralla from different facies (PAPER II). Specimens similar to *P. asper* by Powell and Scrutton (1978), except for the corallite size and corallum shape have been collected from different localities at Slite Beds on Gotland. These localities expose different subunits of the Slite Formation, where facies vary from high-energy environment to steady environment. Tabular coralla are found in coarse-grained crinoidal, high-energy sediments

and bulbous, nodular and domical ones are common in mudstones, low-energy environments (PAPER II). According to Young and Scrutton (1991) the growth form and corallum shape are determined genetically in corals. Columnar and branching forms with the corallites growing upwards are more common in steady environments with moderate influx of sediment (PAPER II). The same is probably valid for branching *Parastriatopora commutabilis*, which is abundant in lagoonal facies of the Rootsiküla Stage (PAPER V, Klaamann 1986).

Remarkable intraspecific variability of *P. asper*, expressed in many different corallum shapes, may reflect a large genetic plasticity of the species. This species is characterised by remarkably wide intraspecific variability. *Halysites catenularius* from Lower Visby Beds of Ireviken biostrome shows less variation in corallite size than *Paleofavosites asper* (PAPER II). The corallite size of *H. catenularius* is less variable than previously thought and this is addressed also in PAPER I.

The relationship between certain types of tabulate corals and environment is also reflected in the structural design of coralla. Both biostromes, Ireviken 1 (PAPER II) and in Blåhäll 1 (PAPER IV), contain heliolitids and halysitids as frame-builders. The coralla are embedded in a mudstone which suggests extensive mud deposition also during their lifetime. These species are characterised by high mud-tolerance; for example, the halysitids have empty spaces — lacunae — between the chains of corallites and mud was removed from the surface of chains into the lacunae (Stel 1978b).

Ordovician — Silurian boundary events, their possible impacts to faunal development

The Late Ordovician glaciation started at about the beginning of the Hirnantian Stage and ended in the later part of the Hirnantian. Two phases of extinctions have been noted in the Late Ordvician event (Sheehan 2001). The first phase of extinction occurred at the start of the Hirnantian (uppermost Ashgill) and the second phase in the mid to late Hirnantian (Brenchley 2004). The first is related to the time of glaciation when epicontinental oceans drained, resulting in a harsh climate in the mid latitudes and changed the nutrient regime supplied by deep ocean currents. The second extinction phase was caused by an abrupt transgression resulting from a stagnation of the ocean circulation, which affected the fauna adopted to the new ecological setting (Sheehan 2001). The following transgression that started in the latest Ordovician *Glyptograptus persculptus* Chron (Baarli et al. 2003) continued into the Lower Silurian. The sea level fall in Scandinavia was 70 m by the latest Ordovician (Johnson et al. 1998).

The event at the end of the Ordovician resulted in only third- and fourth level changes in reef pelagic and benthic settings (Droser et al. 2000) and the extinction was not a major event for reef systems (Copper 1994). The Silurian reefs generally contain the same families of corals known already from the Late Ordovician (Droser et al. 2000).

The changes in composition of tabulate faunas of the East Baltic at the Ordovician and Silurian boundary were mainly expressed at the generic level (PAPER V, Fig. 13.). The Ordovician tabulate taxa did not disappear simultaneously. Some taxa disappeared much earlier than the beginning of the Silurian. In total, 16 Upper Ordovician genera disappeared towards the end of the period and 5 genera continued into the Silurian (Fig. 13) in the Estonian sequence. The Upper Ordovician lichenarids, tetradiids, sarcinulids and heliolitids disappeared, but several species of paleofavositids continued into the Silurian and became more diverse than the extinct cateniporids (PAPER V; Klaamann 1964, 1966). A few heliolitid genera also continued from the Ordovician into the Silurian (PAPER V).

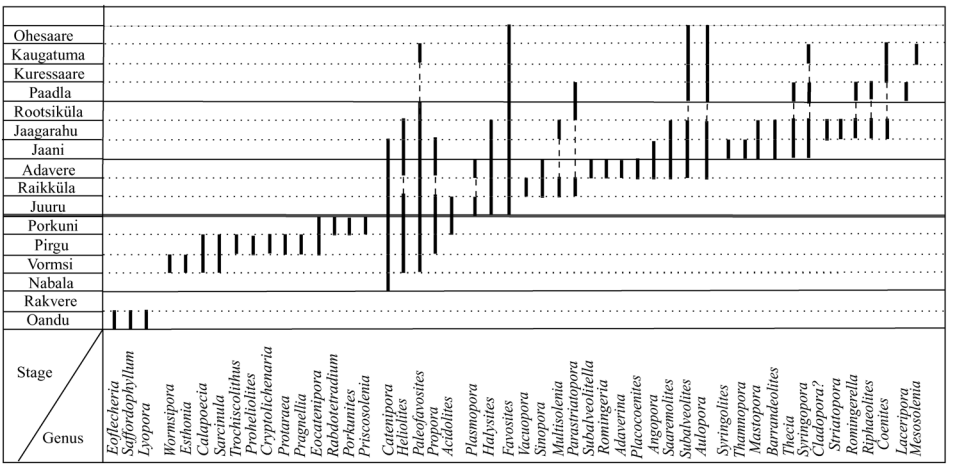

Figure 13. Distribution of tabulate coral genera through the Ordovician and Silurian sequence of Estonia.

The widespread transgressions and ameliorating climates at the beginning of the Silurian induced a rapid emergence of the cosmopolitan species and genera among corals (Copper 1994). In East Baltic, small bioherms are known in Estonia in the Hilliste Member of the Juuru Stage, Rhuddanian. In the early Llandovery the tabulate faunas in Estonia are characterised by low generic diversity, although the species diversity of *Paleofavosites* increased (PAPER V). The early-middle Llandovery macrocycle began with the glacio-eustatic sea level rise and ended with the denudation in marginal areas of the basin (Nestor and Einasto 1997).

According Johnson (1996) and Johnson et al. (1998), the first Silurian sea-level rise took place at approximately the beginning of the Aeronian (Fig. 14). The renewal of faunas in the upper part of the Raikküla Stage occurred at this time in Estonia (Fig.13, PAPER V); the genera *Parastriatopora, Multisolenia*, *Syringopora, Vacuopora* and *Sinopora* appeared. *Favosites* is more abundant than

Paleofavosites in the Raikküla Stage than in the Juuru Stage (PAPER V). The Adavere Stage (Rumba Member) displays the highest diversity of tabulates and the highest ratio of cosmopolitan taxa for the whole Llandovery. This is the beginning of stabilisation stage in the basin development (Nestor and Einasto 1997). The upper part of the Adavere Stage in Estonia comprises marl- and mudstones of deeper facies and contains very few corals. Corals are more abundant in the in the Vik Formation in Oslo Region, which is the same age (Fig. 4).

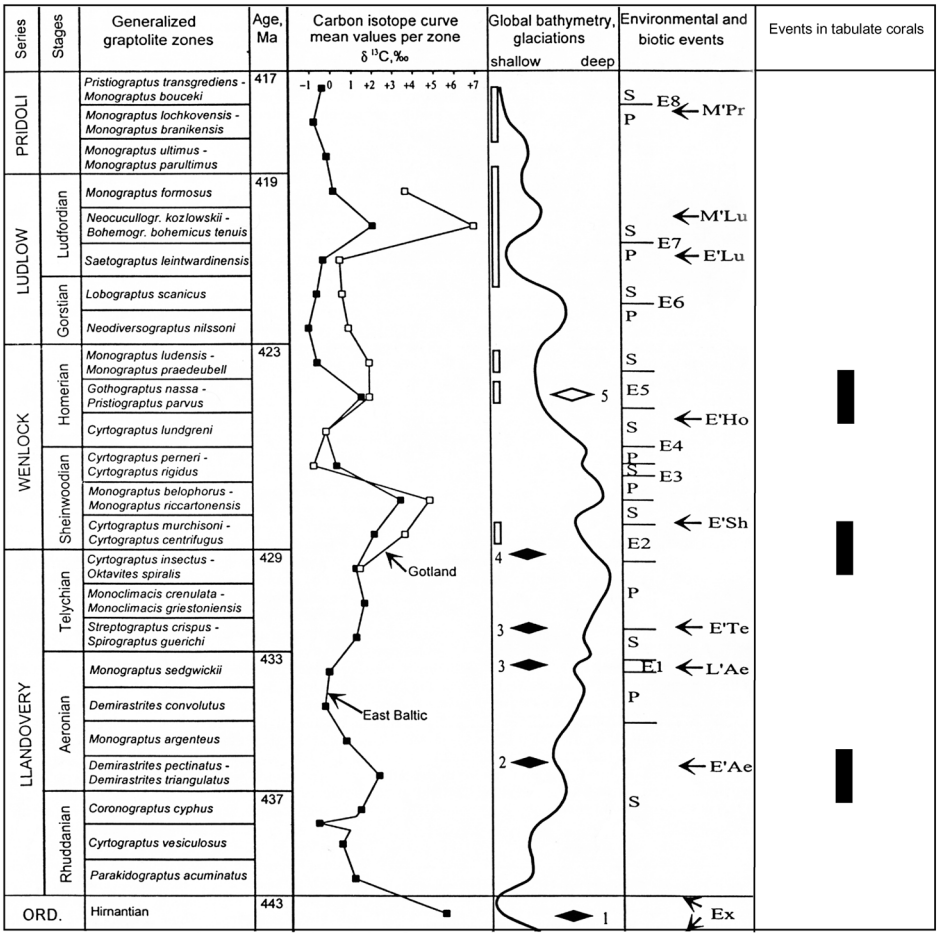

Figure 14. Correlation of East Baltic and Gotland carbon isotope curves and environmental biotic events. Black rhombs are glaciations and white bars mark enchanced oxygenation of bottom waters. Oceanic primo (P) and secundo (S) episodes. Events: E1, Sandvika; E2 Ireviken; E3, Boge; E4, Valleviken; E5, Mulde; E6 Linde; E7, Lau; E8 middle Pridoli. The figure is from Kaljo et al. (1998) with the completion of the events in tabulate coral assemblages marked with black bars.

The major Silurian sea-level rise in uppermost Llandovery is reffered to as the fourth sea-level event by Johnson et al. (1998). The sea-level lowered again at the beginning of Wenlock The Ireviken event in Gotland, which spanned the Llandovery-Wenlock boundary, caused the major extinction of conodonts and trilobites (Jeppsson, 1998). In East Baltic basin, the tabulate fauna changed considerably, new genera appeared (*Thecia*, *Syringolites*, *Mastopora*) and only one of the widely distributed Llandoverian species of *Paleofavosites* continued from the Adavere Stage into the Jaani Stage (PAPER V, Klaamann 1970).

The species and genera of tabulate corals were highly diverse and abundant in the Wenlock. Reefs became widespread and abundant in mid-continental North America and in the Urals during the Wenlock (Copper and Brunton 1991). The correlation between the carbon isotopic changes and environmental cyclicity in the Silurian of East Baltic was investigated by Kaljo et al. (1998, Fig. 14). The sea-level declines, associated with glaciations, were periods of more vigorous circulation and enhanced oxygenation of ocean-bottom waters. The relationship between the positive carbon isotopic peaks and intensive reef growth in Gotland has been confirmed by Sambtleben et al. (1996). The conditions for corals were more favourable in Gotland than in Estonia. Spectacular reefs rich in tabulate corals occur in the Högklint Formation on the northern coast of Gotland (Laufeld and Martinsson 1981). The high-energy shoal facies, which are the most favourable for corals, were absent on Saaremaa at that time (Fig. 15). Smaller biostromes of open shelf facies, rich in heliolitids and halysitids, were spread instead in the Jaani Beds, Ninase Mbr, (Mõtus 2003).

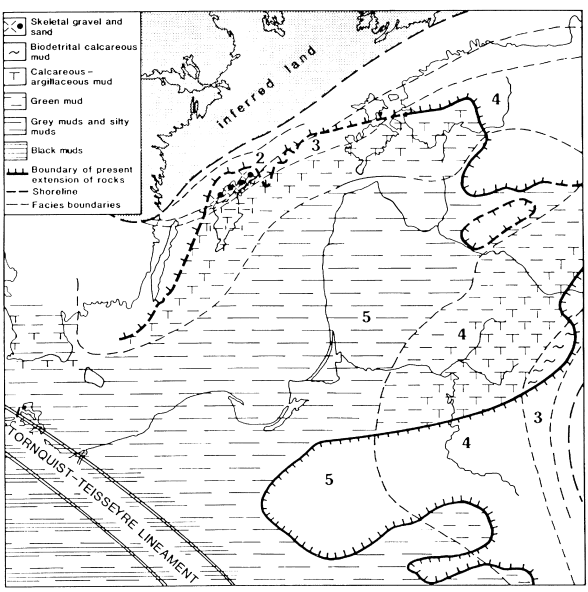

Figure 15. Distribution of early Wenlock (Sheinwoodian) sediments and facies belts from Bassett at al. (1989). Facies belts are follwing: 1, lagoon, 2, shoal, 3, open shelf, 4, transition, 5, depression.

The Jaagarahu Stage in Estonia is characterised by the largest generic diversity of tabulates in the Wenlock (Fig. 13). The most widespread tabulates were favositids, theciids and coenitids. *Palaeofavosites* dominated many bioherms on Gotland and was also abundant on Saaremaa (PAPER II).

The global sea level fall culminating near the top of the *Cyrtograptus lundgreni* Zone and the following rapid transgression in *Gothograptus nassa-Pristiograptus parvus* Zone is marked by transgressive oolites in lowermost Halla Formation on Gotland (Calner 1999, Calner and Säll 1999). A global extinction and disappearance of graptolites, conodonts, chitinozoans and shelly fossils, named the Mulde event by Jeppsson (1998; see also Fig. 14), also affected the reefs on Gotland. The low-diversity biostrome from the Halla Beds of Blåhäll 1 is the first re-appearance of reefs on Gotland after the Mulde event (PAPER IV). A common feature of the Halla and Mulde Formations as well as for the middle of the Klinteberg Formation is their small size (Klaamann and Einasto 1982). A lowering of the sea at the end of the Wenlock is suggested from the appearance of the lagoonal facies in the Rootsiküla Stage on Saaremaa, which contains abundant branching parastriatoporids (Klaamann 1986).

The diversity of tabulate corals in Estonia was low during the Ludlow Epoch (Fig. 13), when the sea was narrowing in Baltoscandia. The high-energy shoal facies with more favourable conditions for corals existed in Gotland, in the Dniestr River Basin and in the Podljassk-Brest area. Heliolitids and halysitids are not found in the Ludlow successions in Estonia, although the former reached the end of Devonian elsewhere and halysitids have been found in the Ludfordian in Gotland and also in the Pridoli of Southern Gaspe Peninsula in Canada (PAPER VI). Disappearance of *Thecia* and *Subalveolitella* is recorded in Estonia at the end of the Wenlock, but they occur in Ludlow of the Dniestr River Basin (Table 3). Large reefs were characteristic of this time in Gotland and Podolia.

The halysitids from the Eke Formation in Gotland are the youngest in Baltoscandia (PAPER VI). The Lau event is one of the largest extinction events among conodonts, graptolites, chitinozoans, some fishes, and brachiopods (Jeppsson 1998). It is noteworthy that the halysitids survived the early parts of the Lau extinction event in Gotland.

BIOSTRATIGRAPHICAL IMPORTANCE OF TABULATE CORALS

Tabulate biostratigraphy has been studied in North America (Young and Noble 1990), South Verkhojanie in Siberia (Khaiznikova 1989), China (Scruton 1989a) and Dniestr River Basin (Bondarenko 1982, Sokolov and Tesakov 1984).

Three Silurian tabulate biofacies and four zones have been established in the Baie des Chaleurs region by Young and Noble (1990). In their opinion, although these zones cannot be applied outside eastern North America because the distribution of species is geographically restricted, they still found it possible to correlate the zones with zones in other regions. Bondarenko (1982) founded seven complex zones and two phylozones for the Pridoli in the Dniestr River Basin (Bondarenko 1982). These phylozones, which were established on the basis of asto-phylogeny of heliolitids, correlated with the tabulate zones of Kazakstania and Middle-Asia. Sokolov and Tesakov (1984) established 25 interzones of Silurian tabulates in the Dniestr River Basin in Podolia.

Klaamann (1982, 1983) proposed several tabulate zones based on assemblages from Gotland and Estonia. The most precise correlation is based on the tabulates from shoal facies (e.g. *Halysites junior* assemblage), whereas assemblages such as *Halysites crassus* and *Halysites laticatenatus – Favosites gothlandicus* in the open shelf environment are long-ranging.

The tabulate coral taxonomy in Baltoscandia is in need of revision. The revised taxa (established on their intraspecific variability) are mostly long-ranging and widespread and therefore less informative in stratigraphy. At the same time the firm taxonomic basis is important because of the higher reliability. According to Klaamann (1986) it is also important that the biostratigraphical conclusions based on tabulates should consider the facies control. The predominant relationship of tabulates to the shallow carbonate facies limits their use in biostratigraphy, but they could still be important when there is insufficient data on biostratigraphically more important fauna, such as conodonts or brachipods.

A case study of the stratigraphical potential of tabulate corals was carried out in Jämtland (PAPER III). Reliable data on conodonts with respect to the age of the Ede and Berge Formations in Jämtland have been published by Dahlqvist and Calner (2004) which is supported by additional evidence on tabulate corals.

The faunas in Jämtland are closely related to those of Estonia and Norway. All Jämtland tabulate species are represented in Estonia (Table 4) showing the close affinities between two areas. The species list contains mostly widespread species, such as *Paleofavosites dualis, P. alveolaris*, *Favosites favosus*, *Propora conferta* and *Catenipora distans* and some regional species, such as *P. hystrix* and *Aulopora assueta.* These species, except for the lower Silurian *F. favosus, C. distans, P. hystrix* and *A. assueta* range from the Upper Ordovician into the lower Silurian (Llandovery). The lower Silurian tabulates in Estonia occur in different facies. *P. hystrix* is characteristic of reef facies, *P. alveolaris* of

interreef facies and *P. dualis* of different facies (reef- and interreef) according to Klaamann (1972). *F. favosus* occurs in shoal facies and parastriatoporids are common in lagoonal facies.

Table 4. Distribution of tabulate corals in Jämtland (localities Ede, Norderön, Verkön) and their ranges in the Estonian sequence. Number of specimens is given in brackets, "+" means presence and "–" is absence of species. Abbreviations: F_Ib, Vormsi Stage; F_Ic, Pirgu Stage; F_{II}, Porkuni Stage; $G_{1–2}$, Juuru Stage; G_3, Raikküla Stage; H, Adavere Stage.

	Jämtland			Estonia					
	Llandovery			Ashgill			Llandovery		
	Ede Fm	Berge Fm		F_Ib	F_Ic	F_{II}	G_{1-2}	G_3	H
	Ede	Norderön	Verkön						
Paleofavosites hystrix	+ (7)	–	–	–	–	–	+	+	–
Paleofavosites alveolaris	–	+ (1)	–	+	+	–	+	+	–
Parastriatopora sp. A	–	+ (2)	–	–	–	–	–	–	–
Catenipora sp. A	–	+ (1)	–	–	–	–	–	–	–
Favosites favosus	–	+ (1)	+ (5)	–	–	–	–	–	+
Paleofavosites dualis ?	–	–	+ (1)	–	–	+	+	+	–
Propora conferta	–	–	+ (1)	–	–	+	–	–	–
Catenipora distans	–	+ (1)	+ (2)	–	–	–	–	–	+
Aulopora assueta	–	–	+ (1)	–	–	–	–	–	+

Several species from the Berge Formation are known from the Raikküla and Adavere stages (Aeronian), but some are found in the Upper Ordovician and Rhuddanian in Estonia (Table 4). The formation of the Berge Formation took place in the middle Aeronian (Dahlqvist & Calner 2004). Some tabulate species occur at a higher stratigraphic level in Jämtland than in Estonia because a large part of the Aeronian successions is absent in west and central Estonia. The bioherm from the Ede Limestone contsists of *P. hystrix*, which occurs in the Juuru to Raikküla Stage in Estonia. Conodont data in Dahlvqvist & Calner (2004) suggests that the upper calcareous parts above the bioherm of the Ede Formation belong to the Rhuddanian–middle Aeronian interval. Based on the affinities of species composition of tabulates in Estonia and Jämtland, an Aeronian age is suggested for the Berge Limestone (PAPER III).

Tabulates might also help to solve some problems in inter-regional stratigraphy, such as the correlations of the East Baltic and Dniestr River Basin.

CONCLUSIONS

(1) The biometric variability studies of tabulate corals from Baltoscandia prove that a number of characters (such as corallum shape and size) are environmentally controlled. The revised diagnoses of the species are based on a careful selection of taxonomically important characters and on exclusion of the non-diagnostic, ecophenotypic characters. The variation measurements of the metric diagnostic characters (e.g. corallite size) are statistically estimated, which is valuable for comparison of the taxa.

(2) The relationship between the intraspecific variability and environment in tabulates and the ecophenotypic character of coralla is exemplified by *Paleofavosites asper*. Tabular coralla of *P. asper* are found in coarse-grained crinoidal, high-energy environments, whereas bulbous, nodular and domical varieties are common in mudstones in low-energy environments. Upward growing coralla (columnar forms) have smaller corallites, whereas spherical coralla have larger corallites because they have more space to grow. *Halysites catenularius* from the Ireviken biostrome of the Lower Visby Beds shows less variation in corallite size than *P. asper*.

(3) The cosmopolitan nature of the species of the Silurian tabulate corals supports the appearance of many synonyms between different regions. Several Baltoscandian tabulate species represent synonyms of widely common cosmopolitan taxa. Some widespread Baltoscandian species have many synonyms in other regions. The high species diversity in some genera is caused by the tendency of "splitting", characteristic of *Paleofavosites* and *Catenipora* in Llandovery. Several genera in Wenlock appear to be synonymous (*Mesofavosites, Solenihalysites* and probably *Mastopora*).

(4) The appearance of new taxa, changes in diversity and the appearance of biostromes can be related to global Silurian events at the lower boundary of the Aeronian, at the beginning of Wenlock and in the middle Homerian. The low-diversity biostrome was the first reef to recover after the Mulde event on Gotland. The disappearance of some tabulate taxa (halysitids and heliolitids) in Estonia in the Wenlock is due to facies changes in that part of the basin. The occurrence of the youngest halysitid from Baltoscandia *Cystihalysites* sp. in Ludlow (Eke Formation) of Gotland confirms that this existed longer in Baltoscandia than previously thought.

(5) The strong facies control over the distribution of corals makes the biostratigraphical use of tabulates relatively regional, but they are useful in cases where there is insufficient data on biostratigraphically more important groups. Based on affinities of the tabulate faunas from Estonia and Jämtland, the Aeronian age is suggested for the Berge Limestone in Jämtland.

ACKNOWLEDGEMENTS

I express my gratitude to my late teachers Valdar Jaanusson and Einar Klaamann. I received good advice from Dr. Graham Young (The Manitoba Museum, Winnipeg) during my Ph.D. course and he has made great efforts in reviewing manuscripts and improving the language. I am also very grateful to Prof. Tõnu Meidla (Institute of Geology at Tartu University) for supervising my work and for his advice. I wish to thank Prof. Dimitri Kaljo (Institute of Geology at the University of Technology) for valuable comments on my work and for advice in all different aspects concerning this work. I am grateful to Dr. Olof Sandström and Dr. Mikael Calner from Lund University for co-operation in the paper. The reviewers, Prof. Klemens Oekentorp (University of Münster), Dr. Björn Neuman, Dr. Stephen Kershaw (Brunel University) and Dr. Robert J. Elias (University of Manitoba) are kindly ackowledged. I thank Dr. Lennart Jeppsson and Mr. Peter Dahlqvist (Lund University, Sweden), Dr. Volodymyr Gritsenko (Kiev National Taras Shevchenko University), Dr. Gregory Webb (Queensland University of Technology) for the personal communications. I am thankful to Prof. Michael Bassett (National Museum of Wales, Cardiff) for his help concerning the material and localities in Jämtland, Dr. Sören Jensen for providing a fieldtrip to Jämtland. I thank Professor Jan Bergström (Swedish Museum of National History) for the field-work arrangements in Gotland, Dr. Robert Szava-Kovats, Dr. Colin Scrutton (University of Durham) and Dr. Ivar Puura (University of Tartu) for the linguistic help.

Last, but not least, I want to thank my family and especially Margus Teder for unconditional support.

This work has been supported by grants No 5042 and No 5290 of the Estonian Science Foundation. The fieldwork in Gotland was supported by Stensiö Fund, The Royal Swedish Academy of Sciences no. 1998 2–4.

SUMMARY IN ESTONIAN

Baltoskandia Siluri (Llandovery-Wenlocki) tabulaatide taksonoomia, paleoökoloogia ja levik

Tabulaadid (alamklass Tabulata) on eranditult koloonialised korallid, kes esinesid ajavahemikul Kesk-Ordoviitsiumist kuni Permi ajastu lõpuni. Eesti alale ilmusid esimesed tabulaadid Oandu eal ning saavutasid oma esimese õitsengu Ordoviitsiumi lõpul. Ordoviitsiumi ja Siluri vahetusel tabulaatide koosseisus suuri muutusi ei toimunud. Perekondade kadumine Hilis-Ordoviitsiumis toimus järk-järgult ja mõned Ordoviitsiumis ilmunud perekonnad eksisteerisid jätkuvalt ka Siluri ajastul. Siluri algul tabulaatide kosmopoliitsus suurenes. Esimene Siluri tabulaatide õitseng saabus Llandovery lõpus. Wenlockis toimus järjekordne tabulaatide mitmekesisuse kasv ning uute perekondade ilmumine kulmineerus Siluri ajastu suurima õitsenguna.

Varasemate uurijate valdavalt tüploogiline liigikäsitlus on muutnud tabulaatide taksonoomia keeruliseks ja see teeb selle rühma taksonoomilise revisjoni hädavajalikuks. Baltoskandias kirjeldatud arvukad tabulaatide liigid on liiga kitsalt piiritletud ja suur osa neist liikidest on laialt levivate, kosmopoliitsete liikide sünonüümid. Neil kosmopoliitsetel liikidel on palju sünonüüme just tänu valdavalt rakendatavale kitsale liigimõistele. Selline "killustamine" (*splitting*) mõjustab loomulikult ka hinnanguid tabulaatide mitmekesisuse muutustele Siluri ajastul. Samal ajal uurimused tabulaadiliikide muutlikkusest Baltoskandias praktiliselt puuduvad, kuid koloonialisuse tõttu on laialdane muutlikkus neile iseloomulik. Kinnituva eluviisi tõttu olid tabulaadid tugevasti faatsiestest sõltuvad. Nad esinesid põhiliselt madalveelises keskkonnas, aktiivse lainetuse vööndis. Tabulaadi morfoloogia peegeldab mineviku keskkonnatingimusi ja see aspekt on oluline liikide kirjeldamisel. Tabulaatide määranguid võimaldab täpsustada biomeetria laiem rakendamine. Biomeetriline käsitlus tugineb tabulaatide puhul meetriliste tunnuste statistilisele analüüsile.

Käesolevas töös on Baltoskandia varajase Siluri tabulaatide kirjeldamisel arvestatud liigisisest muutlikkust ja rakendatud biomeetriat. Uurimus kirjeldab liikide levikut Balti Siluri basseinis ning ja võrdleb seda levikuandmetega Dnestri basseinist ja Podljassk-Bresti piirkonnast. Piirkondlikke levikuandmeid mõjustab läbilõike iseloom ja lünklikkus erinevates piirkondades. Varajase Siluri tabulaadid on teada Oslo regioonist ja Eestist, Wenlocki tabulaatide kohta ona andmeid põhiliselt Gotlandil ja Eestis ning Siluri nooremate kihtide tabulaate on rohkem kirjeldatud Podljassk-Bresti piirkonnast ja Dnestri jõe basseinist. Tabulaadid on valdavalt levinud karbonaatsetes kivimites, nende säilivus on Baltoskandias üldiselt hea, välja arvatud Oslo regioonis ja Jämtlandil.

Siluri tabulaatide arengus on olulised muutused seotud Aeroni ja Rhuddani piiri ning Wenlocki algusega ja on seletatavad globaalsete sündmuste mõjuga. Nii on näiteks halüsitiid/heliolitiidsete biostroomide taasilmumine Halla kihtides Gotlandil kaudselt seotud Kesk-Homeri globaalse sündmusega. Olu-

liste tabulaadiseltside (Heliolitida, Halysitida) kadumine Eestist juba Wenlockis on siiski seotud siinsete fatsiaalsete tingimuste spetsiifilisusega.

Tabulaatide sessiilse eluviisi ja keskkonnatundlikkuse tõttu ei saa neid rakendada globaalse stratigraafilise korrelatsiooni eesmärgil, kuid nende roll võib olla märkimisväärne seal, kus puuduvad teised biostratigraafiliselt olulised fossiiligrupid. Jämtlandi tabulaatide seas leidub mõõdukalt hea säilivusega määratavaid koralle ja see loob eeldused võrdluseks Eesti materjaliga. Jämtlandi ja Eesti tabulaadifaunade võrdluse alusel võib väita, et Jämtlandis esinev Berge lubjakivi on Aeroni-ealine. Gotlandil näib tabulaatide stratigraafiline levik sageli olevat laiem, kuid sellise mulje loovad peamiselt sealsed mitmekesisemad faatsesed ning Eesti läbilõikele iseloomulike lünkade puudumine.

REFERENCES

BAARLI, B. G., JOHNSON, M. E. & ANTOSHKINA A. I. 2003. Silurian Stratigraphy and Paleogeography of Baltica. *In* E. LANDING and M. E. JOHNSON (eds): Silurian Lands and Seas. Paleogeography Outside of Laurentia, 3–34. *New York State Museum Bulletin*, **493**.

BASSETT, M. G., KALJO, D. and TELLER, L. 1989. The Baltic Region. *In* C. H. HOLLAND and M. G. Bassett (eds): *A Global Standard for the Silurian System. Geological Series No 9*, Cardiff, 158–170.

BONDARENKO, O. B. 1982. Prizhidol'sjie geliolitidy: izmenchivost' morfogenez, biostrtigrafiya [Heliolitids of Pridoli: variability, morfogenesis, biostrtigraphy]. *Izvestiya akademii hauk SSSR*, *seriya geologicheskaya*, **5**, 46–58. [In Russian].

BONDARENKO, O. B. 1992. Sistema geliolitoidei. [The system of heliolitids]. 205 pp. Moskovskoe obshchestvo ispytatelej prirody. [In Russian].

BRENCHLEY, P. J. 2004. End Ordovician glaciation. *In* B. D. WEBBY, F. PARIS, M. L. DROSER and I. G. PERCIVAL (eds): The Great Ordovician Biodiversification Event, 81–83. Columbia University Press.

CALNER, M. 1999. Stratigraphy, facies development, and depositional dynamics of the Late Wenlock Fröjel Formation, Gotland, Sweden. *GFF*, **121**, 13–24.

CALNER, M., and SÄLL, E. 1999. Transgressive oolites onlapping a Silurian rocky shoreline unconformity, Gotland, Sweden: GFF, **121**, 91–100.

CARTER, G. S. 1954. *Animal evolution: a study of recent views of its causes*. London. Sidgwick and Jackson.

CLARKSON, E. N. K. 1986. Invertebrate palaeontology and evolution. Second edition. Allen & Unwin. 382 pp.

COCKS, L. R. M. 2001. Ordovician and Silurian global geography. *Journal of the Geological Society, London*, **158**, 197–210.

COCKC, L. R. M and FORTEY R. A. 1998. The Lower Palaeozoic margins of Baltica, *GFF*, **120**, 173–179.

COCKS, L. R. M. and THORSVIK, T. H. 2002. Earth geography from 500 to 400 million years ago: a faunal and palaeomagnetic review. *Journal of the Geological Society*, London, **159**, 631–644.

COPPER, P. 1994. Ancient reef ecosystem expansion and collapse. *Coral reefs 13*, 3–12.

COPPER, P. and BRUNTON, F. 1991. A global review of Silurian reefs. Special Papers in Palaeontology, (44), 225–259.

DAHLQVIST, P. 1999: A Lower Silurian (Llandoverian) halystitid fauna from the Berge Limestone Formation, Norderön, Jämtland, central Sweden. *Examensarbete i geologi vid Lunds Universitiet*, **104**, 1–15.

DAHLQVIST, P. & CALNER, M. 2004. Late Ordovician palaeoceanographic changes as reflected in the Hirnantian — early Llandovery succession of Jämtland, Sweden, 149–164. In M. C. POPE and M. T. HARRIS (eds): New Insights into Late Ordovician Climate, Oceanography, and Tectonics. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **210**.

DIXON, O. A. 1974. Late Ordovician *Propora* (Coelenterata: Heliolitidae) from Anticosti Island, Quebec, Canada. *Journal of Paleontology*, **48**, 568–585.

DROSER, M. L., BOTTJER D. J., SHEEHAN P. M., MCGHEE Jr. G. R. 2000. Decoupling of taxonomic and ecologic severity of Phanerozoic marine mass extinctions. *Geology*, **28**, 675–678 .

DUBATOLOV, V. N. 1971. Taksonomicheskoe znachenie mikrostruktury skeletnykh obrazovanij tabulyat [Taxonomical importance of the skeletal forms of tabulate microstructure], 12–33. *In* V. N. DUBATOLOV (ed.): Tabulyaty i geliolitoidei paleozoya SSSR [Tabulates and heliolitids of the Paleozoic of the USSR], *Papers of II All-Union Symposium on fossil corals of the USSR, Academy of Sciences of the USSR, Siberian branch, Institute of Geology and Geophysics*, **1**, 192 pp. [In Russian with English summary].

EICHWALD, C. E. 1829. *Zooloogia Specialis*, **1**, vi+314, (Vilnae).

EICHWALD, C. E. 1855-1860. *Lethaea Rossica ou paléontologie de la Russie*, **1**, (Part 1), xix + 17–26 + 1–681 pp., (atlas, 1855; text, 1860), E. Schweizerbart, Stuttgart.

FORTEY, R. A. and COCKS L. R. M. 2002. Palaeontological evidence bearing on global Ordovician-Silurian continental reconstructions. *Earth Science Reviews,* **61**, 245–307.

HILL, D. 1981. Rugosa and Tabulata. *In* C. TEICHERT (ed.): *Treatise on Invertebrate Paleontology*, Part **F**, Coelenterata, The Geological Society of America, Inc. and the University of Kansas, F762 pp.

JEPPSSON, L. 1998. Silurian Oceanic Events: Summary of General Characteristics. *In* E. LANDING and M. E. JOHNSON (eds): Silurian Cycles. Linkages of dynamic stratigraphy with atmospheric, oceanic, and tectonic changes. *New York State Museum Bulletin*, **491**, 239–257.

JEPPSSON, L., VIIRA, V. and MÄNNIK, P. 1994. Silurian conodont-based correllations bewteen Gotland (Sweden) and Saaremaa (Estonia). *Geological Magazine*, **131**, 201–218.

JOHNSON, M. E. 1996. Stable cratonic sequences and a standard for Silurian eustasy. 203–211. *In* B. J. WITZKE, G. A. LUDVIGSON and J. E. DAY (eds): Paleozoic Sequence Stratigraphy: Views from the North American Craton. *Geological Society of America, Special Paper*, **306**.

JOHNSON, M. E., BAARLI, B. G., NESTOR, H., RUBEL, M. and WORSLEY, D. 1991. Eustatic sea-level patterns from the Lower Silurian (Llandovery Series) of the southern Norway and Estonia. *Geological Society of America Bulletin,* **103**, 315–335.

JOHNSON, M. E., RONG, J.-Y., KERSHAW, S. 1998. Calibrating Silurian eustasy against the erosion and burian of coastal topography, 3–13. *In* E. LANDING and M. E. JOHNSON (eds): Silurian Cycles — Linkages of dynamic stratigraphy with atmospheric, oceanic, and tectonic changes. *New York State Museum Bulletin*, **491**.

JONES, O. A. 1936. The controlling effect of the environment upon the corallum in Favosites; with a revision of some massive species on this basis. *The Annals and Magazine of Natural History*, **17**, 1–24.

KALJO, D., KIIPLI, T. and MARTMA, T. 1998. Correlation of carbon isotope events and environmental cyclicity in the East Baltic Silurian, 297–312. *In* E. LANDING and M. E. JOHNSON (eds): Silurian Cycles — Linkages of dynamic stratigraphy with atmospheric, oceanic, and tectonic changes. *New York State Museum Bulletin*, **491**.

KALJO, D. and KLAAMANN, E. 1973. In. A. HALLAM (ed.). Atlas of Paleobiogeography. Elsevier, 37–45.

KHAIZNIKOVA, K. V. 1989. Biostratigrafiya i tabulyaty biogermnykh otlozhenij rannego paleozoya (Yzhnoe Verkhojanie), [Biostratigraphy and tabulates of the biohermal deposits of Early Paleozoic (South Verkhojanie)]. Moscow, "Nauka", 218 pp. [In Russian].

KLAAMANN, E. 1959. O faune tabulyat yuuruskogo i tamsaluskogo gorizontov [On the Tabulata fauna in Juuru and Tamsalu Stages]. *Eesti NSV Teaduste Akadeemia toimetised*, **8**, 256–270. [In Russian with English summary].

KLAAMANN, E. 1961. Tabulyaty i geliolitidy venloka Estonii [Tabulates and heliolitids from Wenlock of Estonia]. *Eesti NSV Teaduste Akadeemia, Geoloogia Instituudi Uurimused* **6**, 69–112. [In Russian with English summary].

KLAAMANN, E. 1962a. Tabulyaty verkhnego silura Estonii [Upper Silurian Tabulata of Estonia]. *Eesti NSV Teaduste Akadeemia, Geoloogia Instituudi Uurimused*, **9**, 25–74. [In Russian with English summary].

KLAAMANN, E. 1962b. Rasprostranenie ordovikskikh i silurikskikh tabulyat Estonii (s opisaniem nekotorykh novykh vidov) [Distribution of Tabulata in the Ordovician and Silurian of Estonia (with a description of some new species)]. *Eesti NSV Teaduste Akadeemia, Geoloogia Instituudi Uurimused*, **10**, 149–172. [In Russian with English summary].

KLAAMANN, E. 1964. Pozdneoordovikskie i rannesilurijskie Favositida Estonii [Late Ordovician and early Silurian Favositida from Estonia]. Eesti NSV Teaduste Akadeemia Geoloogia Instituut, 118 pp. [In Russian with English summary].

KLAAMANN, E. 1966. Inkommunikatnye tabulyaty Estonii [The incommunicate Tabulata of Estonia]. Eesti NSV Teaduste Akadeemia Geoloogia Instituut, 96 pp. [In Russian with English summary.]

KLAAMANN, E. 1970. Tabulyata. [Tabulata], 114–125. In D. Kaljo (ed.): Silur Estonii [The Silurian of Estonia], Tallinn, "Valgus", 343 pp. [In Russian with English summary].

KLAAMANN, E. 1971. Über einige korallen aus der bohrung von File Haidar (Gotland, Sweden). *Eesti NSV Teaduste Akadeemia Toimetised **20***, 73–77.

KLAAMANN, E. 1972. O soobshchestvakh tabulyat v Silure Pribaltiki. *Eesti NSV Teaduste Akadeemia Toimetised, Keemia, Geoloogia*, 21, 78–82.

KLAAMANN, E. 1982. Soobshchestva tabulyat (pozdnii venlok i ludlov ostrova Gotland) [The tabulate communities (late Wenlock and Ludlow of Gotland)]. *In* D. KALJO and E. KLAAMANN (eds): Communities and biozones in the Baltic Silurian, 36–60. Academy of Sciences of Estonia, Institute of Geology. [In Russian with English summary].

KLAAMANN, E. 1983. Tabulyaty yaaniskogo i yaajarahuskogo gorizontov (venlok Estonii) i ikh biozony [Tabulates from Jaani and Jaagarahu stages (Wenlock of Estonia) andd their biozones], 3–40. *In* KLAAMANN (ed.): Paleontologiya drevnego paleozoya Pribaltiki i Podolii [Paleontology of early Paleozoic of Baltic and Podolia], Academy of Sciences of Estonia, Institute of Geology. [In Russian with English summary].

KLAAMANN, E. 1986. Soobshchestva i biozonal'nost' tabulyatomorfnykh korallov silura Pribaltiki [The tabulate communities and biozones of the East Baltic Silurian]. *In* D. KALJO and E. KLAAMANN (eds): Theory and practice of ecostratigraphy, 80-98. Academy of Sciences of Estonia, Institute of Geology. [In Russian with English summary].

KLAAMANN, E., EINASTO, R., VIIRA, V., MÄNNIL, R., NESTOR, V., RUBEL, M. and SARV, L. 1980. Fatsial'nye zakonomernosti raspredeleniya fauny v verkhnem llandoveri i venloke severnoj Pribaltiki [Facies conrol in the distribution of fauna in the Llandovery and Wenlock of northern Baltic], 38 – 47. *In* D. L. STEPANOV and L. I. HOZATSKI (eds): Ekostratigrafiya i ekologicheskie sistemy geologicheskogo proshlogo [Ecostratigraphy and systems of ecology of geological past]. Trudy XXII

sessii vsesoyuznogo paleontologicheskogo obshchestva, Leningrad. [In Russian with English summary].
KLAAMANN, E. and EINASTO R. 1982. Coral reefs of Baltic Silurian (structure, facies relations). *In* D. KALJO and E. KLAAMANN (eds): Ecostrtigraphy of the East Baltic Silurian. Academy of Sciences of the Estonian Institute of Geology, Tallinn, Valgus, 35–41.
LAFUSTE, J. and TOURNEUR, F. 1987. Microstructure du genre *Favosites* Lamarck, 1816 (Tabulata) et de Favositides du Silurien, avec une révision du néotype de *Favosites gothlandicus* Lamarck, 1816. *Annales de Société Géologique de Belgique* ***110***, 189–198.
LAUB, S. R. 1979. The corals of the Brassfield Formation (mid–Llandovery; Lower Silurian) in the Cincinnati Arch Region. *Bulletins of American Paleontology* ***75***, 1–457.
LAUFELD, S. and MARTINSSON, A. 1981. Reefs and ultrashallow envioronments. Guidbook to the field excursions in the Silurian of Gotland, Project Ecostratigraphy Plenary Meeting 22nd-28th August, 1981. Project Ecostrtigraphy. 24 p.
LEE, D. J. and NOBLE, J. P. A., 1988. Evaluation of corallite size as a criterion for species discrimination in favositids. *Journal of Paleontology*, **62**, 32–40.
LEE, D. J. and NOBLE, J. P. A., 1990. Colony development and formation in halysitid corals. *Lethaia*, **23**, 179– 93.
LINDSTRÖM, G. 1899. Remarks on the Heliolitidae. *Kungliga Svenska Vetenskaps-Akademiens Handlingar*, ***32***, 1–140.
LINNAEUS, C. 1767. *Systema Naturae. Edition 12,* **1**, 533-1327 + (37). Laurentius Salvius, Holmiae.
MISTIAEN, B. 1988. Tabulés Auloporida du Givetian et du Frasnien de Ferques (Boulonnais – France). *In* D. BRICE (ed.): *Le Dévonien de Ferques, Bas-Boulonnais* (*N. France*), 197–230.
MÕTUS, M.-A. 2003. A small tabulate coral assemblage from the Wenlock of Saaremaa (Estonia). *In* B. HUBMANN, W. E. PILLER, M. RASSER and C. LATAL (eds): 9th International Symposium on Fossil Cnidaria and Porifera. *Berichte des Institutes für Geologie und Paläontologie der Karl-Franzens-Universität Graz/Austria,* **7**. Abstracts, p. 72.
NESTOR, H. and EINASTO, R. 1997. Ordovician and Silurian carbonate sedimentation basin, 192-204. *In* A. RAUKAS and A. TEEDUMÄE (eds): Geology and mineral resources of Estonia. Estonian Academy Publishers, Tallinn, 436 pp.
NOTHDURFT, L. D. and WEBB, G. E. 2003. "Shingle" microstructure in scleractinian corals: A possible analogue for lamellar and microlamellar microstructure in Paleozoic tabulate corals. *In* B. HUBMANN, W. E. PILLER, M. RASSER and C. LATAL (eds): 9th International Symposium on Fossil Cnidaria and Porifera. *Berichte des Institutes für Geologie und Paläontologie der Karl-Franzens-Universität Graz/Austria,* **7**. Abstracts, p. 75.
NOBLE, J. A and LEE, D. J. 1991. First report of allogeneic fusion and allorecognition in tabulate corals. *Journal of Paleontology*, **65**, 67–74.
OEKENTORP, K. W. 1976: Revision und Typisierung des Genus *Paleofavosites* Twenhofel, 1914. *Paläontologische Zeitschrift,* **50**, 151–192.
OEKENTORP, K. W. 2001. Review on diagenetic microstructures in fossil corals — a controversial discussion. *Tohoku University Museum Bulletin*, **1**, 193–209.
PHARAOH, T. C., MERRIMAN, R. J., EVANS, J. A., BREWER, T. S., WEBB, P. C. and SMITH, N. J. C. 1991. Early Palaeozoic arc-related volcanism in the concealed

Caledonides of Southerb Britain. *Annales de la Société Géologique de Belgique*, **114**, 63–91.
POWELL, J. H. and SCRUTTON, C. T. 1978. Variation in the Silurian tabulate coral *Paleofavosites asper*, and the status of *Mesofavosites*. *Palaeontology,* **21**, 307–319.
PREOBRAZHENSKIJ, B. V. 1974. O klassifikatsij i taksonomicheskoj otsenke skeletnykh elementov tabulyatomorfykh korallov [On the classification and taxonomical estimation of skeleton elements of tabulatomorphic corals], 90–99. *In* B. S. SOKOLOV (ed.): Drevnie cnidaria [Ancient Cnidria] I, Novosimbirsk, 284 pp. [In Russian with English summary].
PUSHKIN, V. L., ROPOT, V. F. and ABUSHIK, A.F. 1991: Ecostratigraphy: results of investigations of Silurian deposits in the Byelorussian part of the Podljassk-Brest depression. Byelorussian committee of the international geological correlation programme. Institute of geochemistry and geophysics. Minsk, Nauka i tekhnika. 40 pp.
RESHENYA... 1987. Resheniya mezhvedomstvennogo stratigraficheskogo soveshchaniya po ordoviku i siluru vostochno-evropejskoj platformy 1984 s regional'nymi stratigraficheskimi skhemami. [Conclusion of the meeting of the Ordovician and Silurian stratigraphy in East European platform with the regional strtigraphical scemes]. VSEGEI, Leningrad, 112 pp. [In Russian].
SAMTLEBEN, C., MUNNECKE, A., BICKERT, T. and PÄTZOLD, J. 1996. The Silurian of Gotland (Sweden): facies interpretation based on stable isotopes in brachiopod shells. *Geologische Rundschau*, **85**, 278– 292.
SCHMIDT, F. 1858. Untersuchungen über die Silurichen Formationen von Esthland, North Livland und Oesel. Arch. Naturk. Livlands, Esthlands und Kurlands, Series 1.
SCHOUPPÉ, V. A., and OEKENTORP, K. 1974. Morphogenese und Bau der Tabulata. *Palaeontographica A*, **145**, 194 pp.
SCOTESE, C. R. 2003. Paleomap Project. www.scotese.com
SCRUTTON, C. T. 1987. A review of favositid affinities. *Palaeontology*, **30** (3), 485–492.
SCRUTTON, C. T. 1989. Intracolonial and intraspecific variation in tabulate corals. *Memoir of the Association of Australasian Palaeontologists,* **8***,* 33–43.
SCRUTTON, C. T. 1998. The Palaeozoic corals, II: structure, variaton and palaeoecology. *Proceedings of the Yorkshire geological society*, **52**, (1) 1–57.
SCRUTTON, C. T. and POWELL, J. H. 1980. Periodic development of dimetrism in some favositid corals. *Acta Palaeontologica Polonica*, **25**, 478–491.
SHEEHAN, P. M. 2001. The Late Ordovician mass extinction. *Annual Reviews of Earth Planetary Science*, **29**, 331–364
SIMPSON, G. G. 1944. *Tempo and mode in evolution*. New York Columbia University Press.
SIMPSON, G. G. 1953. *The major features of evolution.* New York Columbia University Press.
SOKOLOV, B. S. 1951a. Tabulyaty paleozoya Evropejskoj chasti SSSR. Ordovik Zapadnogo Urala i Pribaltiki, I [Tabulates from paleozoic of European part of SSSR. Silurian of Baltic, I (Ordovician of West Urals and Pribaltiki)]. *Trudy VNIGRI* , **48**, 1–132. [In Russian].
SOKOLOV, B. S. 1951b. Tabulyaty paleozoya Evropejskoj chasti SSSR. Silur Pribaltiki, II (favositidy llandoverskogo yarusa) [Tabulates from paleozoic of European part of SSSR. Silurian of Baltic, II (favositids from Llandovery Series)]. *Trudy VNIGRI,* **52**, 1–124. [In Russian].

SOKOLOV, B. S. 1952. Tabulyaty paleozoya Evropejskoj chasti SSSR. Silur Pribaltiki, III (favositidy venlokskogo i ludlovskogo yarusov) [Tabulates from paleozoic of European part of SSSR. Silurian of Baltic, III (favositids from Wenlock and Ludlow Series)]. *Trudy VNIGRI*, **58**, 85 pp. [In Russian].

SOKOLOV, B. S. 1955. Tabulyaty paleozoya Evropejskoj chasti SSSR. Vvedenie (Obshchie voprosy sistematiki i istorii razvitiya tabulyat) [Tabulates from paleozoic of European part of SSSR. Introduction (General aspects of systematics and evolution of tabulates)]. *Trudy VNIGRI*, **85**, 527 pp. [In Russian].

SOKOLOV, B. S. 1962. Osnovy paleontologii [Basics of Palaeontology]. Gubki, arheotsiaty, kishechnopolostnye, chervi [Porifera, arheocyatha, anhozoa, vermes]. Izdatel'stvo akademii nauk SSSR, 485 pp. [In Russian].

SOKOLOV, B. S. and TESAKOV, J. I. 1984. Populyatsionnyj, biotsenoticheskij i biostratigraficheskij analiz tabulyat. Podol'skaya model' [The analysis of tabulates in aspects of population, biocoenosis and biostratigraphy]. *Akademiya Nauk SSSR, Sibirskoe Otdelenie, Institut Geologii i geofiziki*, **577**, 198 pp. [In Russian].

SORAUF, J. E. 1996. Biocrystallization models and skeletal structure of phanerozoic corals, 159-184. *In* G. D. STANLEY, Jr. (ed.): Paleobiology and biology of corals. *The Paleontological Society Papers,* **1**, 296 pp.

STASINSKA, A. 1954. Korallowoe Tabulata z devonu Grzegorzowic (Bodania wstepne). *Acta Geologica Polonica*, **4**.

STASINSKA, A. 1967. Tabulata from Norway, Sweden and from the erratic boulders of Poland. *Palaeontologia Polonica*, **18**, 112 pp.

STEL, J. H. 1976, The Paleozoic hard substrate trace fossils *Helicosalpinx, Chaetosalpinx* and *Torquasalpinx*. *Neues Jahrbuch für Geologie und Paläontologie* (12), 726–744.

STEL, J. H. 1978a. Studies on the palaebiology of favositids. Doctor's thesis, Gröningen, 75 pp.

STEL, J. H. 1978b. Environment and quantitative morphology of some Silurian tabulates from Gotland: Scripta Geologica, No. 47, 75 pp.

STEL, J.H. 1978c. Growth and reproduction in the tabulate *Favosites forbesi* from the Silurian of Gotland, *GFF*, **100**, 181–188.

STEL, J. H., 1979. Lateral increase in *Paleofavosites asper* (d'Orbigny, 1850) and other tabulates. *Journal of Paleontology,* **53**, 501–505.

SUTTON, I. D. 1966. The value of corallite size in the specific determination of tabulate corals *Favosites* and *Palaefavosites*. *Mercian Geologist*, **1**, 255–263.

TESAKOV, J. I. 1971. Favositidy Podolii. [Favozitidae of Podolia]. *Akademiya Nauk SSSR, Sibirskoe Otdelenie, Trudy Instituta Geologii i Geofiziki*, 120 pp. [In Russian].

TESAKOV, J. I. 1974. Vnutrividovye podrazdeleniya tabulyat i ikh izmenchivost' s pozitsii biologicheskoj kontseptsii vida. [Tabulata intraspecific subdivisions and their variability in terms of biologic criterion of species]. *In* B. S. SOKOLOV (ed.): Drevnie cnidaria [Ancient Cnidria] I, Novosimbirsk, 128–132. [In Russian with English summary].

TESAKOV, J. I. 1978. Tabulyaty populatsionnyj, biotsenoticheskij i biostratigraficheskij analiz [Tabulata populational, biocoenosoic and biostratigraphic analysis]. *Akademiya nauk SSSR, sibirskoe otdelenie, institut geologii i geofiziki,* **409,** 207 pp. [In Russian].

TORSVIK, T. H. 1998. Palaeozoic palaeogeography: North Atlantic viewpoint. *GFF,* **120**, 109–118.

TRIPP, K. 1933. Die Favositen Gotlands. *Palaeontographica A*, **79**, 75–142.

YOUNG, G. A. and ELIAS, R. J. 1995. Latest Ordovician to earliest Silurian colonial corals of the east-central United States. *Bulletins of American Paleontology*, **108**, 1–148.

YOUNG, G. A. and ELIAS, R. J. 1997. Patterns of variation in Late Ordovician and Early Silurian tabulate corals. *Boletin de la Real Sociedad Espanola de Historia Natural*, **91**, 193–204.

YOUNG, G. A. and ELIAS, R. J. 1999. Relationships between internal and external morphology in *Paleofavosites* (Tabulata): the unity of growth and growth form. *Journal of Paleontology*, **73**, 580–597.

YOUNG, A. and NOBLE, J. P. A. 1990. Silurian tabulate coral biostratigraphy and biofacies of northern New Brunswick and the southern Gaspé Penisnsula. Canadian Journal of Earth Sciences, **27**, 1143–1158.

YOUNG, A. and SCRUTTON, C. T. 1991. Growth form in Silurian heliolitid corals: the influence of genetics and environment. *Paleobiology*, **17** (4), 369–387.

ZOTOV, V. M. 1986. Fauna tselenterat paleozoya belorussii [Coelentarate fauna from Paleozoic of Belarus], 63–65. *In* R. G. GARETSKIJ (ed.): Paleontologya i ee rol' vpoznanii geologicheskogo stroeniya territorii belorussii [Paleontology and its role of geological knowledge of Belarus territory]. Minsk. [In Russian].

PUBLICATIONS

CURRICULUM VITAE

MARI-ANN MÕTUS

Date and
place of birth: July 10, 1970, Tallinn
Address: Institute of Geology at Tallinn University of Technology
Estonia Ave. 7, 10143 Tallinn, Estonia
e-mail: mariann.motus@gi.ee

Education

1988 Tallinn Secondary School No 2
1993 St. Petersburg University, diploma degree in geological survey
1995 University of Tartu, MSc in palaeontology and stratigraphy

Professional experience

January, 2001 – July, 2002 Engineer, Institute of Geology at Tallinn University of Technology
Since July, 2002 Researcher, Institute of Geology at Tallinn University of Technology

Research training

25. March – 08. April 2002 course of Coral Reef Environment, Heron Island, Great Barrier Reef

Main scientific interest

Evolution of Ordovician and Silurian tabulate corals in the seas of Baltica palaeoplate.

CURRICULUM VITAE

MARI-ANN MÕTUS

Sünniaeg ja -koht: 10. juuli 1970, Tallinn
Aadress: Tallinna Tehnikaülikooli Geoloogia Instituut
Estonia pst. 7, 10143 Tallinn, Eesti
e-post: mariann.motus@gi.ee

Hariduskäik

1988 Tallinna 2. Keskkool
1993 Peterburi Ülikool, kvalifikatsioon: geoloogilised otsingud ja uuringud
1995 Tartu Ülikool, MSc paleontoloogia ja stratigraafia erialal

Teenistuskäik

Jaanuar, 2001 – juuli, 2002 insener, Tallinna Tehnikaülikooli Geoloogia Instituut
Alates juuli 2002 teadur, Tallinna Tehnikaülikooli Geoloogia Instituut

Erialane enesetäiendus

25. märts – 08. aprill 2002 korallriffi elustiku kursus, Heroni saar, Suur Barjäärriff.