

Cephalopod Septal Strength Indices (SSI) and depositional depth of Swedish Orthoceratite limestone

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with 13 Text-figures and 11 Tables

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SSI was calculated for 2,994 individual septa measured in sectioned cephalopod conchs from limestones of Arenig to Llandeilo age (Ordovician) in Sweden. Minimum depths assumed on the basis of these calculations serve to illustrate variations in sea-level through time. The sea-level curve for the lower Llanvirn regressive stage agrees with the curve obtained by the same method for the Yangtze Platform.

Septal-Stärke-Indices, für 2994 Kammerwände aus längsgeschnittenen Cephalopodengehäusen arenigischen bis llandeilischen Alters in Schweden errechnet, zeigen Variationen der Ablagerungstiefe an, die für das untere Llanvirn am besten belegt sind. Der Ablauf der regressiven Ereignisse im älteren Llanvirn war nach Vergleich mit in derselben Weise gewonnenen Ergebnissen aus dem Yangtze-Plattform in beiden Regionen ähnlich.

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Introduction

The chambered cephalopods are unique by having developed a fixed-volume phragmocone with subatmospheric internal pressure as buoyancy tank to minimize energy expense; thus their distribution is depth-dependent. Their last septum is assumed to be optimized to minimum weight while attaining a certain level of mechanical pressure resistivity at the depths at which they live. The mechanical resistivity of septa against implosion, expressed as Septal Strength Index (SSI; WESTERMANN, 1973), therefore can give us information on bathymetric limits of certain animals. The validity of SSI for bathymetric study has been supported by several investigations (WESTERMANN, 1973, 1977, 1985; DENTON, 1974; HEWITT & WESTERMANN, 1988; CHEN, 1988 a, b, 1989).

Cephalopods are often assumed to be post-mortem floaters; the fossil record however does not support this contention. Instead, fossil cephalopods would have been mostly post-mortem sinkers that were buried at or near their habitat area (CHAMBERLAIN et al., 1981; CRICK, 1988). Indeed their distribution is known to be facies dependent (CRICK, 1980), possibly as a consequence of different bathymetric situations (CHEN, 1988 a, b). The cephalopod SSI therefore can be expected to provide exceptional evidence of depositional depth of the fossil-bearing stratum.

The purpose of the present study is to investigate cephalopod SSI derived from the Swedish Orthoceratite limestone, with the goal to expand and test our knowledge of the depositional depth of this facies. This depositional depth is subject to prolonged debate in the Scandinavian countries and Estonia (LINDSTRÖM, 1963, 1979; JAANUSSON, 1982; NORDLUND,

1989; STURESSON, 1989), a debate that has been going largely unnoticed in other countries. Our estimates of depositional depths were made from mean habitat depth represented by the peak population of the SSI data in each fossil assemblage with consideration of the distribution of data. We are testing the relevance of our data on the assumption that the SSI depth variations discovered in Sweden are due to eustatic movements of sea-level. If this is indeed the case, then the same variations could occur in the same time intervals in China, where SSI has been investigated in similar facies (CHEN, 1988 a, b, 1989).

Implosion depth

Chambered cephalopods are directly adapted to water pressure. Their shell faces the major functional problem of withstanding ambient hydrostatic water pressure down to the depths at which they live in spite of the fact that gas pressure within the air chambers is less than the atmospheric pressure (DENTON & GILPIN-BROWN, 1966, 1973). The critical water depth at or below which the animals are instantly killed by implosion can give us information on the bathymetric limits of certain animals.

DENTON & GILPIN-BROWN (1966) first argued that the shell of *Nautilus* shows three areas of failure under high pressure: outer shell wall, last septum, and siphuncular wall. The shell wall is considered to be unrelated to implosion depth because it is significantly stronger than septa and siphuncular wall. The significance of the siphuncular wall for the evaluation of the implosion depth is likewise eliminated by variation of mi-

crostructure and morphology between taxa and between living and fossil taxa.

The septa appear to be optimized to minimum weight. Their close relation to the implosion depth is evidenced by frequent occurrences of imploded septa within intact shell wall and with mostly preserved sutural attachment. WESTERMANN (1973) put forward the definition of implosion depth by the Septal Strength Index ($SSI = \delta/R \cdot 1000$, with δ referring to thickness and R to radius of septal curvature) which was calibrated against experimental data from implosion of living *Nautilus* and *Spirula* in a pressure tank, to the effect that one unit of SSI corresponds to a water depth increment of 30 m (WESTERMANN, 1973).

The microstructures of nacreous septa are hardly known in fossil cephalopods. There is as yet no convincing evidence as to whether they were the same or not in fossil and recent cephalopods. Uniform microstructure is assumed by HEWITT et al. (1989), whereas MUTVEI (1983) believes that there are significant differences.

We are using WESTERMANN's (1973) SSI calibration, which is based on the former assumption, because we regard it as consistent with results obtained by our investigations of litho- and biofacies in the rock successions we are dealing with. However, we wish to emphasize that the depths quantified by this standard are not regarded by us as a principal finding; indeed we would accept to regard them as mere guesses for want of an Early Palaeozoic calibration. It is the variation of SSI within the investigated Ordovician successions that is our main interest.

Habitat depth

Pelagic cephalopods lay only a few tens of eggs at maturity (WARD, 1987). Because of the consequent value of the individual for the survival of the species, a broad safety margin is necessary in order to escape mortality from implosion. A habitat depth of $2/3$ the implosion depth is assumed by us. This is less than the $3/4$ assumed by others (WESTERMANN, 1973; DENTON, 1974), but we feel it is justified because it renders our depth figures more conservative. The ecological niches of pelagic cephalopods were restricted mostly to the area of the epicontinental seas in the Early Palaeozoic (CHEN, 1988a). Recent SSI studies indicate that the habitat depth of the benthic forms may have been affected by the local bathymetric situation and the depth of the shelf break as well.

Post-mortem history of cephalopod shells

Many authors have assumed a post-mortem transportation of the cephalopod shell for an unknown distance from the actual

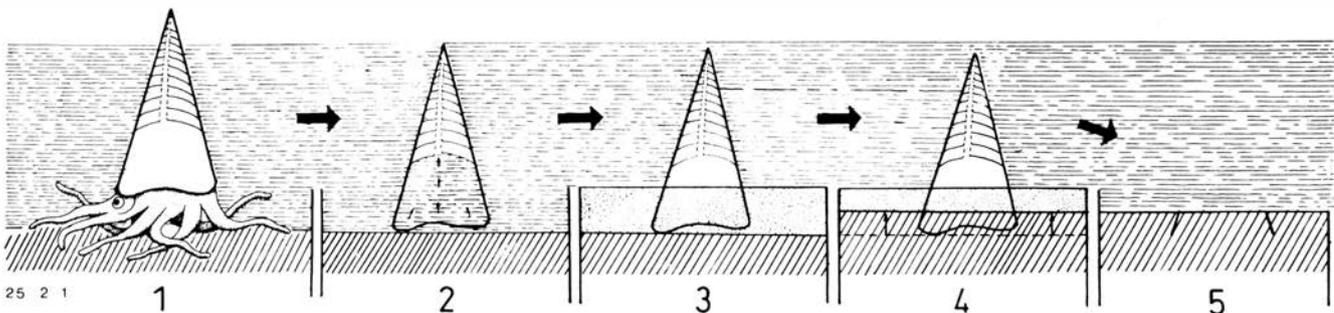
habitat of the animals (see for instance REYMENT, 1958). Uncertainty about this matter has long been a major obstacle to further discussion concerning the cephalopod facies. The fossil evidence suggests that the occurrence of long-drift shells is relatively rare. Our observations indicate that most of the fossils have been little transported, because their distributions are facies-dependent.

The habitat and post-mortem history of fossil cephalopods has been discussed by WESTERMANN (1985). The vagrant benthic mode of life is considered to dominate among those represented in the Ordovician Orthoceratite limestones, in view of their similarity with the forms considered as nekto-benthos in the Silurian. Much of the assumed benthos died on or near the sea-bottom at the dwelling-place. They are likely to have been post-mortem sinkers because their air-chambers are expected to have become flooded after their visceral mass was consumed by scavengers soon after death. A small proportion of the shells might have been transported by current or by turbidity flow into deeper environment before ultimate burial.

Three principal modes of preservation are recognized from Orthoceratite limestones; they are horizontally embedded, vertically embedded, and imploded. Horizontal embedding dominates. A relatively high proportion of fossils in this taphonomic state shows features that suggest that the shells remained intact and without much reworking before ultimate burial. Many air chambers contain abundant cement, indicating that mechanical damage was minimal and the shells were covered with sediment soon after deposition on the sea floor. Because of slow rate of sedimentation and large size, most shells would however face erosion caused by boring, chemical dissolution, or currents before being permanently covered by sediment. Significant portions of such shells were removed. The loss of the upper part of the shells by sea-bed erosion is a characteristic feature of the Orthoceratite limestone.

Vertical preservation (Text-fig. 1) is less common, being typically represented by orthocerids of conic orthocone type with small, centrally located siphuncle. The species are assumed to have maintained equilibrium with their shells in vertical position. The occurrence of vertical preservation indicates that the shells were undamaged and their apical air chambers not entirely flooded before the body chambers were buried in the sea bed. This type of preservation is much less common than the horizontal mode because it requires a consistently calm environment before the body chamber became firmly attached to the sea-bed or before the portion exposed to water was eroded away.

The imploded type of preservation is recognized by the present study to occur in the Folkeslunda Limestone on Öland. The imploded situation is characterized by 1) the repeated occurrence of broken septa within the intact shell, 2)



Text-fig. 1: Sequence of events leading to the vertical preservation mode represented by certain orthocerids of conic orthoconic morphotype. The animal died at or near the sea floor (1); After death its visceral mass was consumed by scavengers, and parts of the air chambers were flooded (2); The adoral part of the shell was buried by sediment (3); The shell became firmly attached to the sea bed due to progressive lithification from below upwards (4); The main part of the shell disappeared during a following erosion event (5).

the values of SSI represented by the imploded septa being significantly lower than the SSI obtained from associated benthic forms, and 3) this preservation being represented by species the epipelagic mode of life of which is indicated by their buoyancy-promoting shell structure with a small, centrally positioned siphuncle.

The SSI value of the imploded septa can give us information about the minimum bathymetry of a given area. The species exhibiting imploded preservation were all apparently epipelagic. After death, the shells may as a rule have been flooded before sinking to their bathymetric limit, in which case no implosion could occur. The implosion is restricted to those individuals of the epipelagic population which reached the bathymetric limit either dead or alive but with their conchs not yet flooded. It is difficult in the fossil record to distinguish whether these individuals were alive or dead. The ratio of imploded to non-imploded conchs within the epipelagic population seems to vary between the species and between different environments. The frequency of occurrence of implosion could rise if the environment was characterized by great and abrupt changes of factors like bottom topography and hydrology. As much as $\frac{2}{3}$ of the specimens observed had imploded in the forereef slope environment on the SW margin of the Sino-Corean Platform during the Late Ordovician (cf. CHEN, 1988a, b), whereas the rate of implosion occurrence is relatively low in the Folkeslunda Limestone in which about $\frac{1}{5}$ to $\frac{1}{4}$ of the epipelagic population had imploded.

Orthoceratite limestone facies

The facies, which in Sweden is traditionally called Orthoceratite limestone, of essentially Arenig to Llandeilo age, consists of medium (2–20 cm) bedded to nodular, calcilitic to calcarenitic limestones with a great proportion of bioclastic (arthropodal and echinodermal) grains in the sand

sizes (JAANUSSON, 1973). It is very rare to find sessile benthos in situ. Except for megafossils, major clasts are generally missing. Burrowing is omnipresent but usually showing very little variation within a stratigraphic interval.

Many bedding-planes are discontinuity surfaces (either firmgrounds or hardgrounds), mostly with either burrows or borings, and frequently with some kind of selective mineralization (JAANUSSON, 1961; LINDSTRÖM, 1979). Glauconite is a common component in parts of the succession. Colour of the limestone matrix as a rule is either grey or reddish, depending on the oxidation state when pore water circulation came practically to an end. Sedimentary structures other than bedding and trace fossils are generally missing.

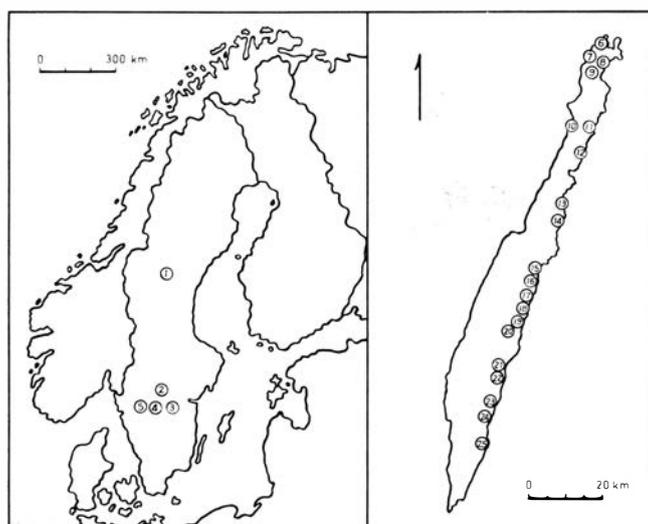
The uniformity of the facies in space as well as in time (many million years) is one of its outstanding features. As far as we have been able to discern, identical facies of identical age is widely distributed on the Yangtze Platform in China. Therefore, studies on cephalopod SSI carried out in both areas can be used for mutual checking of consistency. We do not regard the term »Orthoceratite limestone« as adequate for both facies together, but choose to defer the naming of the facies to a later occasion.

Material and methods

Much of the material consists of specimens collected and stratigraphically determined by V. Jaanusson and H. Mutvei and belonging to Naturhistoriska Riksmuseet, Stockholm. The remainder was collected by the authors. In most cases the cephalopod tests were found to have been dissolved within the sediment before conversion of aragonite to calcite had had time to take place. The hollow spaces left after dissolution were subsequently filled by either calcite cement or internal sediment. A rare mode of preservation consists of phosphatization of the test.

Swedish Orthoceratite limestone sequence					Yangtze platform sequence		Eustatic events
Topostratigraphic units	Conodont		Trilobite	Baltoscandia Stage/Subst.	Litho-units	Megafossil sequence	
	Zones	Subzones					
Folkeslunda	Pygodus serra	Eoplacogn. reclinatus		Lasnamegian	Batiaba Miaopu	Nemagraptus gracilis	Transgression
Seby		Eoplacogn. foliaceus				Glyptograptus teretiusculus	
Skärlov	Eoplacognathus suecicus	Eoplacogn. suecicus - Panderodus sulcatus	Asaphus platyrurus	Aserian	Guniutan	Meitanoceras	Regression
Segestad		E. suecicus - Scalpellodus gracilis	Megistaspis gigas			Kundan	Dideroceras wahlenbergi
Holen	Eoplacogn. variabilis	E.? variabilis M. ozarkodella	Asaphus "raniceps"	Aluojan	Gly. austrudentatus		
		E.? variabilis M. flabellum parva	Asaphus expansus	Valasteian	Dawan	Glyptograptus sinudentatus	
Lanna	Microzarkodina parva		Megistaspis limbata	Volkhovian			Protocycloceras
	Paroistodus originalis		Megistaspis simon				
	Baltoniodus navis Baltoniodus triangularis		Megistaspis lata		Bathmoceras Azygograptus suecicus		

Tab. 1: Ordovician stratigraphic units referred to in the text.



Text-fig. 2: Map of Scandinavia and Öland showing localities referred to in the text. (1) Lundbohm Quarry at Brunflo, Jämtland. (2) Yxhult Quarry SE of Örebro, Närke. (3) Old Ljung Quarry, Östergötland. (4) Våmb S of Skövde, Västergötland. (5) Hälleklis, Västergötland. (6) Hälludden, N Öland. (7) Byxelkrok, N Öland. (8) Sjöstorp, N Öland. (9) St. Mossen, N Öland. (10) Gillberga, N Öland. (11) Källa, N Öland. (12) Persnäs, Öland. (13) Kårehamn, Öland. (14) Löt, Öland. (15) Gärdslösa, Öland. (16) Långlöt, Öland. (17) Folkeslunda, Öland. (18) Lerkaka, Öland. (19) Runsten Öland. (20) S. Bäck, Öland. (21) S. Sandby, S Öland. (22) Brunneby, S Öland. (23) Triberga, S Öland. (24) Hulterstad, S Öland. (25) Segerstad Lighthouse, S Öland.

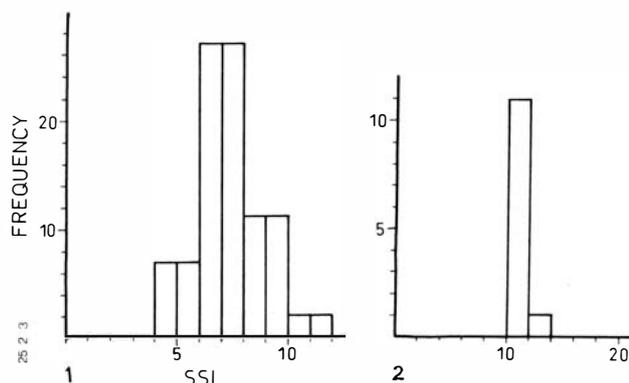
The specimens were sawed and polished as close as possible to a medial plane passing through the siphuncle, which in endoceroids is identical with the plane of bilateral symmetry. Measuring was done with a binocular microscope, using a measuring ocular at 33–50 X magnification. Radius of curvature was determined using a set of transparent templates.

Our observations are based on material which was collected at a number of localities (Text-fig.2) from the following topostratigraphic units (sensu JAANUSSON, 1982): Lanna Limestone, Holen Limestone, Segerstad Limestone, Seby Limestone and Folkeslunda Limestone. They had been dated by conodonts and trilobites with reference to the standard stratigraphy shown in Tab. 1.

Results

Lanna Limestone

The Lanna Limestone belongs to the lower part of the Orthoceratite limestone and is the lowermost part that contains cephalopods in appreciable quantity. It corresponds to the Limbata Limestone in an earlier classification (JAANUSSON, 1955). Its lithology is not markedly different from that of the underlying Latorp Limestone, but the definition is based on trilobites. The unit can be subdivided into biostratigraphic zones by species of the trilobite genus *Megistaspis*, namely from the bottom to the top *M. lata*, *M. simon* and *M. limbata*, and by conodonts (*Baltoniodus triangularis*, *B. navis*, *Paroistodus originalis* and *Microzarkodina parva* Zones). Cephalopods are moderately common and of low diversity. The limestone is a condensed facies consisting of 2–7 m of red or variegated and grey calcilutites. Discontinuity surfaces are numerous, characteristically with yellowish (goethitic) mineralization. The material available for the present SSI study is represented by two fossil assem-



Text-fig. 3: Distribution pattern of SSI assemblages from (1) the *Paroistodus originalis* Zone at Byxelkrok (Fig. 2:7) and (2) the *Baltoniodus navis* Zone at Yxhult Quarry (Fig. 2:2).

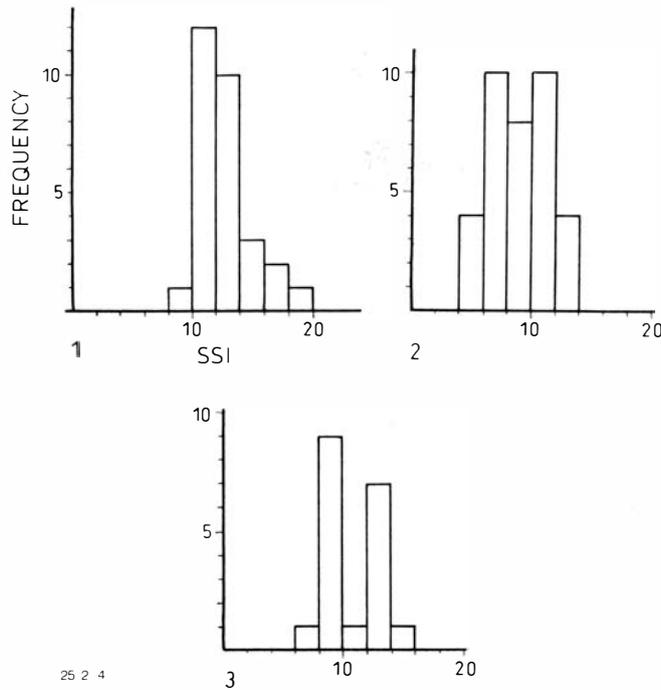
blages collected separately in Närke and Öland at different stratigraphic levels in the middle Lanna Limestone.

The older collecting was carried out in 1987 from half a meter of reddening upward cyclothem sequence at the Yxhult quarry, SE of Örebro, Närke (Text-fig. 2:2). The sequence consists basically of alternatingly greenish grey marly limestone and light reddish grey wackestone to (less commonly) packstone. The bioclasts are sand size with predominance of trilobites and echinoderms. This interval is dated by the occurrence of *Baltoniodus navis*. Estimated habitat depths of about 200 m are based on altogether 43 measurements of septa from 12 specimens (Tab. 2). The SSI distribution pattern (Text-fig. 3:2) is steeply peaked with narrow lateral spreading. Only a small part of the measurements (based on 2 specimens of endocerids) indicates slightly greater habitat depths, about 220–240 m.

48 specimens (Tab. 3) were collected from a 30 cm thick section of variegated limestone, mostly of calcarenite, by the authors in 1990 at Byxelkrok (National Grid Reference 576 728), northern Öland. Conodont dating of this interval showed it to belong to the *Paroistodus originalis* Zone. Discontinuity surfaces are abundant and characteristically knobby, with yellowish (goethitic) mineralization. Cephalopods occur in great numbers, but their diversity is low. The fauna is dominated by two species belonging to *Michelinoceras* and *Dideroceras*. The mean value of the habitat depths of *Michelinoceras* is estimated to be 140 m whereas the habitat depths of *Dideroceras* were deeper, ca 170 m on average. The SSI distribution pattern of the fossil assemblage (Text-fig. 3:1) shows a well defined peak population of SSI at between 6 and 8. The SSI distribution pattern suggests that the fossil assemblage investigated may represent a mixing of adjacent shallow and deeper faunas.

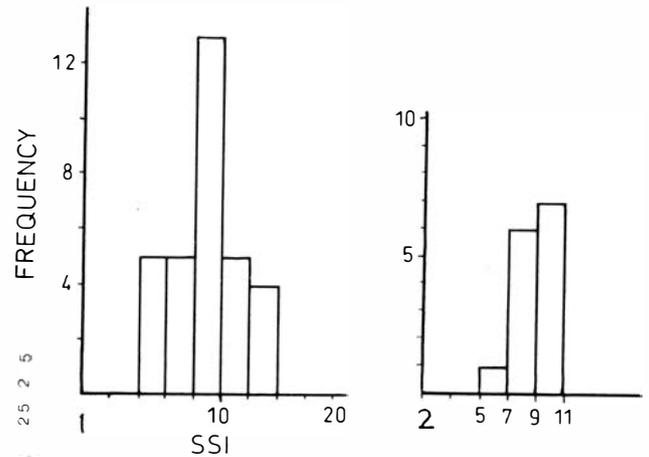
Holen Limestone

The Holen Limestone has previously been known as Vaginatum Limestone. Its lower boundary is defined by a discontinuity surface with a goethitic crust. The upper boundary is drawn by trilobite evidence at the top of the *Megistaspis gigas* Zone. The following subdivisions were erected for the unit by trilobite data (from the bottom): the Zones of *Asaphus expansus*, *A. »raniceps«*, *Megistaspis obtusicauda* and *M. gigas*. The conodont Zone of *Eoplacognathus? variabilis* was erected to represent the lower part of the Holen Limestone while the upper part is represented by the lower part of the *Eoplacognathus suecicus* Zone. The Holen Limestone consists of an 8–10 m thick succession of cal-

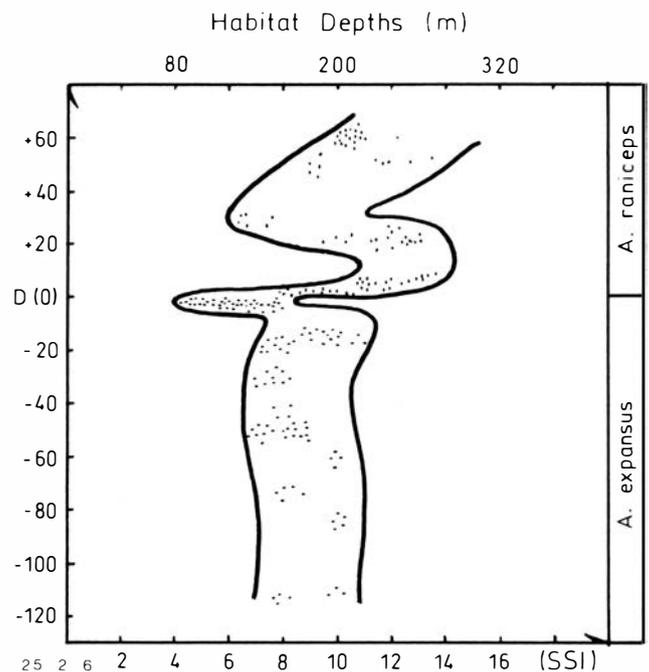


Text-fig. 4: SSI distribution pattern. (1) *Megistaspis obtusicauda* Zone at Old Ljung Quarry (Fig. 2:3). (2) A 1.65 m interval across the smooth discontinuity surface at Hälludden (Fig. 2:6). (3) *Asaphus »raniceps«* Zone at Gillberga (Fig. 2:10).

caremites with evidence of condensation like repeated discontinuity surfaces. The lower Holen Limestone represents an environment that differed considerably from that of underlying and overlying beds. To its significant features belong a shift in colour from reddish to predominantly light grey, and an increase in particle size and faunal diversity with greatly increased abundance of brachiopods and other non-arthropodal benthos. Glauconite and chamosite are abundant, whereas they are rare in immediately underlying and overlying beds. The similarity in lithofacies between the upper part of the Holen Limestone and the underlying Lanna Limestone suggests that the depositional environment may have returned to its previous conditions. A bed by bed sampling of cephalopods was carried out by Mutvei in the upper 100 cm interval of the *A. expansus* Zone and the lower 65 cm of the »*raniceps*« Zone of Hälludden (Text-fig. 2:4), northern Öland. These and other fossils labelled with accurate position within the lower 3.4 m of the Holen Limestone provide us with data concerning the changes of SSI populations through the corresponding, critical time interval. The lithologic sequence of the interval has been measured by JAANUSSON & MUTVEI (1982). The lower 1.9 m consist of glauconite-rich calcarenites dated as *A. expansus* Zone. The basal 0.1 m is rich in limonitic coatings around skeletal grains. The upper 1.5 m, dated as *A. »raniceps«* Zone, are grey, thin bedded calcarenites. Two undulating discontinuity surfaces are recognized at 60 and 105 cm above the base of the *A. »raniceps«* Zone (which is here drawn at a slightly higher level than in JAANUSSON & MUTVEI, 1982). A smooth discontinuity surface with dark mineralization and abundant borings, mostly of *Trypanites* type, occurs at a level 3 to 20 cm above the bottom of the *A. »raniceps«* Zone. 230 measurements of SSI have been obtained from 36 specimens at at least 20 different stratigraphic levels ranging from 115 cm below to 50 cm above the smooth discontinuity surface (henceforth referred to as SDS). The results, relating to SSI variation and bathymetric changes through the investigated interval, sug-



Text-fig. 5: SSI distribution patterns from Hälludden (Fig. 2:6). (1) 80 cm of the lower part of the »*raniceps*« Zone. (2) 1 m of the upper part of the *expansus* Zone.

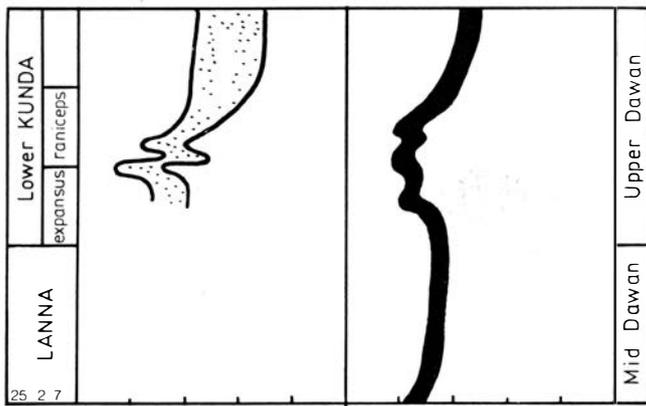


Text-fig. 6: SSI distribution pattern and sea-level curve for upper *Asaphus expansus* and lower *Asaphus »raniceps«* Zones.

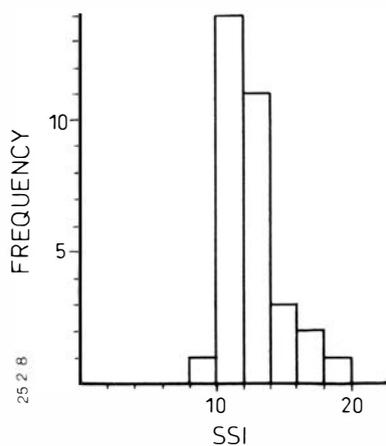
gest that the situation was generally stable during deposition of the lower 110 cm.

The SSI distribution obtained from the Hälludden fossil assemblage has a bimodal pattern (Text-fig. 4:2). The same pattern (Text-fig. 4:3) is also documented from a fossil assemblage (Tab. 5) which was collected by Mutvei in a stratum of the *A. »raniceps«* Zone at Gillberga, Öland. The two fossil assemblages represent nearly the same interval. The occurrence of the bimodal pattern is interpreted as being a result of mixing of shallow and deep water faunas.

The Hälludden fossil assemblage can be divided stratigraphically into two groups. The younger group is represented by 32 specimens obtained from a stratum of ca 80 cm belonging to the lower part of the »*raniceps*« Zone. The distribution (Text-fig. 5:1) from this interval has a normal pattern with a conspicuous peak population at 8–10. The peak population is represented by 13 specimens, the SSI of which provides an estimate of water depth of ca 180–190 m during early »*raniceps*« time. The SSI distribution of the upper *expansus*



Text-fig. 7: Juxtaposition of sea-level curves for eustatic shallowing event documented in the lower Kundan and its equivalent, the upper Dawan Formation of the Yangtze Platform.

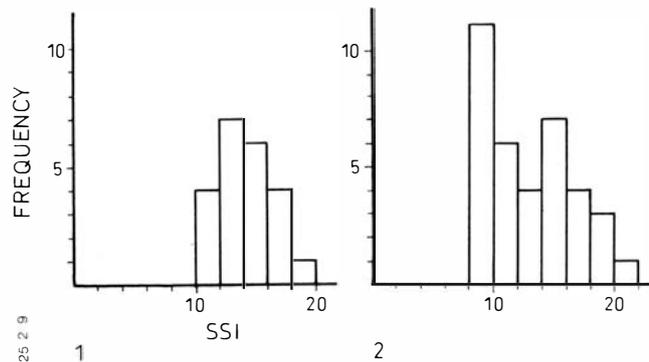


Text-fig. 8: SSI distribution pattern for *Megistaspis obtusicauda* Zone at Old Ljung Quarry (Fig. 2:3).

Zone (Text-fig. 5:2) exhibits a positively skewed pattern, represented by 13 specimens from a stratum of ca 1 m thickness, belonging to the upper part of the *expansus* Zone. Its peak population is at 10–12. Estimated water depth during the time corresponding to the upper *expansus* Zone was about 200 m.

The interval 5 cm below to 20 cm above SDS contains the evidence of a shallowing event; see Text-fig. 6. In our material this is represented by cephalopod populations belonging to oncocerids and *Bathmoceras*. The magnitude of the shallowing is estimated to be 40–60 m. The regression event across SDS was accompanied by the appearance of large brachiopods, transported receptaculitids, trilobite coquina, and cystoids. A tendency toward deepening is recorded to follow the shallowing event. During the Valastean shallowing maximum the water depth is estimated to have been 80–100 m in north Öland. The event is probably coeval with the upper Dawan shallowing event occurring on the Yangtze Platform (Text-fig. 7).

The cephalopods collected by Holm at the Old Ljung quarry, Östergötland (Text-fig. 2:3) are derived from a red, bedded limestone, ca 2.4 m thick and underlying red, finely nodular limestone belonging to the Zone of *Megistaspis gigas*. The stratigraphic level is comparable to the Zone of *M. ob-*



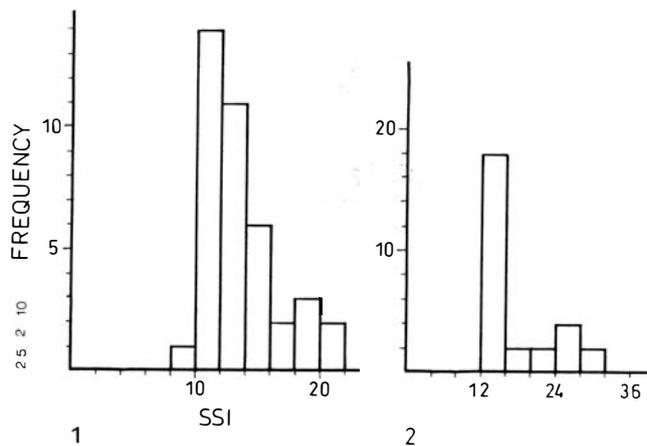
Text-fig. 9: SSI distribution pattern for Segerstad Limestone, Öland. (1) Lower Segerstad Limestone, S. Bäck (Fig. 2:20). (2) Upper Segerstad Limestone, several localities.

tusicauda. 150 measurements were obtained from 32 specimens (Tab. 6), mostly of endocerids, yielding a mean SSI value of 12.6. The local water depth indicated by the mean value of habitat depths of the peak population is estimated to have been about 220 m (Text-fig. 8).

Segerstad Limestone

This unit is represented by red calcilutites to biocalcarenites with a maximum known thickness of just over 6 m. It is characterized by the occasional presence of reddish stromatolitic structures. The cephalopods are abundant, but the fauna is of low diversity and is dominated by endocerids. Lituitids increase in importance toward the upper part. Sedentary macroorganisms were apparently confined to echinodermal epifauna on certain cephalopod conchs. Biostratigraphically the unit belongs to the *Asaphus platyurus* Zone of the trilobite succession and the upper *Eoplacognathus suecicus* Zone of the conodont sequence. Two subdivisions of the Segerstad Limestone have been suggested: a lower one, mainly calcilutites, known as the Kårgårde Limestone (Zone of *Angelinoceras latum*), and an upper one consisting mostly of red and grey, variegated calcarenites, known as the Vikarby Limestone (JAANUSSON & MUTVEI, 1953). 20 specimens (Tab. 7) available for the present SSI study were collected from the lower Segerstad Limestone at S. Bäck quarry by Holm. 130 measurements were obtained from the 20 specimens, most of which are endocerids. The SSI distribution (Text-fig. 9:1) of the lower Segerstad Limestone has a normal pattern with a peak population at 12–14. The local water depths, estimated from the mean value of the peak population were ca 260 m.

The SSI investigation of the upper Segerstad Limestone is based on 38 specimens which were mostly collected by the present authors in 1987 at Segerstad lighthouse (Tab. 8; Text-fig. 2:25). Part of them were collected by Holm at old quarries, Hulterstad (Text-fig. 2:24) and Löt (Text-fig. 2:14), Öland. 154 measurements form the basis of a depth estimate of 280 m. The SSI distribution (Text-fig. 9:2) shows a bimodal pattern with two separate populations at 8–10 and 14–16 respectively. The bimodality is considered to be the result of sedimentary mixing of deeper fauna with shallower fauna because of fluctuating bathymetry during the period of deposition. The water depths are estimated to have been ca 290 m at transgression maximum by evidence of the right peak population whereas they were ca 190 m at their mini-



Text-fig. 10: SSI distribution pattern for Seby Limestone. (1) Several localities on Öland. (2) Lundbohm Quarry (Fig. 2:1).

mum probably by the end of the deposition of the Segerstad Limestone, as indicated by the left peak.

Skärlov Limestone

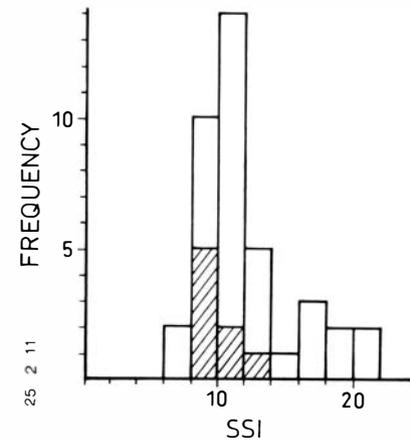
This lithostratigraphic unit is represented by red, nodular calcilutites and argillaceous intercalations. Cephalopods are rare, or absent, providing no material for the present SSI study.

Seby Limestone

At the sampled localities on Öland the unit consists of a 1 m thick sequence of variegated, grey and red biocalcarenes. Biostratigraphically it is dated as middle part of the *Eoplacognathus foliaceus* Subzone. The limestone abounds in diverse cephalopods determined as *Suecoceras*, *Cochlioceras*, *Lituites* and orthocerids. They are assumed to have been mostly vagrant benthos. The habitat depths vary between different genera. *Suecoceras* bears evidence of habitat depths of 220–240 m, whereas the estimated habitat depths were 220–270 m for *Cochlioceras* and 200–300 m for *Lituites*. The habitat depths among the orthocerid group vary greatly from 200 to 440 m, rarely up to 800 m. All 41 specimens considered by the present investigation were collected by Holm from Öland at numerous localities (Text-figs. 2:14, 17, 18, 20, 21). The SSI distribution (Text-fig. 10:1) has a negatively skewed pattern with a conspicuous peak at 10–12. The peak population is represented by 14 specimens, mostly of endocerids and *Cochlioceras*. The mean value of the peak population warrants an estimate of the local depositional depth of ca. 225 m. Nearly the same SSI pattern (Text-fig. 10:2) is also documented from a fossil assemblage which was collected in a stratum ca. 1 m thick, consisting of reddish stromatolite-carrying limestone at the Lundbohm quarry in Brunflo, Jämtland, by the authors in 1987. The stratum is dated by the occurrence of *Eoplacognathus foliaceus* and represents nearly the same stratigraphic interval as the Seby Limestone sampled on Öland. It yields abundant cephalopods, mostly endocerids and lituitids, but also numerous orthocerids. The SSI distribution has a negatively skewed pattern, with a well defined peak population. The depositional depths in Jämtland estimated by the mean habitat depths of the peak population were about 250 m.

Folkeslunda Limestone

The Folkeslunda Limestone is the uppermost unit of the Swedish Orthoceratite limestone and is known as upper grey

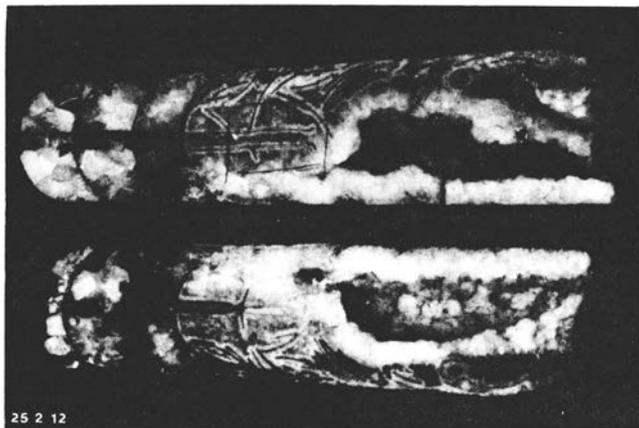


Text-fig. 11: SSI distribution pattern for Folkeslunda Limestone, mainly Öland. Imploded septa indicated by diagonal shading.

orthoceratite limestone according to an old classification. It is a thin unit of grey, mainly calcarenitic limestone dated as upper part of the *Pygodus serra* Zone. It abounds in cephalopods consisting mostly of orthocerids (*Geisonoceras*, *Michelinoceras*, *Polygrammoceras*, *Clinoceras*) and lituitids. Endocerids are less common.

39 specimens were studied by us (Tab. 10). They were collected by Holm, mostly from different localities on Öland. Nine of them (Tab. 11) are imploded. The fossil evidence indicates that implosion preferentially occurred in the adoral portion of phragmocones, whereas the aboral few septa usually remain undamaged. A varying number of septa within the imploded phragmocones were observed to have escaped damage by the implosion event. In some cases implosion occurred independently in separate parts within a single phragmocone. The reason why the septal breakage stopped during implosion is not clear. WESTERMANN (1985) interpreted it to be that septal strength was increased by thickening of septa or by cameral deposits. Although our observations confirm the existence of differences in septal strength between imploded and non-imploded chambers within a single specimen (Tab. 11), the difference is, however, usually minor. Thus it is doubtful if such differences were sufficient to create appreciable differences in resistance against ambient pressure. We consider that water flooding as such would have played an important part in reducing pressure differences and thus saving a number of septa from implosion. If the implosions took place close to the sea-bed the depositional depths indicated by SSI of imploded septa (Tab. 11) were ca. 180–200 m whereas the maximum depth indicated by SSI of non-imploded specimens is in the range 320–400 m (Tab. 10) during deposition of the Folkeslunda Limestone in Öland and Västergötland.

The septal debris from the implosions was deposited adapically, or latero-adapically, or laterally within the imploded air chambers. It is usually closely packed, and oriented with the convex sides either downward or adapically. The differences in orientation may have resulted from two different modes of sinking. Conchs sinking with the apex downwards, as indicated by adapical accumulation of septal debris, are well represented in the fossil assemblages from the Folkeslunda Limestone. This sinking behavior is interpreted to be due to the weight of cameral deposits apically and the density loss adorally (WESTERMANN, 1985). Conchs retaining a horizontal orientation while sinking, as indicated by the convex-downward accumulation of septal debris in imploded air chambers, are less common, being documented only by a specimen of *Polygrammoceras*. The specimen (Text-fig. 12) represents part of a phragmocone 93 mm long, consisting of 9 air chambers. Its adoral four chambers were severely



Text-fig. 12: *Polygrammoceras*, with adoral 4 septa imploded; septal debris accumulated adapically, in convex-downward position. Folkeslunda, Öland, coll. G. Holm. No. 155395. 0.85X nat. size.

damaged by implosion, but part of their septal margin less one fourth radius remains attached to the wall. The siphuncle tube was broken completely, leaving few recognizable fragments. Furthermore, a thick accumulation of septal debris occurs adapically with convex-downward orientation. A layer of internal sediment present at the bottom of the adoral three air chambers shows a conspicuous tendency towards adoral thickening, suggesting that the deposit was introduced through the imploded air chambers. The degree of damage lessens apicad, with presence of but small holes on septa in the following two air chambers. The occurrence of a thick accumulation of septal debris and the debris having a clear preference for convex-downward orientation suggest that the debris was brought into the semi-closed cavities by the shock wave during the implosion event and that it was deposited from suspension when the kinetic energy declined.

The SSI distribution of the fossil assemblage (Text-fig. 11) has a bimodal pattern. The bimodality suggests ecological mixing of epipelagic fauna with benthic fauna. The epipelagic population that is evidenced by a frequent occurrence of imploded septa exhibits what is interpreted as a normal distribution on the left of the diagram whereas the right part of the diagram is believed to represent pelagibenthic forms.

Bathymetric variations and their comparison with the Yangtze Platform

The appearance of the Orthoceratite limestone facies and its equivalents is one of the most dramatic evolutionary developments of the carbonate facies that occurred during the Ordovician Period. In Baltoscandia the facies evolved from an extensively distributed black mud facies in the latest Tremadoc, immediately after an interruption of sedimentation owing to a major regression (LINDSTRÖM & TEVES, 1988). On the Yangtze Platform an equivalent facies known as the Pagoda facies however evolved from a quite different forerunner, namely algae-sponge mud mound shallow carbonates (LINDSTRÖM, CHEN & ZHANG, in press). The developments coincided in time and facies beginning with the *Paroistodus originalis* Chron in Baltoscandia and on the Yangtze Platform. The similarity in facies evolution has been documented by LINDSTRÖM, CHEN & ZHANG (in press) to embrace an interval from the middle Arenig to the Llandeilo. Comparative studies made by the authors have proved the existence of roughly coeval development of characteristic combinations of stromatolite-like bedding-plane structures,

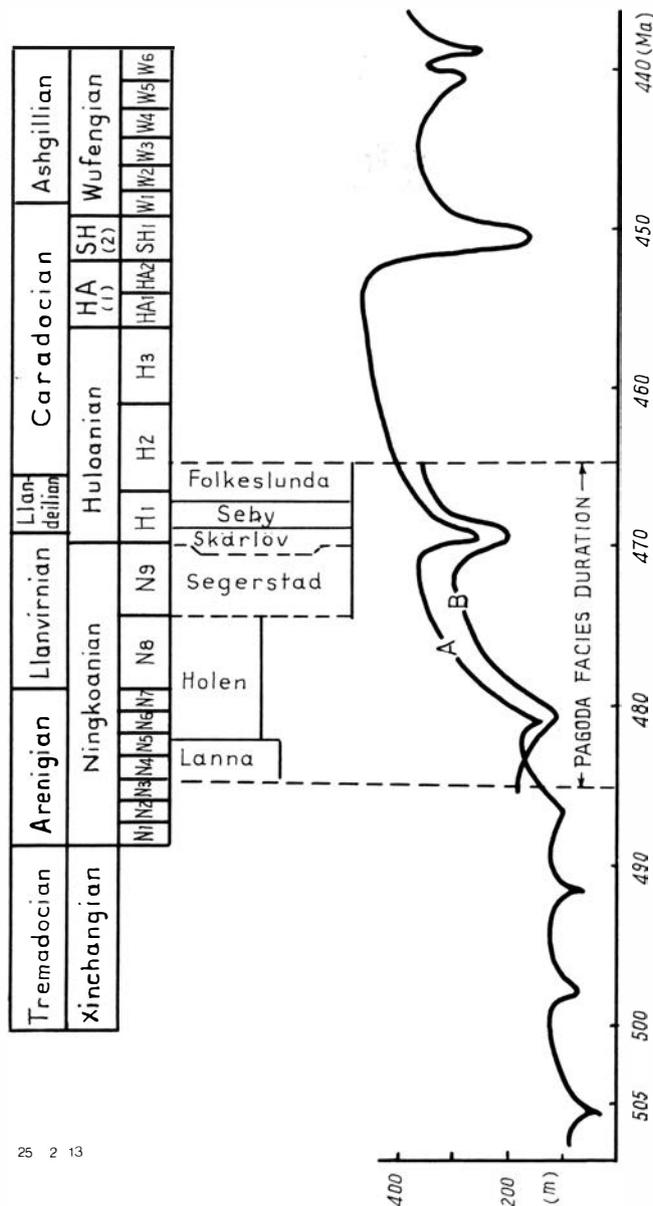
stacked mineralized discontinuity surfaces, and presence of abundant cephalopod conchs carrying similar SSI information.

Although the Orthoceratite limestone facies is well defined by a set of distinctive features, its genesis remains obscure and the interpretation of depositional depths has been debated for years. The occurrence of furrows interpreted as desiccation cracks and other structures that resemble stromatolite mats has led authors to suggest very shallow, probably supratidal conditions (LARSSON, 1973; JAANUSSON, 1973). None of the mentioned evidence, however, excludes relatively deep conditions, suggested by LINDSTRÖM (1984), since the evidence of desiccation is atypical and the distribution of stromatolite-like mats includes their presence within cavities of cephalopods and thus suggests that they may have been formed by the activities of aphotic microorganisms rather than by cyanophytes. The interpretation of the depositional environment as relatively deep has gained support from SSI data (CHEN, 1988a, b, 1989). Judging from these data the deposition of the main part of the Pagoda facies of the Yangtze Platform could have taken place at depths of 140 to 410 m. By the same criterion used in the present study the Orthoceratite limestone in Sweden was deposited at depths of 130 to 300 m (Text-fig. 13).

The SSI of the fossil assemblage from a narrow interval within the *Baltoniodus navis* Zone of the lower Lanna Limestone near Örebro presents a conspicuous peak population, indicating a depositional depth of ca 200 m.

Cephalopod SSI within the *Paroistodus originalis* Zone of the Lanna Limestone indicate a depositional depth of 130 m on northern Öland and a maximum depth of ca 220 m for the epeiric sea at the corresponding time. Presence of stacked discontinuity surfaces and associated yellowish mineralization are characteristic of the *Paroistodus originalis* Zone on northern Öland. An identical facies occurs at a comparable level on the Yangtze Platform within the Dawan Formation, where the SSI data suggest depositional depths of ca 140 m. In Sweden the beds in question are considered to be followed upwards by a regression sequence (NORDLUND, 1989; STURESSON, 1989). The present study indicates that a brief regression did occur during deposition of a narrow interval on both sides of a smooth discontinuity surface of early Valastean age. On northern Öland there was a 40–60 m decrease of water depth as indicated by SSI data. The regression led to introduction of cephalopod fauna which apparently preferred shallow water, large brachiopods and sessile bryozoans, as well as deposition of trilobite coquina and an increase of the content of coarse bioclastics. On the Yangtze Platform the same regression led to a 40 m shallowing according to SSI data. The appearance of rich faunas of large brachiopods and deposits of coquina in the upper part of the Dawan Formation are regarded as related to the shallowing event.

The lower Valastean regressive deposits are followed upwards by a transgressive sequence, with SSI data indicating water depths of 220 m in late Kunda time and 260 m in early Segerstad time. Depths amounting to 280 m are indicated for the time corresponding to the upper Segerstad Limestone. The identical transgression on the Yangtze Platform is represented by the *Glyptograptus teretiusculus* Zone in the uppermost Dawan Formation and the overlying Guniutan Formation. SSI data from these deposits indicate a deepening trend upward from 230 m to 300 m, except for the uppermost 2–3 m of the Guniutan Formation, where SSI data suggest a shallowing of about 100 m. The coeval shallowing in Sweden is revealed by the presence of bimodal SSI pattern in the upper Segerstad Limestone. The regression is assumed to have occurred by the time corresponding to the uppermost Segerstad



25 2 13

Text-fig. 13: Sea-level curves for Ordovician of Yangtze Platform (curve A) and the investigated part of the Swedish Ordovician (curve B) against international, Chinese, and Baltoscandian stratigraphic units.

Limestone and the marly Skärlov Limestone. The water depth is suggested to have been ca 190 m on southern Öland during the maximum of shallowing. We consider the introduction of diverse shallow-water faunal elements such as *Bathmoceras*, *Nybyoceras*, *Hoeloceras*, *Stereoplasmocerina*, *Ctenoceras*, *Allumetoceras*, *Valcouroceras*, *Ruedemannoceras* and *Strandoceras* within the cephalopod shale (probably lower part) in areas surrounding Lake Mjösa to the north of Oslo (SWEET, 1958) as related to the same shallowing event. A shallow and carbonate saturated environment is assumed to have existed during the regression, as indicated by the presence of substantial cameral and endosiphuncular deposits in *Nybyoceras*, *Hoeloceras*, *Ctenoceras* and *Stereoplasmocerina*.

The late Aserian regression was followed by a transgression that is represented by the Seby Limestone and the overlying Folkeslunda Limestone. SSI data suggest water depths of 225 m during Seby time while depths may have reached at least 300 m as indicated by SSI data relating to the following Folkeslunda time on Öland. The latter data include values

calculated for imploded septa. The comparable transgression on the Yangtze Platform is represented by the introduction of the Miaopu graptolite shale. During Miaopu deposition the depths increased from 220 m to 340 m (CHEN, 1988 a, b).

Biogeography and palaeoecology

Although the existence of provinciality during Ordovician time has been well documented through numerous groups of fossils, the mechanisms behind it are unknown. The provinciality of Ordovician cephalopods evolved to development of two distinctive types of fauna which are represented by the Yellow River fauna and the Yangtze River fauna respectively (CHEN, 1976, 1980). The biogeographic development was interpreted as a consequence of different latitudinal positions (CHEN, 1976, 1980) or as a consequence of physical barriers basically due to distance of separation by deep water (CRICK, 1990). The dissimilarity between the faunas appears however to be less dependent on distance of separation than on facies differences. According to the interpretation by CHEN (1988 a, b) the bathymetric environment was first among the environmental factors that controlled the biogeographic development.

The Yellow River fauna consisted largely of shallow-water forms. It was associated with thick carbonate sequences in regions of shallow and warm epeiric seas such as north China, North America, and Western Australia (TEICHERT & GLENISTER, 1954), as well as Malaya. Shells belonging to this fauna have low SSI. The habitat depths indicated by SSI data range from 30 m to 100 m. The taxonomic composition is characterized by the mass occurrence of actinocerids. The endocerids present consist of breviconic forms such as manchiceratids and piloceratids, inhabiting depths of approximately, 40–60 m. Orthocerids are represented by diverse shallow-water forms usually bearing exceptionally heavy endosiphuncular and cameral deposits within their shells. Ellesmerocerids, which are one of the ancestral nautiloid stocks exhibiting wide morphologic variation, are usually associated with stromatolitic mound sequences, with habitat depths of ca 40 m.

The vigorous biocalcification which led to formation of exceptionally heavy calcareous deposits within air chambers and siphuncles in the Yellow River type of fauna may indicate close to optimal conditions for carbonate precipitation in the water mass. However, the endocochlear calcareous deposits might also be considered as stabilizing organ (KAZMIERCZAK et al., 1985).

Compared with the outlined type of fauna, cephalopod fauna of the Yangtze River type comprised forms that preferred the moderate to great depths that existed in regions of slow carbonate deposition such as Baltoscandia and, in China, the Yangtze valley. The faunas of Yangtze River type, as evidenced by SSI studies, possess shells which had high resistance to water pressure. They were thus able to inhabit relatively deep environments. The habitat depths of these faunas are estimated to have been 130–300 m in Baltoscandia and 140–410 m on the Yangtze platform. These faunas were characterized by the mass occurrence of macrochaonitic endocerids represented by *Dideroceras* (with slender apical siphuncle), *Proterovaginoceras* (with bulbous apical siphuncle) and *Suecoceras* (likewise with bulbous apical siphuncle) in Baltoscandia and by *Dideroceras* and *Chisiloceras* on the Yangtze Platform. They possess a relatively large siphuncle, mostly of subventral to ventral position which would have resulted in lowering the centre of gravity to achieve greater stability during horizontal motion. A sluggish nekto-benthic mode of life is proposed for forms which are usually of giant

size. Their habitat depths indicated by SSI range from 140 to 300 m, with maximum frequencies of calculated SSI suggesting that the animals were at optimum water depths at 200–250 m.

Conchs were designed in different ways so as to strengthen them against the ambient pressure. To this category of designs belong the extended septal necks of endocerids, the effect of which certainly was to strengthen the siphuncular wall.

Lituitids are among the most important representatives of the Yangtze River type of fauna. They are characterized by the presence of ocular sinus and a conspicuous hyponomic sinus. Their shells are either conic orthocone or slender to conic orthocone with adapical spiral. Although lituitids evolved during early deposition of the Pagoda facies both in Baltoscandia and on the Yangtze Platform they did not attain numerical dominance till the time of the late Llanvirnian regression and the following Llandeilo-Caradocian transgression, while the frequency of the macrochoanitic endocerids diminished rapidly during this same time. The lituitids of the Swedish Orthoceratite limestone are estimated to have inhabited depths from 150 to 200 m, where they mostly belonged to the pelagic benthos. The presence of imploded lituitids in the Folkeslunda Limestone indicates that lituitids had adapted to an epipelagic mode of life by the time of the Folkeslunda transgression. The same transgression on the Yangtze Platform is accompanied by the introduction of deep, probably pelagic benthos, principally *Simoceras*, which is a dominating genus in the Pagoda Limestone. The transgression furthermore caused the extinction of the endocerids in Miaopu to Pagoda time, as can be verified in numerous sections.

The habitat depths of *Simoceras* are estimated to have been ca 400 m. Orthocerids are less diverse but numerically abundant, with a broad range of bathymetric environments from 130 to 800 m. Most orthocerids lack calcareous deposits within the air chambers and siphuncular tube. Ellesmerocerids are less common and of low diversity, being represented by baltoceratids (*Cochlioceras* and *Bactroceras*). Despite their shallow-water origin, the baltoceratids tended to seek moderately deep environments. Actinocerids are extremely rare.

Biocalcification in the Yangtze River type of fauna is to some extent developed in pseudoorthocones and actinocerids, which are restricted to certain narrow levels usually related to regression. The very low degree of development of biocalcification in the Yangtze River faunas is considered to be a consequence of a relatively high degree of undersaturation with calcium carbonate in the water mass which they inhabited. The frequent occurrence of discontinuity surfaces and the evidence of destruction of skeletal material in the Pagoda facies provides parallel evidence in support of carbonate undersaturation.

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