

**Microscopic echinoderm remains
from the Darriwilian (Middle
Ordovician) of Västergötland,
Sweden - faunal composition and
applicability as environmental proxies**

Christoffer Kall

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Microscopic echinoderm remains from the Darriwilian (Middle Ordovician) of Västergötland, Sweden - faunal composition and applicability as environmental proxies

CHRISTOFFER KALL

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Microscopic echinoderms were studied in acid-insoluble residues from the Lanna and Holen limestones at Hällekis, Västergötland, Sweden. The section studied spans the uppermost Volkhov and lower–middle Kunda Baltoscandian stages, within the Darriwilian global Stage (Middle Ordovician). The echinoderms show an increase in abundance, accompanying falling sea levels during the well-recognized regression initiated in the lower part of the so-called Täljsten interval. The echinoderm abundance reaches its maximum in connection to the lowest water depths, and decreases afterwards. Seven different morphotypes were defined and used to describe fluctuations in ostensive biodiversity. The number of morphotypes present generally follows the same pattern as observed in abundance, until after the lowstand where the number of occurring morphotypes remains high, whereas the abundance decreases. The different morphotypes identified are indicative of an echinoderm fauna dominated by pelmatozoans, mainly crinoids and cystoids. This is partly mirrored at the macroscopic scale by the mass occurrence of cystoids in the 'Täljsten'. Some of the microscopic echinoderms recovered exhibit features common only for holothurians. This would make these specimens the oldest fossil holothurians known thus far.

Keywords: täljsten, echinoderms, microscopic, proxy, ordovician, darriwilian, kunda, volkhov, baltoscandia, lanna limestone, holen limestone, hällekiis, sweden

Supervisor(s): Mats E. Eriksson, Anders Lindskog

Subject: Bedrock geology

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Mellanordoviciska mikroechinodermer från Västergötland, Sverige – faunasammansättning och lämplighet som proxy för miljöförändringar

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Sammanfattning: Mikroskopiska echinodermfossil har undersökts ur prover från täljstensintervallet och intilliggande delar av 'lanna'- och 'holenkalkstenen' i Hällekis stenbrott, Västergötland. Den undersökta sektionen är från översta volkhov och mellersta kunda, darriwilian (mellanordovicium). Tidigare studier har konkluderat att en regression/transgression skedde under den undersökta perioden, vilket bekräftas av en kraftigt förhöjd echinodermabundans såväl som skenbar biodiversitet (baserad på morfotyper) i samband med de lägsta havsnivåerna. Abundansen sjunker efter täljstensintervallet, medan den skenbara biodiversiteten är fortsatt hög. De olika identifierade morfotyperna indikerar att mikroechinodermfaunan domineras av pelmatozoer, främst crinoidéer och cystoidéer, vilket delvis avspeglas på makroskopisk skala i form av massförekomster av cystoidéer. Några av de utplockade exemplaren uppvisar egenskaper vanliga bland holothurier, vilka då skulle vara de äldsta kända. Fortsatta studier krävs för att avgöra om så är fallet.

Nyckelord: täljsten, echinodermer, mikroskopisk, proxy, ordovicium, darriwilian, kunda, volkhov, lannakalksten, holenkalksten

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1 Introduction

The Ordovician deposits in Sweden rarely exceed 150 m in total thickness and a common facies present is named the Orthoceratite Limestone due to its rich abundance of orthoceratite nautiloid cephalopods (Janusson 1982a). The Orthoceratite Limestone has been quarried for centuries and used mainly for construction purposes.

At Kinnekulle, Västergötland, south-central Sweden, the dominantly red Orthoceratite Limestone is interrupted by a distinct grey interval, called the 'Täljsten' (Fig. 1). The succession has been known for a long time and was described already during the 18th century (for a historic review, see Jaanusson 1982a, b). Attention has recently been paid to the 'Täljsten' interval due to the discovery of an anomalous abundance of fossil meteorites and sediment-dispersed extraterrestrial chromite grains, probably originating from a major disruption event in the asteroid belt c. 470 million years ago (e.g. Schmitz et al. 2001; Schmitz et al. 2008; Alwmark et al. 2012). A link between the anomalous influx of extraterrestrial matter and the Great Ordovician Biodiversification Event (GOBE) was proposed by Schmitz et al. (2008).

Faunal analyses were recently performed by Eriksson et al. (2012), who concluded that the microfossil

preservation is better and the abundance is higher in the 'Täljsten' than in the surrounding red limestone. The microfossils of the 'Täljsten' also show a faunal reorganization, with a transition in dominance from trilobites and linguliformean brachiopods to echinoderms within the 'Täljsten'. In the strata above the 'Täljsten' the abundance of brachiopods once again increases. The increase in echinoderms in the 'Täljsten' is also revealed at the macroscopic scale by an extreme prevalence of cystoid echinoderms in the so-called '*Sphaeronites* beds'. Not only the abundance of echinoderms increases within the 'Täljsten' interval, but also conodont and ostracod diversity peak in relation to surrounding strata (Eriksson et al. 2012). Eriksson et al. (2012) suggested that a regression-transgression cycle occurred in connection to the 'Täljsten' interval, and that probably partly explains the faunal reorganization.

The aim of this study is to review Ordovician echinoderms and to examine microscopic echinoderm fossils from the 'Täljsten' and its enclosing strata, in order to assess their diversity and faunal changes throughout the succession. One purpose of this paper is to evaluate the potential for microechinoderms to be used as a proxy for environmental/sea-level fluctuations in the Middle Ordovician. This is done by ana-



Fig. 1 The studied distinctively grey c. 1.5 m thick 'Täljsten' interval and the enclosing strata at the Hällekis quarry, Västergötland, Sweden.



Fig. 2. Planar view of a *Sphaeronites* bed at Thorsberg quarry, Hällekis. Photo by A. Lindskog.

lysing variations in the echinoderm fauna with regards to abundance, diversity and relative frequency of different morphotypes, correlated with trends in sedimentation patterns, variations in inferred water depths, in association with the type of substrate.

1.1 The Ordovician world and faunas

The Ordovician world (c. 485–444 Ma; Cooper & Sadler 2012) was in many ways different from the one we know today. Baltoscandia consisted of two main land areas with little evidence for high relief, 'Fennoscandia' and 'Sarmatia' (Cocks and Torsvik 2005), separated by a large epicontinental sea (Jaanusson 1982a, b). In the Middle Cambrian (c. 510 Ma) Baltica was situated in the southern hemisphere at a latitude of approximately 60°, with reversed cardinal points compared to the modern-day position, and would rotate 120° until the Middle Ordovician. Around the time of the Cambrian–Ordovician transition, Baltica was surrounded by the Tornquist and Iapetus oceans, wide enough to isolate Baltica to the extent that endemic organismal families could form. In the early Late Ordovician (c. 460 Ma) Baltica was entering a latitude of 30°S and as the rotation slowed down, the northward movement increased (Fig. 3). As Baltica travelled northwards, the oceans became narrower and the temperature increased. Hence, the period of isolation was broken and exotic faunal elements could successively invade Baltoscandia. As the temperature increased, so did the abundance and diversity of the benthic faunas (Cocks & Torsvik 2005).

During the late Cambrian and throughout the Ordovician, biodiversity increased continuously until the middle Sandbian (Late Ordovician). The most rapid increase occurred in the Middle Ordovician, and is commonly referred to as the Great Ordovician Biodiversification Event (GOBE). During the GOBE, a general increase in the biodiversity of a wide range of organisms, such as bivalves, brachiopods, bryozoans, conodonts, corals, echinoderms, gastropods, graptolites, nautiloids and trilobites, took place (Sepkoski 1995; Schmitz et al. 2008; Servais et al. 2009). The cause of the diversification is not fully understood, but factors such as extensive epicontinental seas, distinct

faunal provincialism, prominent magmatic and tectonic activity, as well as a relatively low initial diversity probably contributed (Cooper & Sadler 2012). The biodiversification resulted in a gradual replacement of the 'Cambrian Evolutionary Fauna', dominated by detritus feeders, to the succeeding 'Palaeozoic

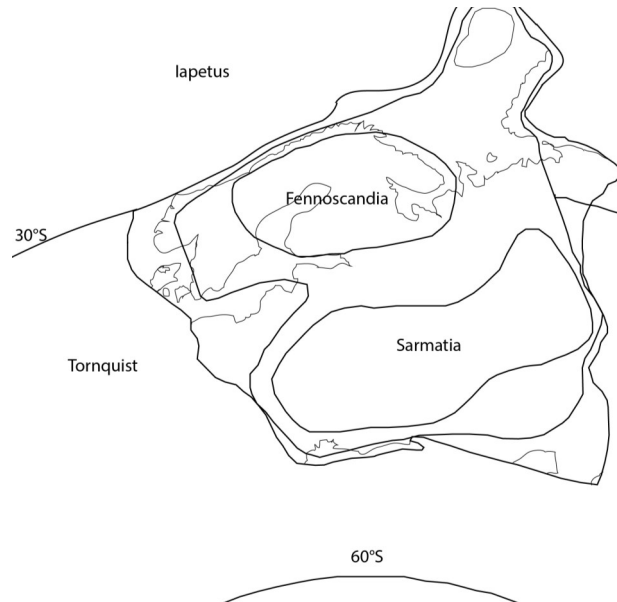


Fig. 3. Baltoscandia during the Late Darriwilian, Middle Ordovician (c. 460 Ma). Baltica was situated in the southern hemisphere between temperate and subtropical latitudes. Isolated by the oceans of Iapetus and Tornquist, and covered by a vast epicontinental sea, which separated the two main land masses of Fennoscandia and Sarmatia. Redrawn and modified from Cocks & Torsvik (2005).

Evolutionary Fauna', dominated by filter feeders (Servais et al. 2010). In the basal Late Ordovician, diversity peaked before entering the late Katian to Hirnantian when approximately 85% of all species became extinct during the end-Ordovician mass extinction. It was probably caused by decreasing water depths as an effect of the Hirnantian glaciation (Sheehan 2001; Servais et al. 2010; Cooper & Sadler 2012).

1.2 Phylum Echinodermata

Most people are familiar with the morphology of asterozoans (starfishes) and echinozoans (sea urchins), but probably less so with the three other today living classes of echinoderms – crinozoans (sea lilies), ophiurozoans (brittle stars) and holothurozoans (sea cucumbers) – all of which are marine, as were their extinct relatives. However, in addition, several extinct classes are known throughout the Phanerozoic. The phylum Echinodermata is subdivided into five subphyla: Crinozoa, which includes the sea lilies; Blastozoa, which includes several extinct classes with similarities to sea lilies; Asterozoa, which includes sea stars; and Homalozoa and Echinozoa, that include the sea urchins and sea cucumbers. The evolutionary history of

echinoderms goes as far back as the late Proterozoic (Sprinkle & Kier 1986).

Features shared by most echinoderms include a pentamer/pentaradial (five-fold) symmetry, calcareous plates and ossicles constituting the skeleton, an ambulacral groove with external tube-feet used for locomotion, food-gathering or attachment, which in turn are part of, and controlled by, the hydraulic water vascular system (Ubaghs 1967; Sprinkle & Kier 1986).

The echinoderm body is composed of soft tissue, which occupies the coelomic fluid-filled cavities, within a meshwork throughout the endoskeleton called stereom. The water-vascular system consists of a central ring with a connection to the outside water, and radiating canals connecting to the tube feet. The digestive system consists, simplified, of a one-way connection from the mouth to the anus through the gut (Sprinkle & Kier 1986).

Distinctive and diagnostic for echinoderms is the stereom of the endoskeleton, in life covered by skin, which can either form a larger unit called theca, or small spicules and sclerites. These separate skeletal elements are connected to each other by muscles and ligaments. For example, in starfishes, the skeletal elements are very rapidly disarticulated after death, while in sea urchins they are better fused. The latter are thus more often preserved articulated. Some echinoderms are equipped with food-gathering arms or, for some extinct classes smaller so-called brachials. Smaller extremities, called pinnules, extend from the brachials (Ubaghs 1967; Sprinkle & Kier 1986).

The echinoderm phylum is divided into two main morphological clades. The first is composed of groups with an attached mode of life called *Pelmatozoa*, including the stalked crinoids, blastoids, and rhombiferans. The second clade comprises the free-moving *Eleutherozoa*, including the asteroids, echinoids and holothurians (Ubaghs 1967; Sprinkle & Kier 1986).

1.3 Ordovician echinoderms

The Late Cambrian echinoderm fauna was dominated by bizarre, archaic forms such as edrioasterids, eocrinoids, rhombiferans and stylophorans. This fauna gradually transferred into a more diverse one dominated by asterozoans, crinoids, diploporans, parablasteroids, and paracrinoids, which expanded in the Middle Ordovician by blastozoans and echinozoans, and eventually during the Late Ordovician, blastoids came into existence (Lefebvre et al. 2013). The diversity of echinoderms increased steadily during the Lower and Middle Ordovician and around the Sandbian–Katian boundary a prominent increase in diversity occurred (Sprinkle & Guensburg 2004). According to Servais et al. (2008) the increase in echinoderm diversity was possibly due to an increased abundance of phytoplankton and zooplankton, which generated more nourishment at higher trophic levels. Planktonic abundance was possibly influenced by the shallow epicontinental seas, which were well distributed at the time (Servais et al. 2009). Global sea levels also seems to

correlate with echinoderm diversity, with higher sea levels coinciding with peak diversity (Peters & Ausich 2008). In Lower Ordovician deposits from many areas the abundance of echinoderm fossils is low until the Darriwilian transgression (Lefebvre 2013). Substrate type has also clearly affected the echinoderm abundance and diversity (Guensburg & Sprinkle 1992; Sprinkle & Guensburg 1995). Around the Cambrian–Ordovician boundary, the expansion of hardground formation in low-latitude areas likely promoted the diversification of pelmatozoans, for example crinoids (Lefebvre et al. 2013). During the Middle Ordovician, crinoids developed root-like holdfast devices and could thus settle in soft-substrate environments, allowing them to migrate further offshore and thus come to dominate the Palaeozoic echinoderm fauna (Lefebvre & Fatka 2003; Lefebvre 2007a). The diversification of echinoderms was probably initiated in the eastern regions of low-latitude Gondwana, and then spread from there to other regions (Roshnov 2010). Below follows brief descriptions of the main Ordovician echinoderm groups.

1.3.1 Asterozoans

Asterozoans are star-shaped eleutherozoans typically with five arms, or more (Sprinkle & Kier 1986). In the Early Ordovician the asterozoans, including the classes *Asterozoa* and *Ophiurozoa*, diversified by the addition of the new class *Somasteroidea*. During the Early Ordovician, somasteroids were the most frequent asterozoans, but their dominance decreased through the Middle and Late Ordovician. The first known ophiuroids are from the Early Ordovician and during the Late Ordovician they reached their highest diversity globally (Lefebvre et al. 2013). Asteroids are composed of tiny skeletal plates that disarticulate very rapidly (Hunter et al. 2011). The earliest diversity peak in asteroids is from the Late Ordovician of Avalonia, and a very high diversity is known from the Upper Ordovician Lady Burn Starfish bed in Scotland (Lefebvre et al. 2013).

1.3.2 Blastozoans

Most blastozoans were stalked brachial-bearing suspension feeders (Sprinkle & Kier 1986). They first appeared in the Early Cambrian (Sprinkle 1973). During the Ordovician the classes *Blastoidea*, *Coronoidea*, *Soluta*, *Eocrinoidea*, *Parablastoidea*, *Paracrinoida*, *Rhombifera* and *Diploporita* were present, of which the latter two were most diverse. The occurrence of blastozoans increased significantly throughout the Ordovician. According to Lefebvre et al. (2013), it is conceivable that Ordovician blastozoans responded to climatic and latitudinal trends, as their distribution is provincial. As Avalonia drifted northward and approached Baltica, faunal exchange became possible and similarities between the respective faunas are apparent, but also between more separated areas from the same latitudes (Cocks 2000;

Lefebvre et al. 2013). Climatic changes during the Hirnantian were likely responsible for a Late Ordovician decrease in blastozoan diversity (Marshall et al. 1997).

1.3.3 Crinoids

Crinoids are stalked suspension feeders, with a relatively large bowl-shaped theca on which the arms are attached (Sprinkle & Kier 1986). The first unambiguous crinoids appeared in the Lower Ordovician (Guensburg & Sprinkle 2009). Crinoids diversified during the Middle Ordovician and became the dominant echinoderms in the Late Ordovician. Diversity peaked during the Sandbian. The most diverse crinoid faunas were those of Laurentia and Baltica, whereas the Gondwanan ones were less diverse (Lefebvre et al. 2013). Crinoid assemblages are mainly associated with carbonate environments, probably reflecting more favourable conditions for preservation rather than remarkable abundance. Ordovician crinoids were not likely to attach to soft substrates and are generally found on hardgrounds or attached to bioclastic debris (Guensburg 1992; Guensburg & Sprinkle 2001). In the Middle Ordovician, however, crinoids began to evolve holdfasts and could thus inhabit softer substrates (Lefebvre et al. 2013).

1.3.2 Echinozoans

Echinozoans are free-moving eleutherozoans, with a globular (e.g. sea urchins), cylindrical (e.g. sea cucumbers) or flattened (e.g. sand dollars) shape. They typically lack arms or brachials (Sprinkle & Kier 1986).

1.3.2.1 Echinoidea

The first known echinoids appeared in Baltica during the Darriwilian (Pisera 1994). However, their palaeogeographical origin is ambiguous, as most echinoid genera have been found in Laurentia, and only a few from Baltica (Lefebvre et al. 2013). Rozhnov (2010) suggested that Baltica can be regarded as a storehouse for echinoderms, to which many forms migrated but did not originate from.

1.3.2.2 Holothuroidea

According to Reich (2010), the oldest holothurian fossils are from the early Middle Ordovician. The understanding of the holothurian evolutionary history is poor, as there are more recent species than fossil ones. This is caused by the fact that the holothurian endoskeleton very rapidly disarticulates post mortem and is only preserved articulated under very favourable conditions (Smiley 1994; Kerr 2003; Lefebvre et al. 2013). The oldest undisputable holothurian calcareous rings accompanied by sieve plates are from the Darriwilian, late Middle Ordovician, of Sweden (Lefebvre et al. 2013).

1.3.2.3 Ophiocistoidea

Ophiocystoids are free-moving echinozoans, placed

between holothurians and echinoids (Smith 1984). The oldest ophiocystoids are from the Middle Ordovician (Reich & Haude 2004; Reich 2007).

1.3.2.4 Cyclocystoidea

The oldest known cyclocystoids are from the Darriwilian, Middle Ordovician, of Sweden (Berg-Madsen 1987). The cyclocystoid skeleton disarticulates immediately after death (Lefebvre et al. 2013).

1.3.2.5 Edrioasteroids

The oldest edrioasteroids are from the Middle Cambrian. During the Ordovician they could inhabit a variety of different substrates (Meyer 1990; Sumrall & Zamora 2011), but usually not soft ones. Edrioasteroid diversity reached its maximum during the early Late Ordovician (Lefebvre et al. 2013).

1.3.2.6 Stylophorans

The first stylophorans are from the Middle Cambrian and their main diversification took place during the Late Cambrian to Middle Ordovician, which coincided with a low geographical dispersion (Lefebvre et al. 2013). The distribution of stylophorans was likely dependant on temperature and substrate type (Lefebvre 2003, 2007b). Most stylophorans were cold-water living species and therefore occurred in deeper-water environments at lower latitudes and vice versa for higher latitudes (Lefebvre 2007b). The echinoderm diversification during the Darriwilian resulted in additional groups adapting to (and thus living in) soft-substrate settings, thus decreasing the stylophorans' relative influence on echinoderm diversity. During the Late Ordovician stylophorans expanded into lower latitudes, possibly as a response to global cooling. During the Silurian, stylophorans exclusively occurred in shallow, low-latitude environments and they eventually became extinct during the Late Carboniferous (Lefebvre et al. 2013).

1.4 Pelmatozoan morphology

Most echinoderm elements treated in the present study likely derive from pelmatozoans, and therefore a review of pelmatozoan morphology is needed in order to establish and define different morphotypes as well as for understanding their ecology. Some of the information is, however, applicable also to echinoderms in general.

Pelmatozoans are passive suspension feeders, filtering water in search for nutrients, and are therefore dependent on currents. As for echinoderms in general, the crinoid endoskeleton shows pentamerous symmetry. The endoskeleton is composed of separate calcite ossicles bounded by ligaments. The bulk of the crinoid is constituted by the skeleton, which contains numerous calcite plates. The water-vascular system is composed of a ring canal, from which radial canals spread out. Oxygen is taken up through the body wall and is then transported by the coelomic fluid. The crinoid

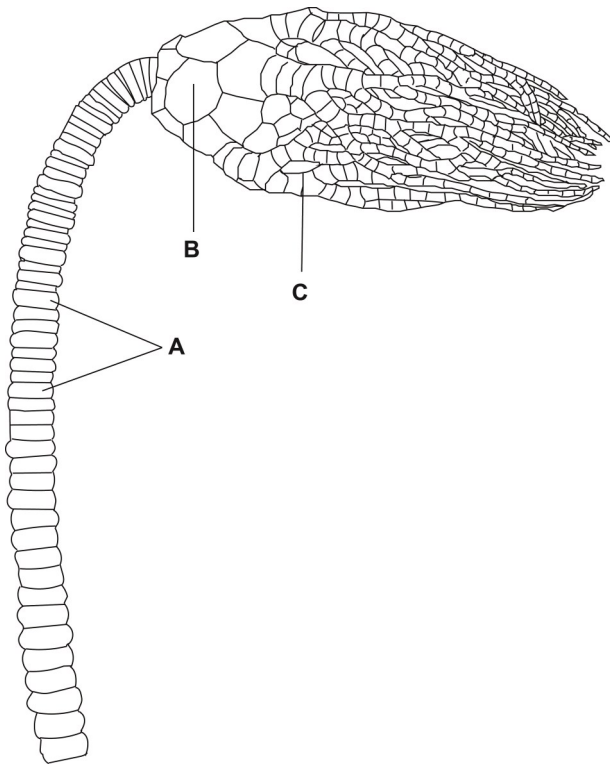


Fig. 4. The basic morphology of a crinoid. A. Columnals constituting the stem. B. Theca composed by several different plates. C. Brachials. Redrawn and modified from Hess et al. (1999).

crown is elevated from the seafloor by a stem, which is attached to the substrate in different ways (Fig. 4). The lower crown is called the calyx and houses the majority of the animal's soft parts, such as the digestive, haemal and sensory system. It is composed of several plates, commonly as interlocking bands of five plates. According to Hess et al. (1999), there are eleven common designs of aboral cups (the bowl-shaped part of the calyx). The arms, or brachials, are attached to the calyx and function as food gatherers, by means of the tube feet, distributing the intercepted particles to the mouth (Fig. 4; Hess et al. 1999).

The function of the stem is to attach the animal to the substrate, and also to elevate the calyx and the food gathering arms into waters where feeding is more efficient due to faster flowing currents, thus allowing the animal to filtrate a larger volume per time unit. Several columnals joined together composes the stem (Fig. 4), penetrated by a central canal that houses the coelom and nervous system. The columnals form just below the calyx, thus generating smaller and more immature ones in the proximal area and larger, more mature, ones in the distal area. The columnals are further divided into nodals, where the brachials are attached, and internodals, lacking brachials. Disarticulated, the columnals can be separated from each other by differences in morphology. Some columnals are equipped with ridges that can hook into each other, thus resisting the forces that otherwise would twist the stem. In

general, forces of tension and shearing are resisted by ligaments (Hess et al. 1999).

The stem is often anchored horizontally in the substrate by protrusions of the stereom. Simpler forms of attachment include cementing onto harder substrates, thus restricting the animal to those substrates during episodes of low sedimentation rates, whereas more recent forms can be attached by outgrowths known as cirri (Hess et al. 1999).

Since crinoids are composed of calcareous plates jointed by soft tissue, they disarticulate very rapidly after death. In order to be completely preserved they need to be buried rapidly in an environment free from burrowing organisms. To avoid re-excavation by currents the environment should also be calm (Donovan 1991). Although they rapidly disarticulate into small fragments, echinoderms often appear to be found nearby where they once lived (Meyer & Meyer 1986; Llewellyn & Messing 1993). Processes resulting in the required rapid burial could for example be turbidites and tempestites (Hess et al. 1999).

In describing the blastozoans, cystoids will be used as a model and especially *Sphaeronites* which according to Paul & Bockelie (1983) share many common features with cystoids in general. *Sphaeronites* also appear in extreme concentrations as macrofossils within the 'Täljsten' interval, literally constituting the bulk of the '*Sphaeronite* beds' (Fig. 2). The cystoid equivalent to the calyx is formed as a capsule and called theca, constituting a protective envelope for the internal organs (Regnéll 1945). The spherical theca is composed by individual plates as a meshwork of calcite, collagen and soft tissue. Like other pelmatozoans, cystoids were epifaunal filter feeders, attached to the substrate. Unlike crinoids, the theca was directly attached to the substrate and not elevated by a stem. *Sphaeronites* are often found in association with rich brachiopod faunas. *Sphaeronites* were diploporan cystoids, diplopores being the main respiratory organ and in life covered by soft tissue, through which oxygen and carbon dioxide diffused between sea water and internal coelomic fluids (Paul & Bockelie 1983).

2 Geological setting

The Hällekis quarry is situated just southwest of the village of Hällekis by the south coast of Lake Vänern, on the northwestern slope of Mount Kinnekulle in the province of Västergötland, Sweden (Fig. 5). At the Hällekis quarry, a section of approximately 40 m of limestone is exposed and it is Dapingian–Darriwilian (Middle Ordovician) in age (Lindskog 2014). The interval of main interest for this study, the 'Täljsten' interval, is located at approximately 14 m above the quarry floor and is easily identified as a horizontally continuous, grey c. 1.5 m thick interruption enclosed in the otherwise rusty red limestone. Stratigraphically, the 'Täljsten' interval belongs to the lower Kunda Baltoscandian Stage (Lindskog et al. 2014).

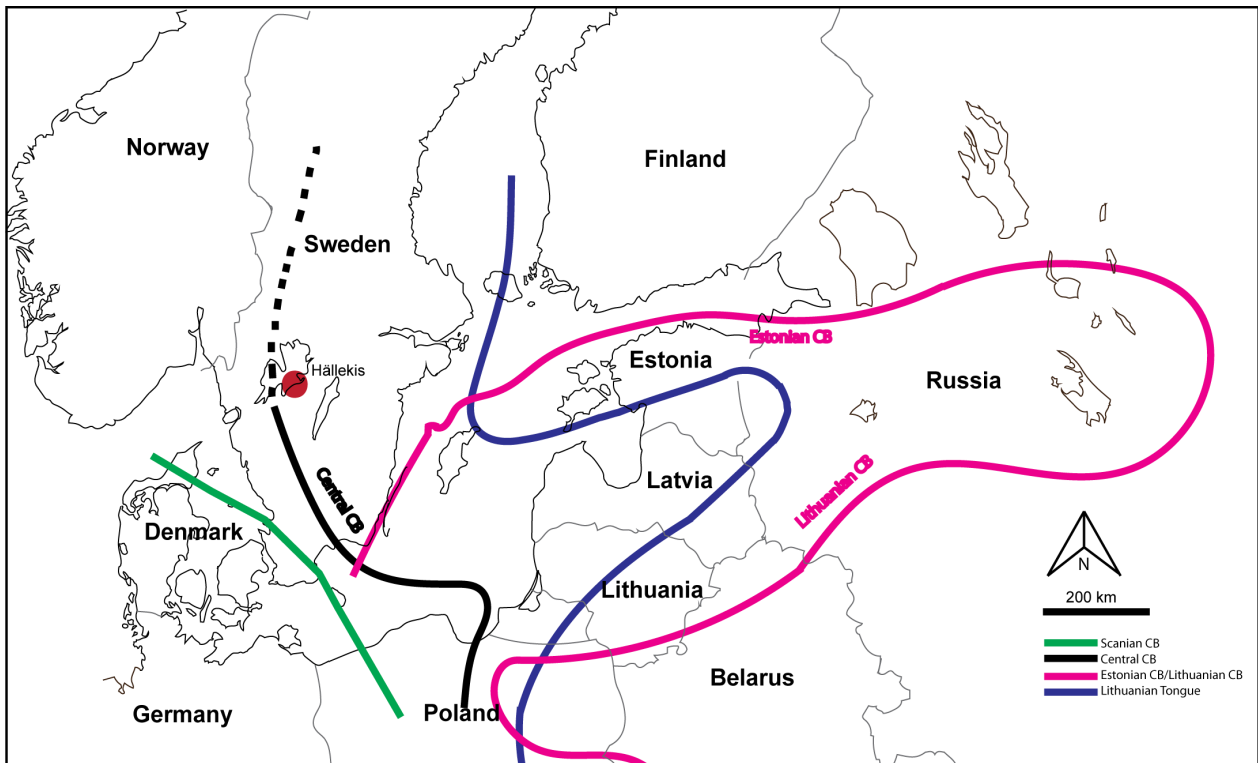


Fig. 5. Map of Baltoscandia showing the position of the sampled location in Hällekis and the boundaries of the confacies belts (CB). Redrawn and modified from Eriksson et al. (2012).

A depth zonation runs from the west-southwest to the east-northeast through the Baltoscandian palaeocontinent. This zonation is termed confacies belts, each with relatively well-defined palaeontological and sedimentological properties (Jaanusson 1973). The distribution of the Central Baltoscandian confacies belt, which the Hällekis limestones belong to, is shown in (Fig. 5). Through the Ordovician, the features of sedimentary deposits from Baltica indicate a transition in water temperature from cooler to warmer, in accordance with the northward movement of Baltica into lower latitudes (Lindström 1971; Jaanusson 1973; Cocks and Torsvik 2005). Deposition is commonly considered to have taken place in a moderately shallow epeiric sea, although some authors have argued for greater depths (see Lindskog 2014). According to calculations performed by Chen & Lindström (1991) for some Orthoceratite Limestone areas, the general depth might have been up to 200–300 m. Based on studies of oncooids and stromatolites, however, Lindskog (2014) concluded that parts of the Hølen Limestone were deposited in shallow settings of a few tens of meters, which were also supported by lithological observations. The ‘Täljsten’ interval appears to record exceptionally shallow conditions, and conodont studies from the ‘Arkeologen’ bed beneath the ‘Täljsten’ indicates an initial regressional phase, continuing throughout the ‘Täljsten’ until the ‘Blåmåkka’ where the regression reached its climax, resulting in mass occurrence of cystoids. Subsequently, the top of the ‘Täljsten’ shows signs of a transgression (Mellgren & Eriksson 2010). Kinnekulle is the type area for the Orthoceratite Li-

mestone, a cool-water carbonate, which at the locality is sub-divided into a lower part called the Lanna Limestone and an upper part, including the ‘Täljsten’ interval, called the Hølen Limestone (Jaanusson 1982b; Tinn & Meidla 2001). The Lanna Limestone corresponds to the Volkhov Baltoscandian Stage and Hølen Limestone to the Kunda Baltoscandian Stage. The joint boundary between the rock units and stages is located c. 2.6 m below the base of the ‘Täljsten’ (Lindskog et al. 2014). According to Lindskog et al. (2014), these boundaries have often been placed at different levels by different authors, and published results are therefore not always easily compared.

The Orthoceratite Limestone is biostratigraphically divided into different biozones based on trilobites and conodonts. The studied succession spans the trilobite zones of *Megistaspis limbata*, *Asaphus expansus* and *Asaphus raniceps* – *Asaphus vicaarius* and the conodont zones of *Baltoniodus norrlandicus*, *Lenodus variabilis*, *Yangtzeplacognathus crassus* and *Eoplacognathus pseudoplanus* (Fig. 6; Zhang 1998; Villumsen et al. 2001; Rasmussen et al. 2007; Mellgren & Eriksson 2010). The transition between the *M. limbata* and *A. expansus* trilobite zones marks the Volkhov–Kunda boundary (Villumsen et al. 2001). The ‘Täljsten’ interval is traditionally divided into eight divisions, from the lower ‘Golvsten’ through ‘Botten’, ‘Gråkartan’, ‘Blymåkka’, ‘Fjällbotten’, ‘Likhall’, ‘Flora’, to the upper ‘Mumma’. The bordering strata are the subjacent ‘Arkeologen’ and the superjacent ‘Rödkartan’ (Fig. 7; Schmitz et al. 2001).

The Orthoceratite Limestone at Hällekis, speci-

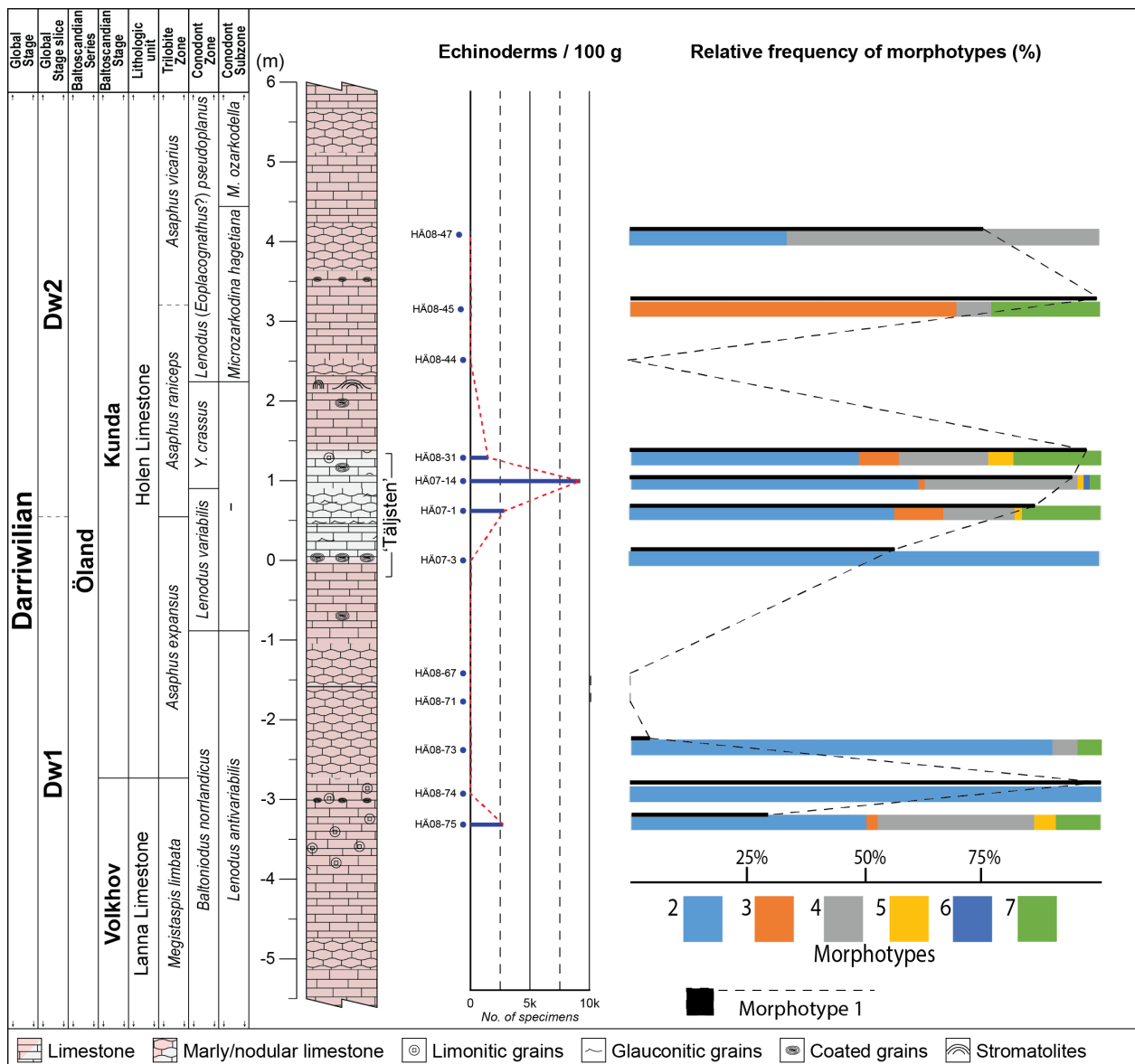


Fig. 6. Sedimentary profile of the studied section at Hällekis and its stratigraphic context. Studied samples, echinoderm grain abundance and relative frequency of abundance among morphotypes 2-7 are plotted. The relative frequency of morphotype 1 is too large to be plotted together with the other morphotypes and is therefore plotted alone (black staples) in percentage of all morphotypes. Actual numbers are found in the text. Based on figure by A. Lindskog.

fically the Lanna and Hølen succession, including the 'Täljsten' interval, is commonly composed of wackestone and packstone (Tinn & Meidla 2001; Eriksson et al. 2012; Lindskog et al. 2014). The limestone is typically very condensed (Tinn et al. 2007), as a result of the very low sedimentation rates, calculated to some 1–9 mm/1000 years (Nielsen 2004). The typical red colour is due to hematite impregnation, indicating oxygenated conditions (Lindström 1963; Jaanusson 1973). The section is typically poor in macrofossils, with some exceptions, one notable being the 'Täljsten'. The main macrofossil groups observable at different levels are cephalopods, trilobites and cystoids (Jaanusson 1982a, b). The lithologic properties of the local Orthoceratite Limestone have been studied in detail by, for example, Lindström (1979),

Eriksson et al. (2012) and Lindskog et al. (2014).

3 Materials and methods

A total of 9 samples from an approximately 7.5 m thick interval at Hällekis, embracing the 'Täljsten', form the basis of this study (Fig. 5). These samples have been analysed in detail with regards to the content of microscopic echinoderms. Each sample initially weighed c. 100 g. The samples were dissolved in buffered acetic acid by A. Lindskog and M.E. Eriksson and the microfossil-yielding sample residues were put at my disposal.

The microscopic echinoderm fossils were studied with a binocular light microscope. The abundance

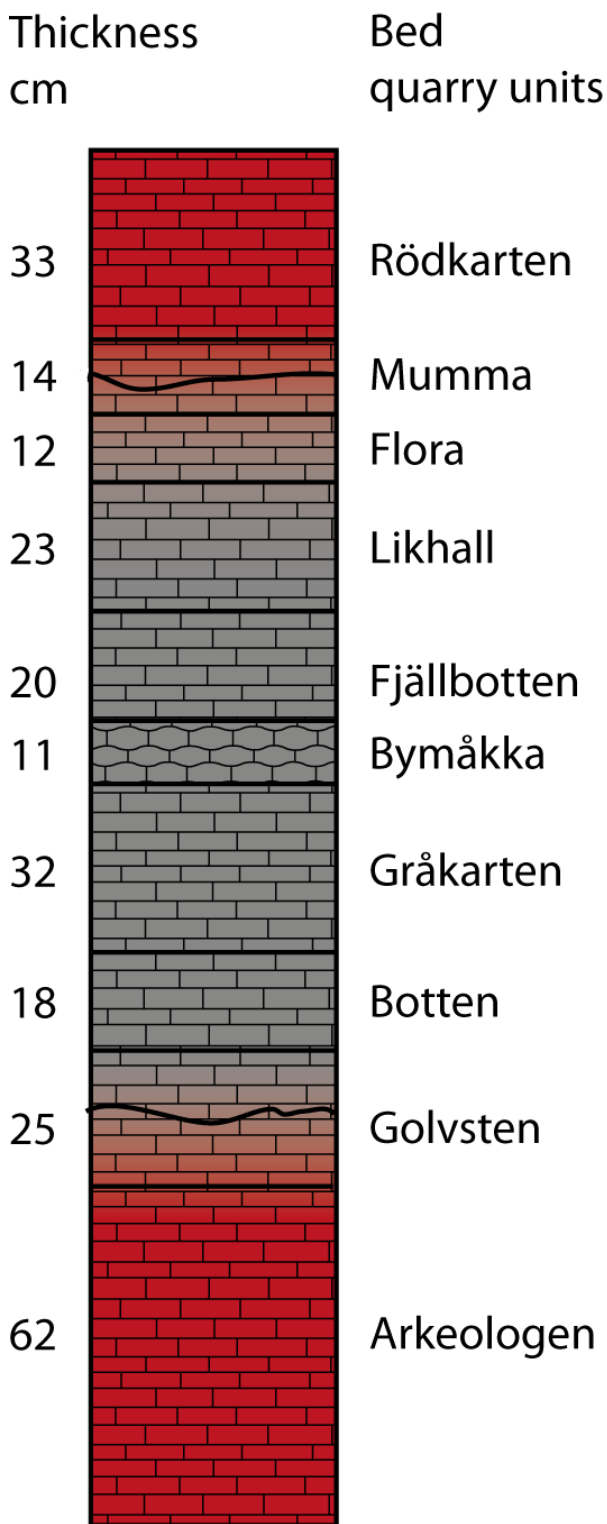


Fig. 7. The traditional division of the 'Täljsten' interval in quarry units and their thickness (cm). Redrawn and modified from Schmitz et al. (2001).

(specimens/100 g of rock) was calculated, and the relative frequency (in percent) of different morphotypes (see below) was determined. All grains identified as deriving from echinoderms were picked with a brush and stored in microfossil slides. Selected specimens, showing the full range of morphological variation,

were photographed in a binocular light microscope fitted with a digital camera. Whereas some well-preserved specimens were studied in closer detail and an effort was made to assign them to certain taxonomic groups (see systematic palaeontology below), most were referred to as different morphotypes.

Seven different morphotypes (Fig. 8) were defined based on the sample materials, and in accordance with the published literature. To be useful, these morphotypes should be relatively easy to distinguish and possible to relate to a certain subphylum or class.

All figured specimens, together with the remaining samples material, are stored at the Department of Geology, Lund University, Sweden.

A short field study was carried out, for photographing and ocular examination of the sampled section.

4 Results

The red parts of the Orthoceratite Limestone is generally poor in microscopic echinoderm fossils, with one exception in the uppermost Lanna Limestone that shows a relatively high abundance. Nevertheless, the abundance is clearly higher within the 'Täljsten' interval compared to the enclosing strata, see Fig. 6. The echinoderm abundance shows a gradual increase, peaks in the middle of the interval, subsequently decreases before entering the red part of the Holen Limestone above the 'Täljsten'.

The diversity of morphotypes referable to any taxonomical level lower than the phylum (all categories except morphotype 1) is also clearly higher in the 'Täljsten' interval than in the underlying strata. This heightened diversity continues high above the 'Täljsten' and follows in general the same pattern as the echinoderm abundance, that is low diversity below the 'Täljsten', increasing diversity in 'Blymåkka' (HÄ07-1) at the base of the 'Täljsten', reaching its maximum in 'Likhall' (HÄ07-14) of the middle-upper 'Täljsten', thereafter decreases and is once again low above the 'Täljsten'. Interestingly, one sample from far below the 'Täljsten' interval (HÄ08-75) shows a peak in absolute abundance, morphotype diversity as well as high relative frequency among the morphotypes 2-7. This sample is from the uppermost Lanna and Holen limestone, and thus close to the Volkhov-Kunda boundary, which is characterised by coarse carbonate textures, indicating low water depth (Fig. 7; see Lindskog et al. 2014). The lithological properties of the samples generally show differences in colour and porosity related to preservation, for example due to impregnation of hematite, limonite, glauconite, chamosite, and phosphate.

The material at hand reveal that the main subphyla represented is Crinozoa, dominated by crinoids and cystoids. Some of the better preserved specimens and/or those with a distinctive morphology could be assigned to different taxa, albeit at a high taxonomic level. These are briefly discussed below.

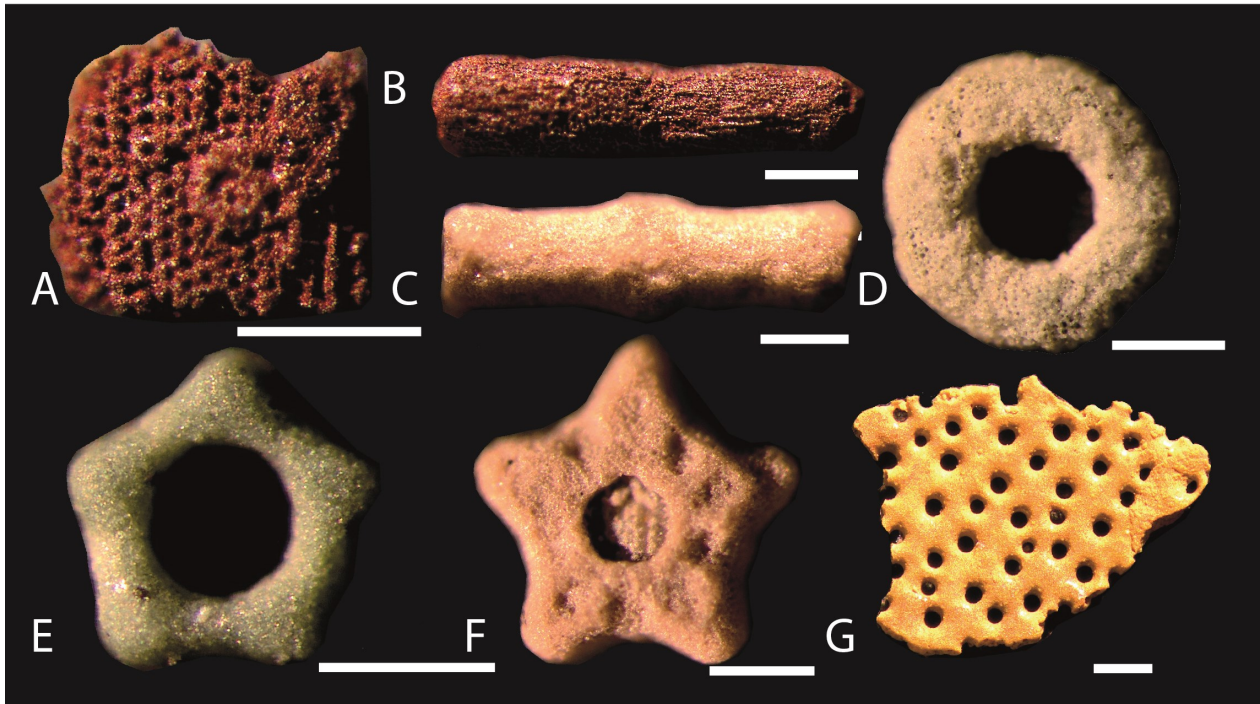


Fig. 8. Photographic plate showing selected specimens representative for each of the distinguished morphotypes. **A.** Morphotype 1 (from sample HÄ08-32). **B.** Morphotype 2 (from sample HÄ08-38). **C.** Morphotype 3 (from sample HÄ07-6). **D.** Morphotype 4 (from sample HÄ07-14). **E.** Morphotype 5 (from sample HÄ07-14). **F.** Morphotype 6 (from sample HÄ07-8). **G.** Morphotype 7 (from sample HÄ08-31). Scalebars are 200 μ m.

4.1 Morphotypes

The characteristics of each morphotype are described below.

4.1.1 Morphotype 1

This category is the dominant morphotype throughout all samples. It is defined by a distinct stereom structure, but without other externally recognisable morphological features (Fig. 8A). Thus, it is not possible to assign the specimens of morphotype 1 to any other taxonomic level than phylum Echinodermata. Though beyond the scope of this study, it might have been possible to further subdivide the specimens included in morphotype 1. The total number of specimens sorted in morphotype 1 is 5560.

4.1.2 Morphotype 2

This is a relatively frequent morphotype, defined by showing a distinct stereom structure, as well as an external cylindrical morphology (Fig. 8B). The origin is ambiguous, but they could represent more distal columnals of small (or juvenile) crinoids, or blastozoan spines (Jones 1956; Hess et al. 1999). The total number of specimens sorted in morphotype 2 is 178.

4.1.3 Morphotype 3

This category shares similarities with the previous morphotype. The external morphology is cylindrical, however, increasing in diameter towards the middle in what is probably best described as a bulb (Fig. 8C).

Specimens of this morphotype could derive from blastozoans as well as crinoids (Jones 1956; Svensson 1999). The total number of specimens sorted in morphotype 3 is 23.

4.1.4 Morphotype 4

This morphotype shows a distinct stereom structure, is cylindrical in shape, preferably but not exclusively with a single central perforation (Fig. 8D). These specimens represent crinoid or blastozoan columnals (Jones 1956; Hess et al. 1999). The total number of specimens sorted in morphotype 4 is 66.

4.1.5 Morphotype 5

This morphotype shows a distinct stereom structure and a polygonal outline with a central circular or quadrangular perforation (Fig. 8E). These columnals probably derive from crinoids or blastozoans (Jones 1956; Hess et al. 1999). The total number of specimens sorted in morphotype 5 is 7.

4.1.6 Morphotype 6

This morphotype is very distinct but rare. The external morphology composes a pentamerous star, with a central perforation (Fig. 8F). They typically resemble a crinoid columnal (Jones 1956; Hess et al. 1999). Total number of specimens sorted in this morphotype is 1.

4.1.7 Morphotype 7

This morphotype is defined as plates with regular, circular perforations, typically more or less aligned (Fig. 8G). They could derive from crinoid radial plates, echinoids or holothurians (Jones 1956; Hess et al. 1999). The total number of specimens sorted in this morphotype is 33.

4.2 Analysed acid-insoluble residues

The nine samples analyzed in closer detail are, in stratigraphically ascending order: HÄ08-75, HÄ08-74, HÄ08-73, HÄ07-3, HÄ07-1, HÄ07-14, HÄ08-31, HÄ08-45, HÄ08-47 (Fig. 6). The characteristics and echinoderm fossils of these are described below. In addition to the above mentioned samples, A. Lindskog provided picking results from three other samples, with no observed echinoderm fragments; HÄ08-71, HÄ08-67, HÄ08-44. These samples derive from conodont samples with an original weight of c. 1 kg. Only samples yielding echinoderms are described below. Some sample residues were so large and rich in echinoderm fragments, that subsamples had to be collected from them. The abundances from those subsamples were then multiplied by the quotient of the weight of the sample and the subsample, before the data was presented below. The subsamples are of HÄ07-1, HÄ08-75, HÄ08-31 and HÄ07-14.

4.2.1 Subsample HÄ08-75 Lanna Limestone

General description: The sample was collected far into the stratigraphically lower red section of the Lanna Limestone, approximately 3.25 m below the base of the 'Täljsten' (Fig. 6). In general, the abundance of echinoderm fragments is very high, as well as the diversity among morphotypes. The specimens are relatively well-preserved and the morphotypes easy to distinguish. Echinoderm fragments are preferentially brownish in colour, probably limonite, or greenish, probably glauconite.

Echinoderm abundance: 2747 specimens/100g

Morphotypes present: 1, 2, 3, 4, 5, 7

Relative frequency of morphotypes is shown in Fig. 6.

4.2.2 Sample HÄ08-74 Lanna Limestone

General description: The sample was collected in the uppermost Lanna Limestone. The abundance in echinoderm fragments is low and preferentially reddish/brownish in colour, probably hematite impregnated.

Echinoderm abundance: 16 specimens/ 100g

Morphotypes present: 1, 2

Relative frequency of morphotypes is shown in Fig. 6.

4.2.3 Sample HÄ08-73 Holen Limestone

General description: The sample was collected in the lowermost red Holen Limestone, approximately 2.25 m below the base of the 'Täljsten' interval. The general colour of the sample is brown to reddish brown. Numerous porous 'grains' occur in the sample residues, making it difficult to discern echinoderm frag-

ments.

Echinoderm abundance: 79 specimens/100g

Morphotypes present: 1, 2, 4, 7

Relative frequency of morphotypes is shown in Fig. 6.

4.2.4 Sample HÄ07-3 Holen Limestone, 'Täljsten', 'Golvsten'

General description: The sample was collected at the base of the 'Täljsten', from the upper 'Golvsten' bed. Grain colour is generally white, red, turquoise, grey and golden with a metallic lustre, the latter probably from pyrite impregnation. Echinoderm fragments are preferentially hematite impregnated. Pyrite abundance is relatively high.

Echinoderm abundance: 55 specimens/100g

Morphotypes present: 1, 2

Relative frequency of morphotypes is shown in Fig. 6.

4.2.5 Subsample HÄ07-1 Holen Limestone, 'Täljsten', 'Blymåkka'

General description: The sample was collected from the 'Blymåkka' unit at the middle of the 'Täljsten'. The colour varies from grey to green (glauconite). Grain residues after acid digestion and picking of other fossil groups are large. The abundance of echinoderm fragments is high. Approximately half of the sample was analysed. A needle-shaped grain was found, with similarities to those shown by some holothurian sclerites.

Echinoderm abundance: 2842 specimens/100g

Morphotypes present: 1, 2, 3, 4, 5, 7

Relative frequency of morphotypes is shown in Fig. 6.

4.2.6 Subsample HÄ07-14 Holen Limestone, 'Täljsten', 'Likhall'

General description: The sample was collected in the middle 'Likhall' unit, in the upper part of the 'Täljsten'. The colour is white (phosphatized) and green (from glauconite) with moderate porosity. The preservation of echinoderm fragments is mainly glauconitic.

Echinoderm abundance: 9223 specimens/100g

Morphotypes present: 1, 2, 3, 4, 5, 6, 7

Relative frequency of morphotypes is shown in Fig. 6.

4.2.7 Subsample HÄ08-31 Holen Limestone, 'Täljsten', 'Mumma'

General description: The sample was collected in the 'Mumma' unit, at the top of the 'Täljsten'. Grain colour is distinctively yellow (limonite), brown (chamosite/phosphate) and green (glauconite/chamosite). The abundance of echinoderm fragments is high, as is the relative frequency of different morphotypes. A wheel-shaped grain was found, with similarities to those shown by some holothurian sclerites, see Fig. 9AB. Approximately half of the sample was analysed.

Echinoderm abundance: 1488 specimens/100g
Morphotypes present: 1, 2, 3, 4, 5, 7
Relative frequency of morphotypes is shown in Fig. 6

4.2.8 Sample HÄ08-45 Holen Limestone

General description: The sample was collected in the upper red Holen Limestone, at some 3 m above the base of the 'Täljsten'. The grain colour is light brown to reddish brown. Pyrite grains occur. Numerous porous 'grains' occur in the sample residues, making it difficult to discern echinoderm fragments.

Echinoderm abundance: 48 specimens/100g
Morphotypes present: 1, 3, 4, 7

Relative frequency of morphotypes is shown in Fig. 6.

4.2.9 Sample HÄ08-47 Holen Limestone,

General description: The sample was collected far into the upper red part of Holen Limestone. The colour is red, probably from hematite.

Echinoderm abundance: 25 specimens/100g
Morphotypes present: 1, 2, 4

Relative frequency of morphotypes is shown in Fig. 6.

4.3 Systematic palaeontology

Phylum Echinodermata

4.3.1. Subphylum Crinozoa—Class Crinoidea

Pentagonocyclicus

Fig 9A

Remarks.- Limonitic well-preserved disc-shaped specimen with pentamerous star-shaped lumen. Similarities to those crinoids identified by Svensson (1999) as *Pentagonocyclicus*. It relates to morphotype 4.

Vialovicystis sp.

Figs 9B-D

Remarks.- Phosphatized and/or glauconitic specimens, moderate to well-preserved. Similar to those specimens assigned to *Vialocystis* sp. by Pisera (1994). It relates to morphotype 2 or 3.

Crenatocrinus biplex

Fig 9E

Remarks.- Phosphatic and well-preserved specimen similar to one assigned to a *Crenatocrinus biplex* columnal by Pisera (1994). Areola and lumen are limited and gives place to a relatively large crenula. It relates to morphotype 4.

Baltocrinus sp.

Fig 9F

Remarks.- Phosphatic and well-preserved pentameric columnal similar to *Baltocrinus* sp., as described by Svensson (1999). It relates to morphotype 5.

Crinoid radial plate

Fig 9G

Remarks.- Phosphatic, moderately well-preserved specimen, possibly a crinoid radial plate (for comparison, see Jones 1956). It relates to morphotype 7.

Crinoid columnals

Figs 9H, I, L-N

Remarks.- Specimens range from phosphatic, glauconitic, limonitic and chamositic and from poorly to very well-preserved. The well-preserved phosphatic quadrangular specimen with a central perforation (Fig. 9H) is similar to the quadrangular crinoid columnals described by Svensson (1999). It relates to morphotype 5. The well-preserved specimen shown in Fig. 9I is a putative crinoid columnal (cf. Jones 1956; Hess et al. 1999) and similar to the holomeric pentagonal column described by Svensson (1999). It relates to morphotype 6. Specimens shown in Figs. 9L-N are pentamerous crinoid columnals (see Pisera 1994; Svensson 1999), sometimes with a coarse stereom (Fig. 9M) (cf. Hess et al. 1999) and relates to morphotype 5 or possibly 6.

Distal columnal or brachial facet

Fig 9J

Remarks.- Phosphatic, moderately well-preserved specimen, conceivably a distal crinoid columnal or brachial facet. It relates to morphotype 2.

Crinoid brachial

Fig 9K

Remarks.- Well-preserved, glauconitic/chamositic specimen, conceivably a crinoid brachial (cf. Hess et al. 1999). It relates to morphotype 4.

4.3.2. Subphylum Crinozoa—Class Cystoidea

Glyptocystoid columnals

Figs 9O-R

Remarks.- Specimens range from phosphatic, glauconitic, hematitic and chamositic and from moderately to very well-preserved. All are similar to glyptocystoid columnals as described by Pisera (1994) and Svensson (1999). The well-preserved phosphatic specimen (Fig. 9O) is similar to that by Pisera (1994) classified as a distal columnal. It relates to morphotype 3. The moderately well-preserved specimen (Fig. 9P) has an areola which is glauconitic, whereas the lumen is chamositic/phosphatic. It relates to morphotype 4. The phosphatic ring-like columnal (Fig. 9Q) is similar to specimens that both Pisera (1994) and Svensson (1999) described as proximal columnals. It relates to morphotype 4. Specimens shown in Figs. 9R, S are moderately well-preserved hematitic columnals and relates to morphotype 2, 5 or possibly 6. The moderately preserved hematitic specimen (Fig. 9R) resembles a glyptocystoid columnal as described by Svensson (1999). It relates to morphotype 5 or 6, respectively 2.

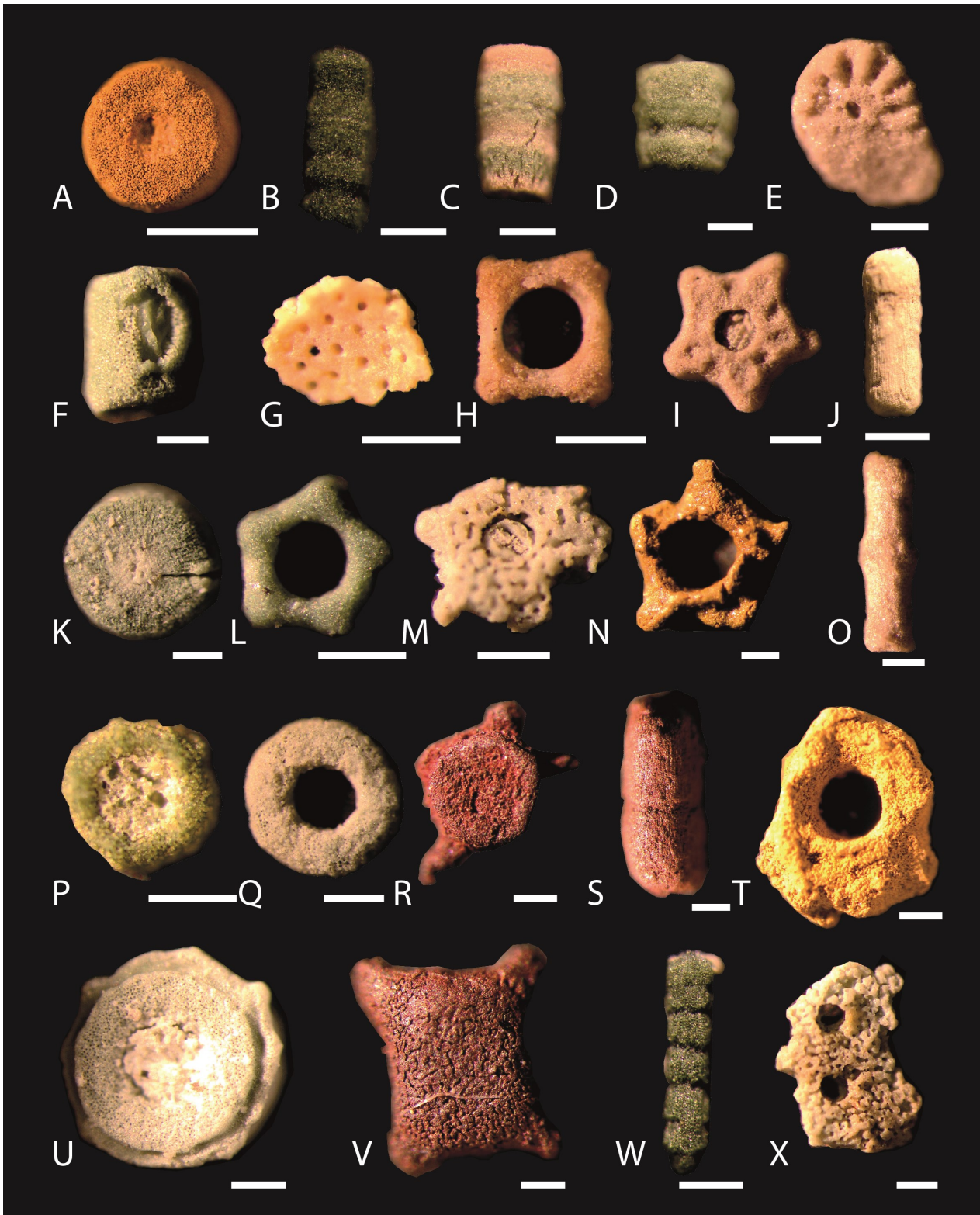


Fig. 9. Photographic plate showing selected echinoderm specimens. A. *Pentagonocyclicus* B. *Vialovicystis* sp. C. *Vialovicystis* sp. D. *Vialovicystis* sp. E. *Crenatocrinus biplex* F. *Baltocrinus* sp. G. Crinoid radial plate H, I. Crinoid columnals J. Distal columnal or brachial facet K. Crinoid brachial L. Crinoid columnal M. Crinoid column N. Crinoid columnal O. Glyptocystoid columnal P. Glyptocystoid columnal Q. Glyptocystoid columnal R-S Glyptocystoid columnals T. *Schizocrinus cuckarensis* or Glyptocystoid U. *Schizocrinus cuckarensis* or rhombiferan column V. *Schizocrinus cuckarensis* or rhombiferan column W. Blastoid column. X. Echinocystitid. A, H are from HÄ08-75. B, C, E, G, O are from HÄ07-6. D, I are from HÄ07-8. F, J-M, Q, U, W, X are from HÄ07-14. N, T are from HÄ08-31. P is from HÄ07-1. R is from HÄ08-33. S, V are from HÄ08-38. B, C, D, J, S, W relates to morphotype 2. B, C, D, O, W, S relates to morphotype 3. A, E, K, P, Q, T, U, V relates to morphotype 4. F, H, L, M, N, R relates to morphotype 5. I, N, R relates to morphotype 6. G, X relates to morphotype 7. Scalebars are 200 μ m.

4.3.3. Subphylum Crinozoa—Class Crinoidea or Cystoidea

Schizocrinus cuckarensis or glyptocystoid
Fig 8T

Remarks.- Glauconitic/chamositic and well-preserved. Similar specimen described as a barrel shaped spinose columnal and referred to *Schizocrinus cuckarensis* by Pisera (1994). Another similar specimen is by Svensson (1999) described as a glyptocystoid columnal. It relates to morphotype 4.

Schizocrinus cuckarensis or rhombiferan columnal
Figs 9U, V

Remarks.- The well-preserved phosphatic and the poorly preserved hematitic specimens (Figs 8U, V) resembles those by Pisera (1994) described as *Schizocrinus cuckarensis* as well as by Svensson (1999) described as a rhombiferan columnals. They relate to morphotype 4.

4.3.4. Subphylum Blastozoa—Class Blastoidea

Blastoid columnal
Fig 9W

Remarks.- Glauconitic/chamositic, well-preserved blastoid columnal (cf. Ubaghs 1967). It relates to morphotype 2 or 3.

4.3.5. Subphylum Echinozoa—Class Echinoidea

Subphylum Echinozoa
Class Echinoidea

Echinocystitid
Fig 9X

Remarks.- Moderately well-preserved phosphatic specimen similar to what Pisera (1994) described as an echinocystitid ambulacral plate. It relates to morphotype 7.

4.3.6. Subphylum Echinoidea—Class Holothuroidea

Holothurian seiv plates?
Figs 10A-B

Remarks.- Limonitic and moderately well-preserved plates, with some features similar to those of holothurians (cf. Sprinkle & Kier 1987). They relate to morphotype 7.

4.3.7. Unidentified columnals

Figs 10C-I, O-U

Remarks.- Specimens range from phosphatic, glauconitic, hematitic, limonitic and chamositic and from

poorly to well-preserved. The well-preserved hematitic pentamerous specimens, one with a flat rectangular perforation (Fig. 10C) and one with frayed edges (Fig 10D) and another phosphatic moderately well-preserved (Fig. 10I) relate to morphotype 5. The poorly preserved hematitic and frayed limonitic disc-shaped columnals (Figs 10E-F) relate to morphotype 4. The glauconitic, moderately and well-preserved specimens (Figs 10G-H) probably represents pelmatozoan distal columnals. They relate to morphotype 2. The moderately well-preserved limonitic specimen (Fig. 10O) has a six-fold symmetry and relates to morphotype 5. Another well-preserved limonitic specimen (Fig. 10P) has a quadrangular perforation and relates to morphotype 4. The poorly preserved limonitic specimen (Fig. 10Q) has a pentamerous symmetry and relates to morphotype 5. The moderately well-preserved limonitic specimen (Fig. 10R) has a flat rectangular perforation. It relates to morphotype 5. The poorly and moderately well-preserved, limonitic specimens (Figs 10S, T) relates to morphotype 4. The poorly preserved phosphatic specimen (Fig. 10U) has pentamerous symmetry and frayed edges. It relates to morphotype 5.

4.3.8. Other specimens

Pinnular
Fig 10J

Remarks.- Glauconitic/chamositic, relatively well-preserved specimen, similar to that by Pisera (1994) described as a pinnular. It relates to morphotype 1.

Thecal plates
Figs 10K-N

Remarks.- The phosphatic and moderately well-preserved specimens (Figs 10K-M) are perhaps fragments of thecal plates with ambulacral groove (cf. Jones 1956; Ubachs 1967). They relate to morphotype 7. The well-preserved limonitic specimen with four-fold symmetry (Fig. 10N) is probably a thecal plate (cf. Jones 1956; Ubachs 1967). It relates to morphotype 5.

Specimen with four-fold symmetry
Fig 10V

Remarks.- 'Pillow'-shaped well-preserved hematitic specimen with four-fold symmetry and coarse stereom. It relates to morphotype 5.

5 Discussion

The results of this study clearly show that the abundance of microechinoderms is considerably higher in the 'Täljsten' interval than in the enclosing strata (Fig. 6). The actual numbers should, however, not be confused with the number of once living echinoderm individuals, as each individual can result in numerous fragments.

Within the relatively diverse sample in the lower Lanna Limestone (HÄ08-75), morphotypes 2, 4 and 7

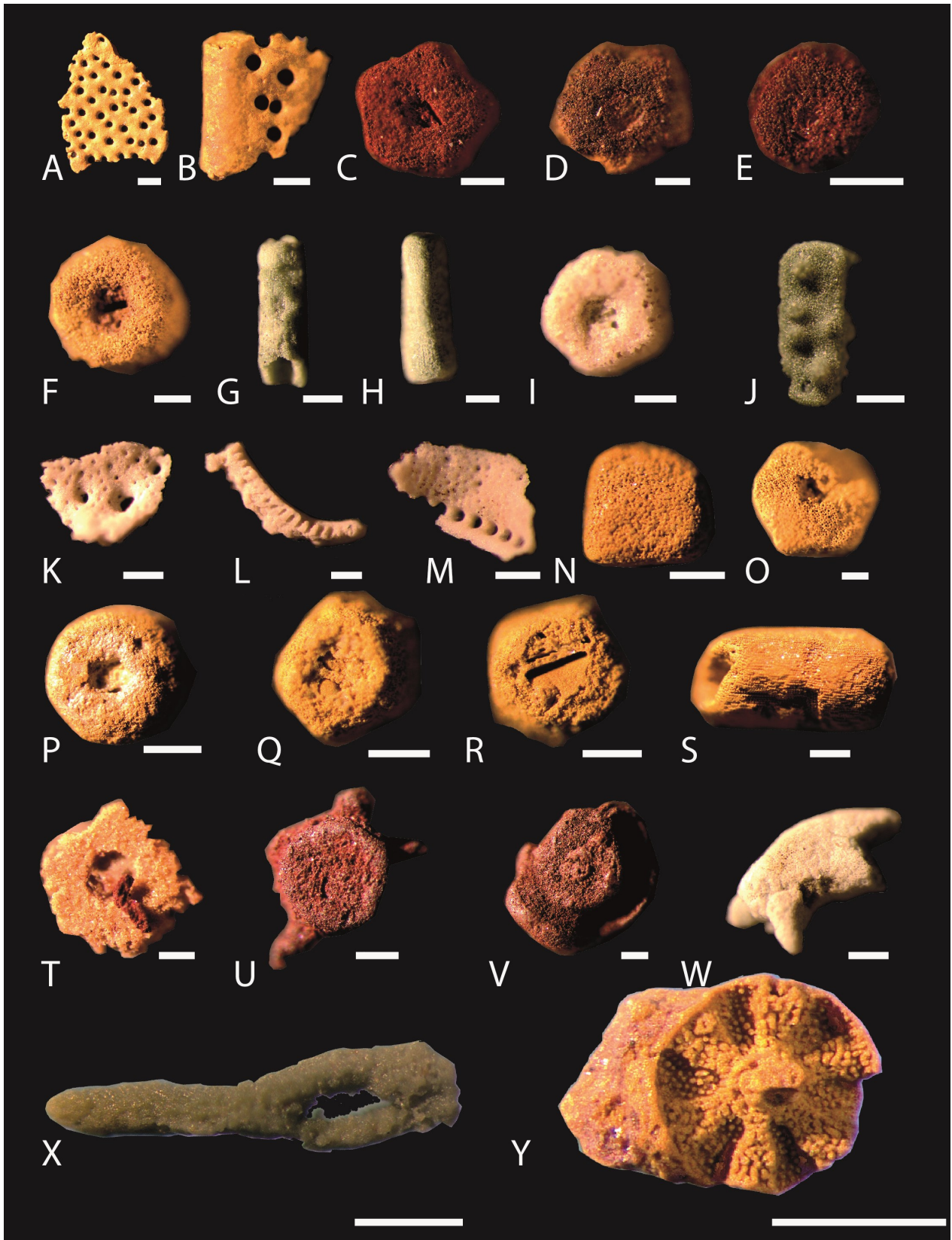


Fig. 2. A, B. Holothurian siev plates? C-I. Pentamerous columnals J. Pinnular K-M. Thecal plate with ambulacral groove N. Thecal plate O-U. Pentamerous columnals V. Specimen with four-fold symmetry W. X. Holothurian? Y. Holothurian? A, B, N, Y are from HÄ08-31. C-F are from HÄ08-75. G, H are from HÄ07-8. I, X are from HÄ07-1. J is from HÄ07-11. K-M, W are from HÄ07-14. T, U are from HÄ08-33. V is from HÄ08-38. J, V relate to morphotype 1. G, H relate to morphotype 2. E, F, P, S, T relate to morphotype 4. C, D, I, N, O, Q, R, U, V relate to morphotype 5. A, B, K, L, M relate morphotype 7. Scalebars are 200 μ m.

dominate. These are thought to represent crinoids and/or blastoids, indicating some extrinsic change, for instance the development of hardgrounds, fluctuations in sea level or changes in redox conditions. In the subsequent samples HÄ08-74 and HÄ08-73 morphotype 2 dominate, indicating the presence of crinoids and blastozoans, although accompanied by an overall low abundance of echinoderms. The relative frequency of morphotype 1 is very high in HÄ08-74 and drops drastically in HÄ08-73, indicating increased preservation. Upwards in stratigraphy an interval barren of echinoderms (HÄ08-71, HÄ08-67) follows. The next sample (HÄ07-3) is from the 'Golvsten' in the lowermost 'Täljsten' which shows an increase in abundance. It is largely dominated by morphotype 2, indicating the occurrence of crinoids and blastozoans. The observed changes are likely linked to the regression beginning in the lower 'Täljsten' interval as well as the extensive formation of hardgrounds throughout the section. The increased abundance of echinoderms in the 'Golvsten' was also observed by Eriksson et al. (2012) from thin-section studies, whereas other taxa declined. In this same sample pyrite grains are first noted, indicating less oxygenated conditions, which also is supported by the shift in colour from red to grey (Eriksson et al. 2012). In the 'Blymåkka' (HÄ07-1) the increase in morphotype diversity continues, with high relative frequency among all morphotypes except for morphotype 6. The abundant morphotypes indicates the presence of crinoids, blastozoans, and possibly holothurians (cf. Gutschick 1954). This is also the sample in which the different morphotypes are most equally represented. The maximum echinoderm abundance as well as morphotype diversity (with morphotypes present) is reached in the 'Likhall' (HÄ07-14) in the upper 'Täljsten' interval. This same bed also shows a very high abundance of echinoderms in thin sections, and at the macroscopic scale cystoids are often badly damaged, implying that many echinoderm fragments derive from cystoids (Eriksson et al. 2012; A. Lindskog, pers. comm., 2014). The impaired preservation at the macroscopic level is supported by the high relative frequency of morphotype 1, indicating poor preservation. However, most identified specimens probably derive from crinoids. The high abundance probably reflects the lowest water depths during the regression. A decrease in abundance throughout the 'Mumma' (HÄ08-31) in the upper 'Täljsten' to HÄ08-44 above the 'Täljsten', where no echinoderms were present, is probably a response to the transgression initiated in the 'Flora' and 'Mumma' of the upper 'Täljsten' interval (Eriksson et al. 2012). Above sample HÄ08-44, an increase is once again apparent throughout HÄ08-45 and HÄ08-47, resulting in a relatively low abundance but a relatively high morphotype diversity.

Relating the morphotype most abundant (morphotype 1) to specific taxa is beyond the scope of this study, and it would be difficult or even impossible in most cases. However, it is useful as the relation

between morphotype 1 and the other morphotypes is indicative on the state of preservation, as morphotype 1 relates to damaged echinoderm fragments with no distinguishable diagnostic features. The other morphotypes that are relatively abundant within the 'Täljsten' can be referred to pelmatozoans, e.g. crinoids and blastoids. During the Ordovician, these classes were living in relatively shallow water settings compared to crinoids of today, which also inhabit the deeper ocean floors to depths of c. 9000 m (Hess et al. 1999; Oji et al. 2009). In the Baltoscandian palaeobasin, echinoderm abundance increased from west to east, as the water depth decreased, suggesting that the echinoderm fauna preferred shallower water depths (see, e.g., Ölgun 1987). Crinoid diversity was also found to be higher at shallow, inner-shelf settings by Guensberg & Sprinkle (1995), from a similar Ordovician locality. Morphotype diversity (Fig. 6.) increases within the 'Täljsten', decreasing afterwards but remains higher than in the pre-'Täljsten' strata, because of persisting relatively shallow water-depths (Lindskog 2014; Lindskog et al. 2014). The loss in echinoderm abundance above the 'Täljsten' is probably due to less favourable conditions for fossil preservation (cf. Eriksson et al. 2012).

Crinoid and cystoid microechinoderms are abundant throughout the whole section. Not surprisingly is the peak of crinoids reached within 'Likhall' (HÄ07-14), which is in accordance with the peak in absolute abundance and morphotype diversity. Cystoids do not really show any peak, but are still found in most samples. The results indicate that crinoids were more abundant than cystoids, which is in sharp contrast to the macroscopic fossil record.

The unusually common development of hardgrounds during the 'Täljsten' interval probably contributed to the increase seen in echinoderms, promoting especially pelmatozoans, which at the time lacked holdfast devices and required hard substrates or harder objects like skeletal debris to attach to. Pelmatozoans could therefore inhabit the shallow environments during the formation of the 'Täljsten' interval (cf. Lefebvre et al. 2013).

The increase in diversity throughout the 'Täljsten' interval could to some extent reflect the successively narrower oceans facilitating faunal exchange when Baltica successively approached other palaeocontinents, such as Avalonia. New groups could be introduced to the province and when the environmental factors were favourable, those could settle. In a wider context the diversification could then be part of the Great Ordovician Biodiversification Event, driven by several factors probably in several pulses, throughout a relatively long period of time (Servais et al. 2009; Lefebvre et al. 2013).

As proposed by various authors (e.g. Jaanusson 1982a, b) the grey colour of the 'Täljsten' interval most likely represents reducing conditions, compared to its enclosing red hematite impregnated strata, indicating oxygenated conditions. Eriksson et al. (2012)

concluded that the mass-occurrence of diploporite cystoids also supports a reducing environment, due to their pore structure, which probably is a response to lowered oxygen-levels.

The respiration of echinoderms mainly functions by oxygen diffusion through the body walls. The oxygen demand is proportional to thecal volume, increasing by size and for echinoderms with a radius above 3 mm, diffusion has to be complemented by respiratory surfaces (Paul 1977). The relatively large size (c. 1–4 cm) of the highly abundant macroscopic cystoids throughout the ‘Täljsten’ could thus also be a response to oxygenated conditions, as the oxygen demand increases by size. Although Paul & Bockelie (1983) noted that the ‘*Sphaeronites* beds’ show similarities to lag deposits, that is probably not the case, as Paul & Bockelie (1983) also noted that many cystoids had geopetal infills as well as that younger cystoids attached to older, suggesting that the cystoids were not transported from their habitat. However, the general size of the cystoids increases within the ‘Täljsten’ interval according to (Eriksson et al. 2012), which could reflect increasingly higher oxygen levels as the water became shallower and the higher energy could oxygenate the water. Curiously, specimens in the ‘Likhall’ bed, where the echinoderm fauna peaks in abundance, tend to be relatively small (A. Lindskog, pers. comm., 2014). Most identified pelmatozoans at the microscopic level from ‘Likhall’ were probably crinoids. The exception from the cystoid size trend in the ‘Täljsten’ could indicate that the cystoid fauna was partly outcompeted by crinoids and that cystoids were not allowed to grow as large as before. Crinoids lack respiratory organs and have a high oxygen demand. Therefore the increase of crinoids may reflect an increase in oxygen levels (cf. Hess et al. 1999).

According to Eriksson et al. (2012), the fossil preservation is better within the ‘Täljsten’ interval than in enclosing strata. The echinoderm abundance is in large parts of the ‘Täljsten’ interval several times higher than in other parts of the studied strata. At the peak in ‘Likhall’, abundance is hundreds of times higher than in surrounding beds. This extraordinary abundance is probably, but not only, a question of preservation. This is supported by the fact that different taxa show peaks in different sections, as well as that the echinoderm abundance also peaks in ‘Likhall’ in thin sections (A. Lindskog, pers. comm., 2014).

The needle-shaped grain found in HÄ07-1 (Fig. 10X) and the wheel-shaped grain found in HÄ08-31 (Fig. 10Y), both share similarities with those of holothurian sclerites. For instance, the symmetry of the ‘wheel’ is not pentameral, a detail common in some holothurians (see Sprinkle & Kier 1986). According to Reich (2010), the oldest unequivocal holothurians are from the Middle Darriwilian, Kunda Baltoscandian stage, early Llanvirnian (c. 464 Ma), and were found in a glacial erratic boulder in northern Germany, originating in the Orthoceratite Limestone of Sweden. The holothurian sclerites referred to by Reich (2010) are

from within the *Eoplacognathus suecicus* conodont zone, whereas the ‘Täljsten’ interval is within the stratigraphically lower *Lenodus variabilis* to *Yangtzeplacognathus crassus* conodont zones (Mellgren & Eriksson 2010). Thus, if the herein described specimens represent holothurians, they would be the oldest ones known from the geological record. However, additional material and detailed studies are needed to fully resolve this.

6 Conclusions

The ‘Täljsten’ and immediately enclosing strata yield a diverse and abundant fauna of microscopic echinoderms. The microfossils are generally preserved as hematite, limonite, glauconite, chamosite and phosphate. Numerous specimens are well-preserved. The distributional pattern of echinoderms throughout the ‘Täljsten’ interval and its enclosing strata undoubtedly reflects a period of dramatic environmental changes, and thus fits well into the results reported by several authors.

From a very low abundance prior to the ‘Täljsten’ interval, the pelmatozoan-dominated echinoderm fauna increases dramatically in abundance as well as diversity throughout the succession, likely reflecting a drop in sea level (regression). The peak in echinoderms is reached in the ‘Likhall’ of the upper ‘Täljsten’, which probably coincides with the maximum regression. Thereafter, echinoderm abundance decreases in conjunction with putative transgression through the upper ‘Täljsten’.

The microscopic pelmatozoan fauna appear to be dominated by crinoids in contrast to the cystoid dominated macroscopic fauna.

As it seems like the abundance and diversity of microechinoderms follows the changes in water-depth throughout the regression-transgression event, these fossils can be used as a proxy for relative sea-level, at least throughout the Volkhov–Kunda Baltoscandian stages in the Darriwilian of the Middle Ordovician. After a total absence in the beds immediately above the ‘Täljsten’ interval, the echinoderm fauna partly recovers, reaching a higher diversity compared to pre-‘Täljsten’ strata, suggesting that sea levels were still relatively low.

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