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ÅRSBOK 76 NR 5

YNGVE GRAHN

CHITINOZOOPHORAN
PALAEOECOLOGY IN THE
ORDOVICIAN OF ÖLAND



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ABSTRACT

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A special study has been made across the Arenig-Llanvirn boundary at Hälludden, northern Öland, as part of an investigation of chitinozoophoran palaeoecology in the Ordovician of Öland. Chitinozoophoran ecology has been analysed with regard to 1, the general palaeogeographical conditions in the area, 2, co-occurrence with large macrobenthos and, secondarily, small macrobenthos and planktic organisms, 3, affinity to different sediments reflecting different water energy levels and to some extent depth. The chitinozoophorans were either marine benthic metazoans that attached their eggs and egg capsules to firm objects, or marine metazoans that were holoplanktic or merely planktic during the spawning season and which dispersed their eggs and egg capsules unattached in the water. The propagation bodies (so-called chitinozoans) occur commonly in shallow water limestone facies, but very high water energy seems to have been unfavourable to most of them.

INTRODUCTION

This study is the third and last in a series of papers on Ordovician Chitinozoa from Öland. It is an attempt to interpret the palaeoecology of chitinozoophorans (*sensu* Grahn 1981b:30). There are different opinions on the systematic affinity of Chitinozoa, but it is generally believed that they are eggs and egg capsules of marine metazoans for which the general term chitinozoophorans has been introduced (cf. Grahn & Afzelius 1980).

The taxonomy and biostratigraphy of the Öland Chitinozoa have been described earlier (Grahn 1980, 1981a). This paper includes a special study across the Arenig-Llanvirn boundary in the Hälludden section (cf. Grahn 1980:10–12) as part of a project initiated by the CIMP Subcommission on Chitinozoa.

The Ordovician bedrock of Öland has a thickness of about 44 m. The early Tremadocian beds consist of alum shale and glauconitic argillites, while late Tremadocian and younger beds are developed as limestones. The Ordovician sea-floor of the Öland area was extraordinarily flat and had a very gentle slope from the shore of a land area in an advanced state of peneplanation, and consequently with very low relief (Jaanusson 1973:19). There are no traces of calcium carbonate ooids in the Öland sequence, and these sediments probably accumulated in a sea with a temperature below that at which aragonite can be precipitated (Jaanusson 1973:14). It has been suggested that the Baltoscandian epicontinental sea was situated in a temperate climatic zone during most of Ordovician time (Troedsson 1928; Spjeldnaes 1961; Jaanusson 1973). The carbonate mud was produced by particle-size reduction and disintegration of skeletal material, and possibly also by non-calcareous algae (Jaanusson 1973:15). The predominance of carbonate sedimentation is probably due to very low supply to terrigenous material.

THE HÄLLUDDEN SECTION

The Hälludden section (Figs. 1, 3) is a well-known locality in the early Ordovician sequence of Sweden (cf. Grahn 1980:10–12). The section comprises beds from the *Megistaspis simon* Zone (Upper "Limbata") to the lower part of the *Asaphus raniceps* Zone (Lower Valaste). (See Fig. 2.) The cliff section was sampled for fossils both qualitatively and quantitatively in the course of field work 1948–1950 led by Harry Mutvei. This paper is based on the chitinozoans which I extracted from a series of limestone samples collected in that work. Previous contributions to "Project Hälludden" are Jaanusson (1957) and Skevington (1963, 1965a, 1965b).

LITHOLOGIES

The lithologies in the Hälludden section are very similar to equivalent strata in Bödahamnborrningen 1 (Jaanusson 1955, pers. comm. 1981 and Grahn 1980:7–8, Fig. 4). In the description of the section the thickness of beds is given in cm.

VALASTE (Zone of *Asaphus raniceps*)

- 127+ Mostly sparitic calcarenites, light-grey and thin-bedded (2–4 cm). The limestone is interbedded with thin marl layers, and has a moderate content of glauconite. The lowermost 20–30 cm consist of micritic calcarenites.

Discontinuity surface.

Dark-coloured, smooth and with abundant organic borings.

HUNDERUM (Zone of *Asaphus expansus*) 218

- 212 Predominantly micritic calcarenites, grey to greenish-grey and thin-bedded (2–4 cm). The limestone is interbedded with thin marl layers, and has an abundant to moderate content of glauconite. There are two thin discontinuity surfaces, 10 and 17 cm below the top of the unit, respectively.

- 6 Oolitic limestone.

Thin-layered limestone with elliptical limonitic ooids.

LANGEVOJA (Zone of *Asaphus lepidurus*) 216

- 216 Predominantly sparitic calcarenites, grey and thin-bedded (2–5 cm). The limestone is interbedded with thin marl layers, and has a moderate content of glauconite.

"LIMBATA" (Zone of *Megistaspis simon*) 99+

- 81 Micritic calcarenites, pale brownish-grey and thin-bedded (2–5 cm). The limestone is interbedded with thin marl layers, and has a moderate content of glauconite.
- 18+ Calcarenitic calcilutites, reddish-brown and delimited upwards by a discontinuity surface enriched in haematite (the "Blood Layer"; cf. Bohlin 1949:532–533).

FOSSILS

The macrofossils of the Hälludden section are mainly benthic. Trilobites and orthocone nautiloids are the most common representatives of the large (>0.5 cm) shelly fossils in the lower part of the section, but at the end of Langevoja times the macrobenthos became more diverse, and reached maximum diversity during late Hunderum times (Fig. 3). Both soft- and hard-bottom forms occur in the shelly fauna. The fossils will be briefly surveyed in systematic order.

PLANTS – The presence of algal grazers (e.g., gastropods) and algal borings (Jaanusson, pers. comm. 1981) in shell fragments indicates that algae formed an important component of the bottom communities. Green, blue-green and red algae have been mentioned as possible borers. These algae are limited to depths generally less than 50 m (Milliman 1974:254). They are also able to form algal mats (Bathurst 1971:125).

Receptaculitids are generally considered as ancient Dasycladales (cf. Gould & Katz 1975:5–6). Recent dasycladaceans are restricted to warm waters at depths generally less than 30 m and with a maximum abundance at about 3–5 m. Most species grow on soft bottoms in protected lagoons (Flügel 1978:265). Nitecki (1972:306) reported Ordovician receptaculitids from northwest Africa. This suggests that receptaculitids might occur also in cold waters, since the South Pole was located in that area during late Ordovician (Beuf *et al.* 1971).

PROTOZOA – Two foraminiferan species, *Archaeochitinoso clausa* and *Arenosiphon minima*, which belong to the families Allogromiidae and Textulariidae, have been described from Hälludden (Eisenack 1976:186). Specimens of Textulariidae are common on sandy clays and in shallow-water algal facies (Loeblich & Tappan 1964:120).

METAZOA – The lamellibranchs in the Hälludden section are mainly endobyssate suspension feeders (Cyrtodontacea and Modiomorphacea; cf. Soot-Ryen 1969:176 and Stanley 1972, Fig. 33). Their success can be attributed to their ability to maintain stable positions in soft substrates at the sediment-water interface (Stanley 1972). Other forms were free burrowers (e.g., *Babinka oelandensis*; see Soot-Ryen 1969 and Stanley 1972, Fig. 33), but lacking capacity for deep burrowing, and therefore at a competitive disadvantage in an agitated environment (Stanley 1972).

The euomphalid *Lesueurilla* (e.g., *Lesueurilla infundibulum*; see Koken 1925) is the most common gastropod at Hälludden (cf. Bohlin 1949), and another important group of gastropods are the bellerophonaceans. The



Fig. 1. Map showing Ordovician localities used for ecological study. Filled circles indicate outcrops and open circles borings.

euomphalids were filter feeders and the bellerophonaceans mainly active algal grazers (Linsley 1978:440).

The cephalopods at Hälludden are insufficiently known (see Holm 1893, 1895 and Foerste 1932), but there are some unfinished studies with ecological implications. Conchs of orthocone cephalopods tend to be concentrated on bedding planes, at Hälludden especially in the "Limbata" and Langevojan Limestones. In the course of the fieldwork for "Project Hälludden" in 1949, Björn Kurtén determined the orientation of cephalopod conchs on a number of successive bedding planes at Hälludden. Anders Martinsson started a study in 1965 on the embedding conditions for large fossils in the Ordovician limestones of Öland and measured the orientation of large numbers of cephalopods on the bedding planes. Graphic display of the results shows more or less distinct patterns of preferred orientation, which have not yet been tested statistically. With regard to orientation the cephalopods in the Öland limestones seem to represent a diversified picture, depending on the length and preservation of the embedded shell portions. Orientations can be both transverse to and along the current directions, and in quiet environments the shells could be left standing vertically long enough for the living chamber or even older chambers to become embedded in that position in the rock (Martinsson, pers. comm. 1981). All these types of orientations occur in the Hälludden section.

Besides brachiopods, trilobites are the most common macrobenthos at Hälludden. Parts of the faunas have been described by Bohlin (1949,1960), Jaanusson (1957), Whittington & Bohlin (1960), and Bruton (1968). The smooth exterior and the wide rhachis in illaenines, asaphids and nileids are probably an adaptation to burrowing habits (Bergström 1973:62), and these forms are common at Hälludden. Odontopleurids also occur, and these were probably benthic crawlers (Bergström 1973).

Most bryozoans require a hard substrate for attachment and many forms are adapted to life in very turbulent waters (Dodd & Stanton 1981:63). The bryozoans at Hälludden (e.g., *Orbipora acanthophora* and *Orbipora indenta*; see Bassler 1911) include some which were encrusting or attached by holdfasts, but many formed massive colonies and were obviously ambitopic (Jaanusson 1979:269).

Brachiopods are common at many levels. Recumbent soft bottom forms, e.g. *Pseudocrania*, occur throughout the sequence, whereas infaunal soft bottom forms, represented by lingulaceans, are rare at most levels (Mutvei, unpublished). Pedunculate articulate brachiopods with thick shells probably attached to a firm substrate. At Hälludden *Chitambonites zonatus* and *Orthis callactis* can be included in this category.

The graptolites at Hälludden have been described by Bulman (1936),

BRITISH SERIES	BALTOSCANDIAN STAGES	BALTOSCANDIAN SUBSTAGES	FORMATIONAL UNITS ON ÖLAND	GRAPTOLITE ZONES	CONODONT ZONES	
CARADOC	KUKRUSE	NOT DEFINED	[Vertical lines]	NEMAGRAPTUS GRACILIS	PYGODUS ANSERINUS	
LLANDEILO			UHAKU			DALBY
	PERSNÄS			GLYPTOGRAPTUS TERETIUSCULUS	PYGODUS SERRA	
LLANVIRN	LASNAMÄGI		KÄLLA			FOLKESLUNDA
			SEBY			
			SKÄRLÖV			
	ASERI		SEGERSTAD	DIDYMOGRAPTUS "BIFIDUS"	AMORPHOGNATHUS VARIABILIS	
	KUNDA		ALUOJA			GIGAS
			V ALASTE			R ANICEPS
ARENIG	VOLKHOV		HUNDERUM	EXPANSUS	DIDYMOGRAPTUS HIRUNDO	MICROZARKODINA PARVA
		LANGEVOJA	LEPIDURUS			
	LATORP	"LIMBATA"	LIMBATA	DIDYMOGRAPTUS EXTENSUS	PAROISTODUS ORIGINALIS	
		BILLINGEN	BILLINGEN			
		HUNNEBERG	HUNNEBERG	HUNNEBERG	(TETRAGRAPTUS APPROXIMATUS)	PAROISTODUS PROTEUS
			BALTONIODUS NAVIS	BALTONIODUS TRIANGULARIS	PRIONIODUS EVAE	PRIONIODUS ELEGANS
TREMADOC	CERATOPYGE	NOT DEFINED	CERATOPYGE	BRYOGRAPTUS	PALTODUS DELTIFER	
PAKERORT	DICTYONEMA		DICTYONEMA FLABELLIFORME	CORDYLODUS ANGULATUS		

Fig. 2. Diagram showing correlation of Ordovician rocks on Öland. Based on Bergström (1971, 1973, written comm. 1980), Jaanusson (1955, 1960a, 1960b, 1973, pers. comm. 1979, 1980) and Lindström (1971).



Fig. 3. Hälludden 1. Sample levels, chitinozoan abundance (specimens per gram of rock) and relative frequencies (% of all specimens), and the relative frequencies (% of all specimens) of dominant macrofossil groups. Stratigraphical column and relative frequencies of macrofossils after Mütvei (unpublished)

Skevington (1963, 1965b) and Eisenack (1976:183). They show maximum abundance 0.23–0.26 m above the Hunderumian–Valastean boundary (c. 6% of the macrofauna), and a less pronounced maximum 1.18–1.20 m below the boundary. The planktic taphocoenosis at Hälludden consists only of surface-water graptolites (Erdtmann 1976:626, Fig. 1, Table 4–5).

PROBLEMATICA – The hyolithids in the Hälludden section were described by Holm (1893). There is strong evidence that they lay on the flat side on the bottom, partly buried in the sediment (Dzik 1980:229), and they were possibly filter feeders. Hyolithids are most common in argillaceous sediments but are found in all types of marine sedimentary rocks except for those of hypersaline, dolomitic or reef origin (Fisher 1962:117).

Other fossil groups from Hälludden, but without particular ecological relevance here, are acritarchs (Eisenack 1976:190–197), conodonts (cf. Löfgren 1978:35), conulariids (Holm 1893:144), cystoids (cf. Regnéll 1945), dendroids (Skevington 1963), hydroids (Skevington 1965a and Eisenack 1976:185), ostracodes, scolecodonts (Eisenack 1976:184–185), and tasmanitids (Eisenack 1976:185). It should be added that dendroids and hydroids reached their maximum diversity above the Hunderumian–Valastean boundary at the same level as the graptolites.

INTERPRETATION OF THE ENVIRONMENT

The closest land area during early Ordovician times was probably situated in the northeast (Männil 1966 and cf. Jaanusson 1973:18, Fig. 2). The land area was in an advanced state of peneplanation. A regression started in Latorp times and reached its maximum in northern Öland during the early Valastean. The depth of the sea during late Langevoja time was probably some tens of metres, but shallowing during Hunderum time. The benthic fossils are dominated by soft-bottom forms that lived on and in a sandy sediment. The currents were strong enough to bring finer particles into suspension. Occasionally the sediments may have been under the influence of oscillatory wave motions (cf. Gnoli et al. 1979).

ECOLOGICAL CONCLUSIONS

The most striking feature in the frequency curves (Fig. 3) is that the chitinozoans increased in diversity and abundance parallel with the large macrobenthos. However, Chitinozoa as a group show no pronounced relation to any other benthic or planktic fossil group studied, although it should be noted that no comparisons have been made with conodonts and

ostracodes. Individual chitinozoan species have been tested statistically for possible relation to the large macrobenthos (quantitative data for individual macrobenthic species have not been available) but without positive results. The chitinozoans from the Hälludden section are well-preserved (Grahn 1980), and the differences in size of species exclude sorting. "Limbata" beds with reddish and brownish limestones are devoid of chitinozoans. This is due to the oxidizing conditions within the sediments, which prevented preservation of the chitinozoans (cf. Grahn 1981b:31). In the Hälludden section the chitinozoans occur exclusively in grey glauconitic calcarenites, and they have their maximum abundance and diversity in the micritic sequences. This is also true of the macrobenthos and the planktic organisms at this locality. In the Ordovician of Öland graptolite abundance maxima coincide, with few exceptions, with peaks in the abundance and diversity of Chitinozoa, which indicates that some chitinozoophorans were probably planktic during spawning. Whether differences in water energy levels are also related to water depth cannot be stated with certainty in the Hälludden section, since the deep differences in the section must have been comparatively small. Through the whole Hälludden sequence, independent of lithology, trilobite pygidia dominate numerically over glabella (Jaanusson, pers. comm. 1981), and this sorting effect might on the whole imply comparatively high water energy. However, very high water energy seems to have been unfavourable to most chitinozoophorans. Since the fluctuations in chitinozoan abundance are not related to any group of shelly fossils, nor to lithology, physical factors like temperature, salinity, nutrient input may provide an explanation (cf. Grahn 1981b:36). It is also possible that chitinozoophorans were soft-bodied animals which left no trace in the fossil record.

REVIEW OF CHITINOZOOPHORAN ECOLOGY IN THE ÖLAND AREA

In the ecological interpretations below, data available from the Ordovician of other parts of Sweden are included (Laufeld 1967; Grahn 1978, 1981b, 1982). Four major types of carbonate sediment can be distinguished in the Baltoscandian area (Jaanusson 1973:12, 1979:20), viz. sparitic calcarenites, micritic calcarenites, calcarenitic calcilutites and calcilutites. These types of sediments roughly reflect different water energy levels. The 32 chitinozoan species in the Ordovician of Öland can be divided in three major ecological categories reflecting these water energy levels: 1. Chitinozoans with preference for comparatively high water energy (shallow water). 2. Chitinozoans with preference for comparatively low water energy. 3. Chitinozoans "independent" of the type of sediment.

CHITINOZOANS WITH PREFERENCE FOR COMPARATIVELY HIGH WATER ENERGY (SHALLOW WATER) – Half the chitinozoan species belong to this category. Seven species, viz. *Angochitina cf. capillata*, *Conochitina cf. comma*, *Cyathochitina regnelli*, *Cyathochitina sebyensis*, *Cyathochitina stentor*, *Desmochitina elongata*, and *Lagenochitina tumida* (not recovered from Hälludden in this study, see Grahn 1980) are restricted to calcarenites in general, and nine chitinozoans, viz. *Conochitina aff. claviformis*, *Conochitina aff. elegans*, *Desmochitina amphorea*, *Desmochitina cocca*, *Desmochitina complanata*, *Desmochitina minor*, *Desmochitina ovulum*, *Desmochitina rugosa*, and *Eisenackitina oelandica* reach their maximum relative frequencies in micritic calcarenites.

Desmochitina species have their maximum frequencies in calcarenitic sediments. They are also known to occur in chains and cocoons. Their preference above all for micritic calcarenites which indicate a somewhat turbulent environment, implies that they were attached to firm objects by the chitinozoophorans. A vagile life habit for the chitinozoophorans is necessary for this type of egg-laying. Currents, storms etc. were able to transport some of the pseudoplanktic chitinozoans into both shallower and deeper waters. The same is probably also true for other chitinozoans with preference for shallow and turbulent water. Very high water energy, here represented by sparitic calcarenites, seems to be unfavourable for most chitinozoophorans (cf. Laufeld 1979). It should also be noted that no chitinozoans are restricted to or show preference for sparitic calcarenites. Other very shallow water sediments have yielded very poor chitinozoan faunas (cf. Laufeld 1974; Grahn 1978).

CHITINOZOANS WITH PREFERENCE FOR COMPARATIVELY LOW WATER ENERGY – Three chitinozoans, viz. *Conochitina pelfifera*, *Conochitina wesenbergensis* and *Cyathochitina striata*, reached their maximum relative frequencies in different types of argillaceous rocks in the west Baltic area, and *Conochitina clavaherculi* is restricted to calcarenitic calcilutites. Low water energy does not necessarily indicate relatively deep water.

Conochitina wesenbergensis is known from many types of sediments, and in the Gotland area it has a maximum frequency in calcilutites rich in algae and deposited in a shallow but calm environment (Grahn 1982:58). *Conochitina pelfifera* and *Cyathochitina striata* also occur in micritic calcarenites. However, in the Öland area the calcilutites reflect deeper water than the calcarenites. The bathymetric conditions for the chitinozoophorans are exemplified by the conditions during Uhakuan times (Fig. 2), when different types of sediments, deposited at different depths, occurred in the Öland area. In the early Uhakuan, calcarenitic calcilutites were present in the north and calcilutites in the south of Öland. The

chitinozoan diversity (number of chitinozoan species) in the latter is 75% of that in the former. Change of sedimentary conditions in north Öland during the middle Uhakuan, from calcarenitic calcilutites to micritic calcarenites, is reflected by a slight difference in chitinozoan diversity. The maximum chitinozoan diversity in calcilutites in south Öland is 68% of that in micritic calcarenites in north Öland. It is not possible to say whether these differences depend on preference for a firmer bottom, or are a reflection of the shallower sea in north Öland. In any case, the depth differences between north and south Öland were probably relatively small.

CHITINOZOANS "INDEPENDENT" OF THE TYPE OF SEDIMENTS –

Twelve chitinozoans, viz. *Conochitina capitata*, *Conochitina conulus*, *Conochitina micracantha*, *Conochitina minnesotensis*, *Conochitina primitiva*, *Cyathochitina calix*, *Cyathochitina campanulaeformis*, *Cyathochitina kuckersiana*, *Cyathochitina latipatagium*, *Lagenochitina esthonica*, *Rhabdochitina gracilis*, and *Rhabdochitina magna* show no pronounced preference for any specific type of bottom. Some of these species may have been planktic and accordingly been dispersed freely in the water by the chitinozoophorans. This and the fact that many chitinozoans have a wide palaeogeographical distribution imply that respective chitinozoophorans were holoplanktic or planktic only during the spawning season. In the Gotland area, *Conochitina micracantha*, *Rhabdochitina gracilis* and *Rhabdochitina magna* reached high frequencies in calcilutites rich in algae and deposited in a shallow but calm sea. Since these species are also important elements in the chitinozoan fauna in the sparitic calcarenites at Hälludden, which were deposited in a shallow but turbulent sea, it seems likely that these chitinozoophorans were bathymetrically controlled and preferred shallow water, independent of water energy. Worthy of note is that *Rhabdochitina magna* does not occur in the calcilutites in southern Öland. This is in agreement with the interpretation that this species preferred shallow water, and that the Uhakuan calcilutites were deposited in relatively deeper water.

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PRISKLASS B

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