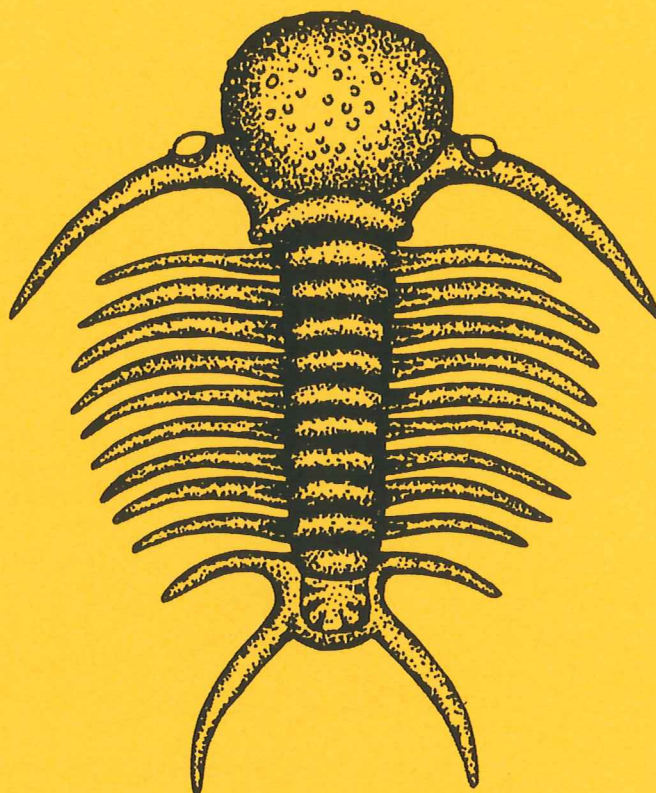# EXAMENSARBETE I GEOLOGI VID LUNDS UNIVERSITET

Historisk geologi och Paleontologi

Phosphatized echinoderm remains from upper Lower Ordovician strata of northern Öland, Sweden - preservation, taxonomy and evolution

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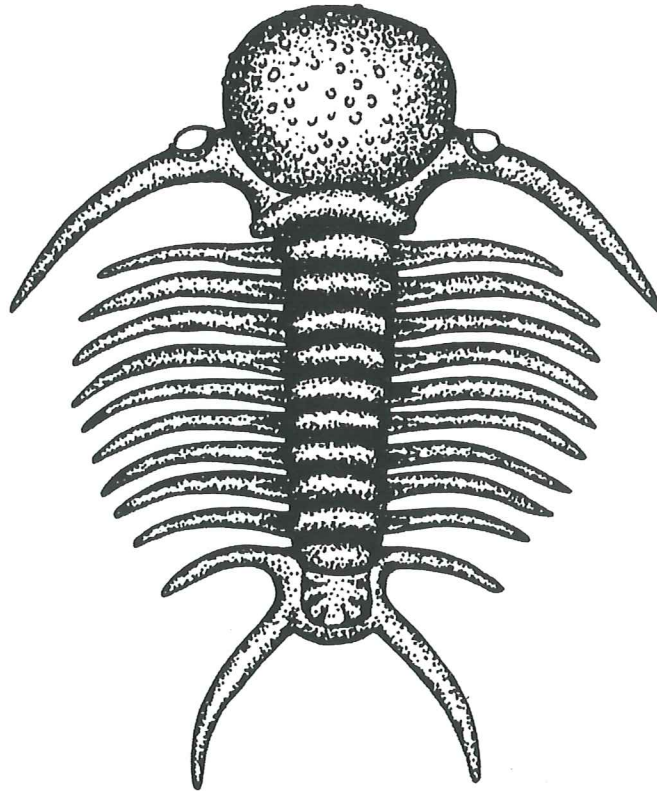
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Phosphatized echinoderm remains from upper Lower Ordovician strata of northern Öland, Sweden - preservation, taxonomy and evolution

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Abstract: Phosphatization of late Early Ordovician echinoderm fragments from N Öland has resulted in excellent preservation of the echinoderm stereom ultra structure. The stereom investigated shows a close relationship to different types found in recent echinoderms. The several different types of phosphatic preservation found have been controlled by diagenetic relationships. The original stereom structures have also been a controlling factor in the distribution of three-dimensional preservational types. The stratigraphically oldest samples from the Gillberga quarry, N Öland, SE Sweden, are dominated by rhombiferans while the youngest samples are dominated by crinoids. This might reflect that the distribution of echinoderm classes in Gillberga has mainly been controlled by changing bottom conditions. The distribution and dominance of the different articulation types in echinoderm columnals closely follow the evolutionary pattern of columnal articulation as described by various other authors. It is also shown that amongst crinoids the species domination has mainly been controlled by articulational type. A major faunal shift is evident across the Arenig - Llanvirn boundary, and this could be linked to evolutionary and palaeoenvironmental controls on the echinoderm fauna. Asterozoans are rather common in some samples and they have obviously played a more important role in the echinoderm fauna at this time than has been recognised before. Amongst the asterozoans, the ophiuroids clearly dominate the samples. A possible occurrence of asteroids is also noted. The distribution of stylophorans could also most likely be linked to the depositional environment. Cyclocystoids, previously reported from other localities in Öland, have also been found. Thus the best-yielding levels, just below the Llanvirn boundary, contained fragments representing at least five different echinoderm classes, and also within these there is a surprisingly high diversity.

Keywords: Echinodermata, Lower Ordovician, phosphatization, Gillberga, Öland, Sweden, stereom, Stylophora, Asterozoa, Crinozoa, Echinozoa, Cyclocystoidiea, Palaeozoic fauna

The history of phylum Echinodermata starts in Cambrian time with a first diversification which is followed by a second, early Ordovician radiation of new classes (see e.g. Nichols 1969). Especially the middle Ordovician is a time of rapid diversification of pelmatozoan echinoderms. This second radiation made echinoderms more important sediment contributors than ever before (see for example Jaanusson 1976; Sprinkle 1992).

Phosphatized echinoderm fragments have been found at various stratigraphic levels in the Ordovician of Öland (see e.g. Berg-Madsen 1987; Bohlin & Jaanusson 1955). Some levels have shown a better preserved fauna than others and some levels are also especially rich in echinoderm parts. This study deals with a sequence from the coastal quarry Gillberga. Except for echinoderm remains the section studied also contains a very diverse and complex fauna of for example conodonts, brachiopods, hyolithids, ostracods, molluscs, trilobites and many other types of organisms. Some of these groups have been phosphatized while others have not. Especially phosphatized internal moulds of ostracods are very common at some levels, as are phosphatic-shelled brachiopods.

This investigation deals exclusively with microscopic remains. It is also the first study dealing qualitatively as well as semi-quantitatively with all kinds of microscopic echinoderm fragments from the Ordovician of Öland. Other essays (for example Regnéll 1945) concerning the Ordovician of Öland have shown that the echinoderm fauna was complex and diverse at this time. Some types of echinoderms have been found that were not previously known from Öland (e.g. ophiuroids and asteroids), adding to the diversity of the fauna. Another aspect of this essay is to describe the different states of phosphatic preservation that were encountered in the samples. Some palaeoecological and taphonomical aspects are thus also briefly dealt with.

Overall the echinoderm fauna described shows an excellent preservation except at a few stratigraphic levels. It shares a great deal of similarities with a Polish fauna from the Holy Cross Mountains of approximately the same age and type of preservation described by Pisera (1994).

Geological setting / Lithology

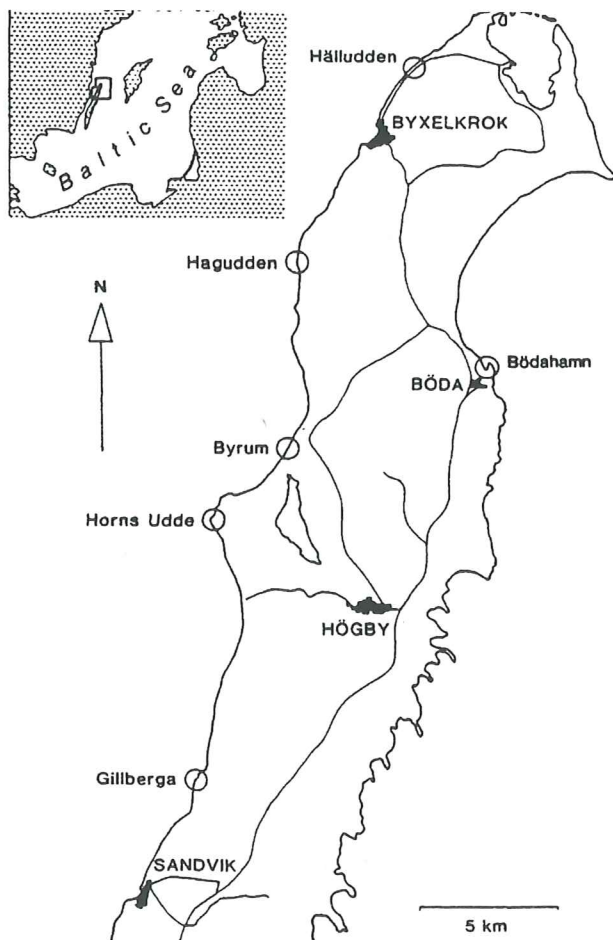Gillberga is an extensive active coastal quarry situated in the northern part of Öland, Sweden (Fig. 1). Just to the

Fig. 1. Map of N Öland, showing the location of the Gillberga quarry. Taken from Nordlund (1989b).

noderms and also including many erosional structures (e.g.; disconformities) within the limestone due to the slow rate of deposition with many depositional breaks. One wall section from Gillberga (north side) is illustrated in Fig. 2. Fig. 3 illustrates the palaeogeographic location of Baltica during Early Ordovician time.

Jaanusson (1976) distinguished a series of Ordovician confacies belts with different types of deposition. These belts are: the Scanian (the southernmost), Central Baltoscandian (middle), North Estonian and Lithuanian confacies belts. Öland was part of the central Baltoscandian belt, which continues up through Västergötland and crops out in the Caledonian front area in the northern parts of Norway. This also means that deposition and tectonic stability in the area are both affected by the ongoing Caledonian orogenesis. The main effect of this situation is that regional subsidence gives rise to sediments with varying thickness. In the studied area tectonic stability mainly rules. Jaanusson (1976) also noted that the central confacies belt had deeper water deposits in comparison with the more eastern confacies belts. Lindström (1984) noted that "the finer grained and more argillaceous sediments occur towards the west" of these confacies belts. This situation has most likely influenced the distribution of different echinoderms as certain taxa are more depth dependent than others and some are more sensitive to sedimentation rate and mud influence.

The lithology of rocks from northern Öland was thoroughly described by Bohlin & Jaanusson (1955) when working with a core from Böda hamn. Fig. 4 depicts the distribution of major and rather easily recognised lithological horizons within the Gillberga quarry.

Bohlin & Jaanusson (1955) also recognised different levels on a microscopic scale within the core, which yielded ferroan minerals, phosphorite, oolites and certain horizons which were extremely rich in different types of fossils (e.g. echinoderms). The fossils found were also to some extent described. They also studied the presence of certain minerals (e.g. sulphur and $CaCO_3$ content). It should be noted that Böda hamn is located some distance (more than 15 km) from Gillberga (see Fig.1), which means that lateral facies changes are of great importance and lithology description and chemical analysis as made by Bohlin & Jaanusson (1955), would with most certainty not apply to the whole area that lies in between Böda hamn and Gillberga.

Nordlund (1989b) made a more detailed sedimentologic study of northern Öland and he also suggested a model for lateral facies changes. The localities he studied were Hälludden, Hagudden, Byrum, Horns Udde, Gillberga and Böda hamn (see Fig.1 for localities). Based on his observations he subdivided the sections into 4 micro lithological zones (after a correspondence analysis), which are

south of Gillberga lies Sandvik, another active coastal quarry (Fig. 1) recently much extended to the north from where some samples have been examined in search for echinoderm fragments. Samples from this location are less important and these will not be dealt with further.

The section at Gillberga has its base in the upper middle Arenig and reaches up into the lower Llanvirn. The samples examined consist of orthoceratite limestone. Calcareous mud forming this limestone was part of the sea bottom in Europe ranging from the end of the Tremadoc to the beginning of the Caradoc (e.g. Lindström et al. 1991). Characteristics of this limestone are; grey to red colour, containing fragments of trilobites, molluscs, echi-

2

Fig. 2. The north wall of the Gillberga quarry.

Early Ordovician (Arenig)
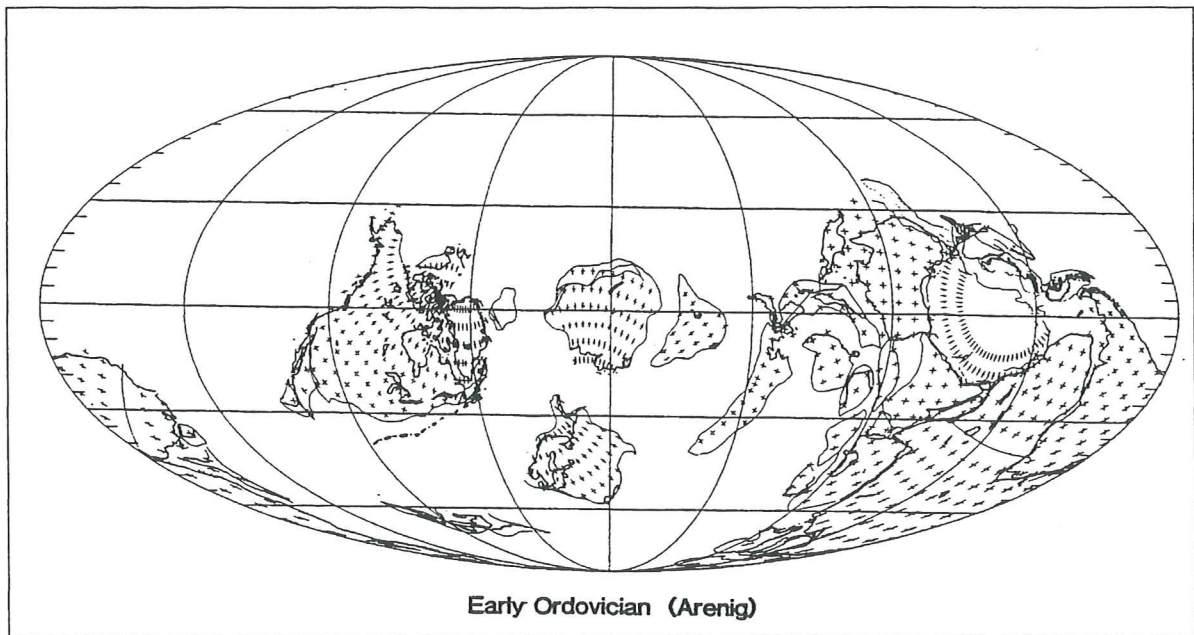
Fig. 3. The location of Baltica during Early Ordovician time. Taken from Scotese & McKerrow (1990)

recognisable in all the localities studied. Furthermore he noted that "the sequences at Horns Udde and Gillberga are generally thicker and have a more homogeneous appearance than those to the north". He also showed that a thick marly unit, which does not exist in the other locali-ties (except for Horns Udde) is developed in Gillberga. Part of that particular unit has been investigated here.

His conclusions from this study were:
1. A regressive phase can be distinguished in the lower parts of the sections studied. In Gillberga this zone
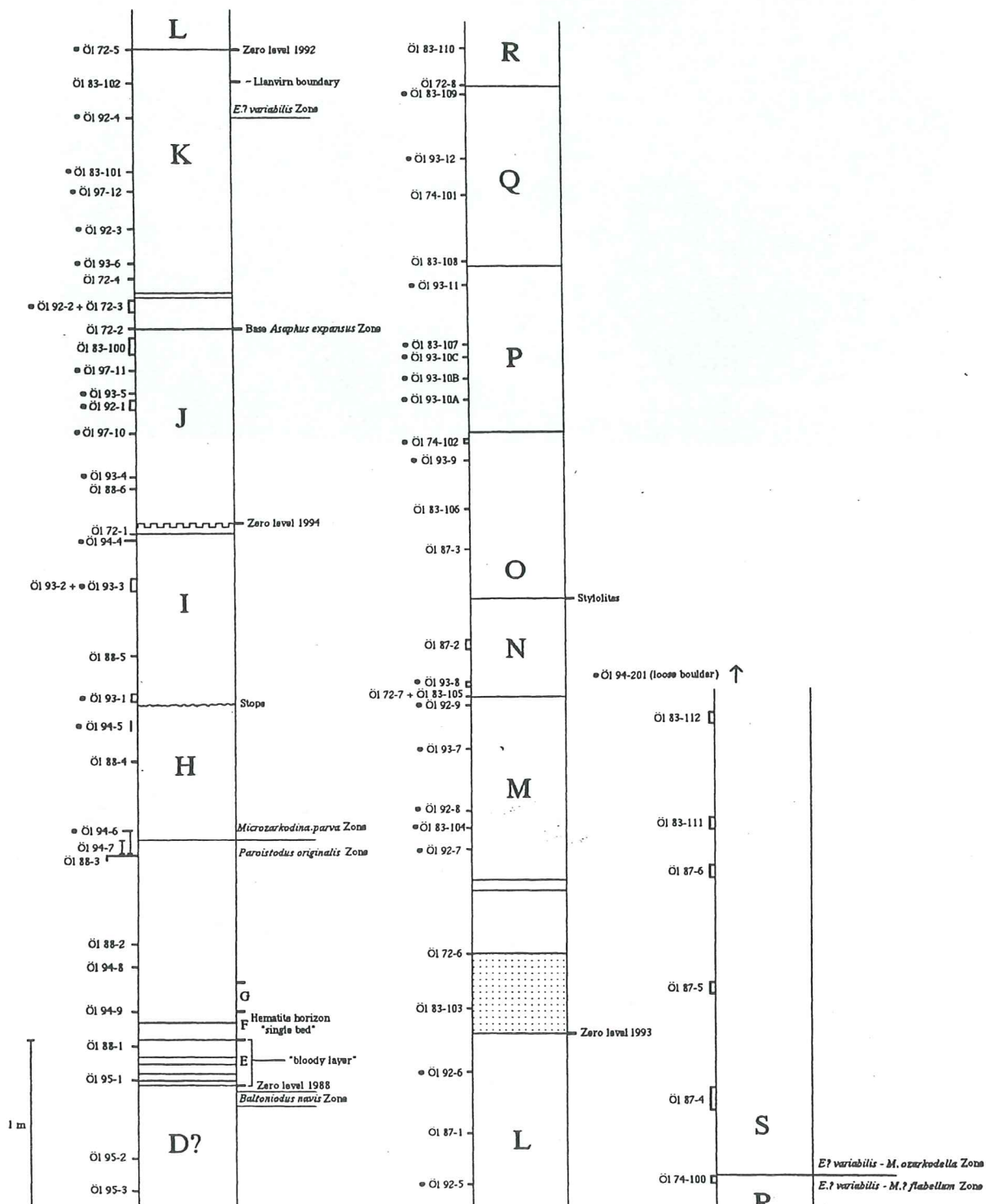
Fig. 4. Log from the Gillberga quarry based on the samples and data collected by A.Löfgren. All samples shown have been investigated for conodonts. Samples with dots have been searched for, and also yielded echinoderm fragments although in some cases only fragmentary ones. Biozonation has been carried out by A.Löfgren. Letters are used for easier recognition of certain intervals within the section.

roughly extends from the base of the "bloody layer" and about 4 meters up in the section (see Nordlund 1989b, fig.8). In Fig. 4 this roughly corresponds to a zone, which extends from base "bloody layer" to Öl 97-11.

2. "A slight slope of the sea floor towards the south and east has influenced the facies pattern in the upper part of the sequence". This means that the Gillberga sequence was deposited in the deepest part of the basin in comparison with the other localities.

3. An ooid horizon, which was found in all the localities (at the top in Gillberga, see Nordlund 1989b, fig. 8) "represents a migrating high-energy deposit".

The conclusion that can be drawn from this is that the lithology in northern Öland varies because of lateral facies change.

Nordlund (1989a) also suggested a model for the genesis of phosphatic hard grounds in northern Öland. He concluded that trapping of organic material (from e.g. storm-deposition) on non-permeable hard grounds under periodically semi-emergent to emergent conditions would generate enough phosphate that would be released to the interstitial water under reducing conditions. An increasing temperature, pH and photosynthesis (by cyanophytes) would then lead to the phosphatization of the sediment (Nordlund 1989a). He also noted that the trapping mechanism during the peak of regression would inhibit "any lateral movements of the phosphate-rich water". This resulted in extremely high ionic concentrations. The only problem with this model is the lack of evaporites (e.g. sabkha traces), which have been found at other localities for which this model has been proposed and the lack of traces from the large quantities of organic matter that would have been needed for the generation of the phosphatic hard grounds. Other authors have also suggested this kind of model for the generation of phosphate in a shallow carbonate producing sea (e.g. Soudry & Lewy 1988; Jarvis 1992). This depositional model is often observed in combination with a regressive phase that often allows the trapping of material as described above.

Lindström (1984) noted that a regressive phase spanned the boundary between the Arenig and the Llanvirn. He also noted that the *P. originalis* Zone in the basal part of the Gillberga quarry showed some signs of a beginning regressive phase with "increased content of biogenics, relative increase of echinoderm debris, and occasional fragments of sessile forms". This might also imply that several different lowstand episodes could have been responsible for the distribution of phosphatization levels within the quarry studied.

The role of bacteria in replacing carbonate with phosphate is also very important (see e.g. Soudry & Lewy 1988; Lamboy 1990). Especially Lamboy (1990) stressed this role of bacterial communities and he even separated

between two different types of bacterial communities, which gave rise to different types of phosphate.

Dr. A. Löfgren (not published) has established a biozonation based on conodonts for the Gillberga quarry. For the distribution of conodont biozones in Gillberga see Fig. 4. She has also noted the state of preservation of some of the conodonts examined (see Table 1). For a description on the Baltoscandian stages involved and their correlation see Fig. 5.

British Series	Baltic Stages and Substages	Finngrundet			
		Trilobite Zones (Tjernvik & Johansson 1980)	Conodont Zones and Subzones		(m)
Llanvirn	Valaste	Asaphus "raniceps" Zone	E.? variabilis – M. ozarkodella Subzone	E.? variabilis Zone	-18.33 -18.50
	Kunda		E.? variabilis – M.? flabellum Subzone		-20.50 -32.30
	Hunderum	Asaphus expansus Zone			-39.00 -39.10
Arenig	Langevoja	Megistaspis (M.) limbata Zone	Microzarkodina flabellum parva Zone		-45.48 -45.60
	Volkhov	Megistaspis (M.) simon Zone	Paroistodus originalis Zone		-51.07 -51.50
		Megistaspis (M.) lata Zone	Baltoniodus triangularis and Baltoniodus navis Zones		-56.50 -58.00
	Billingen	Megistaspis (V.) estonica Zone	Oepikodus evae Zone		-59.94
		Megalaspides (M.) dalecarlicus Zone			-61.00 -61.10
	Latorp	Transition Beds	Prioniodus elegans Zone ?		-61.23 -61.32
	Hunneberg	Megistaspis (V.) planilimbata Zone	Paroistodus proteus Zone		-62.17
		Megistaspis (E.) armata Zone			-62.68

Fig. 5. Correlation chart and Baltoscandian stages in the Early Ordovician (from Löfgren 1985).

Material and methods

This study is mainly based on samples collected by A. Löfgren (not published) in the search for conodonts. Three samples were taken at a later stage by myself (those beginning with Öl 97 followed by sample number). For the sample levels see Fig. 4. My samples were taken at levels that I thought were of special interest (after having gone through almost all the other samples). Especially the K-level interval shows a rich and well-preserved echino-

Sample number	Sample split	Fractions examined	Preservation types	Erosion of conodonts	Other fossils
Öl 94-201	No	nMf	phosphatic	*	
Öl 83-109	No	>1 mm	sugary	-	
Öl 93-12	No	> 0.5 mm nMf	brown phosphatic, sugary	Ø	
Öl 93-11	No	> 0.5 mm nMf	phos. almost sug., brown inner, inner white	-	molluscs
Öl 83-107	No	> 1 mm	sugary, brown phosphatic	-	
Öl 93-10C	No	> 0.5 mm nMf	white phosphatic, sugary'	0	
Öl 93-10B	No	> 0.5 mm nMf	white phosphatic, sugary, brown inner	0	
Öl 93-10A	No	> 0,5 mm nMF	sugary + brown inner	0	
Öl 74-102	No	> 0.063 < 1 mm		-	
Öl 93-9	No	> 0.5 mm	sugary, pyritic, white phosphatic	Ø	
Öl 93-8	No	nMf	sugary, coated, sugary-rind,	0	ostracods (most orn.), trilobites
Öl 92-9	No	> 0.5 mm	phosphatic, almost sugary, some brown	Ø 0	ostracods
Öl 93-7	No	> 0.5 mm	sugary	0	foraminifers
Öl 92-8	No	nMf	white phosphatic, sugary	Ø	
Öl 83-104	No	> 1 mm	sugary	-	
Öl 92-7	No	nMf	white phosph., sugary, rather poorly preser.	Ø 0	
Öl 92-6	No	nMf	almost sugary, inner brown	Ø	
Öl 92-5	Yes	nMf		Ø 0	
Öl 72-5	No	> 0.5 mm nMf	sugary	-	
Öl 92-4	No	nMf		0	
Öl 83-101	No	> 1 mm	glauconitic	0	
Öl 97-12	No	> 0.5 mm nMF	phosphatic		
Öl 92-3	Yes	nMf	white phosphatic	Ø	
Öl 93-6	No	nMf	sugary, white phosphatic	Ø	ostracods (most unornamented)
Öl 92-2	No	> 0.5 mm	sugary, coated	0	ostracods, trilobites
Öl 97-11	Yes	> 0.5 mm nMf			molluscs, brachiopods
Öl 93-5	No	> 0.5 mm nMf		*	molluscs
Öl 92-1	Yes	nMf	white phosphatic	Ø 0	
Öl 97-10	Yes	> 0.5 mm nMf			molluscs, brachiopods
Öl 93-4	No	> 0.5 mm nMf	sugary	0 *	
Öl 94-4	No	>0.5 mm nMf		*	molluscs
Öl 93-3	No	nMf	white phosphatic	*	molluscs
Öl 93-1	No	nMf	sugary	*	
Öl 94-5	No	nMf	white phosphatic, sugary, glauconitic	0 *	molluscs
Öl 94-6	No	nMf < 0.5 mm	white phosphatic	*	

Table 1. The preservation of certain conodonts shown together with the preservational types encountered amongst the echinoderms. Conodont preservation is based on observations by Löfgren (1998) on the conodont taxon *Decoriconus* (Ø: base detached, *: good preservation and O: bad preservation). Samples were split when residues were large. In theses cases only half of the sample was investigated for echinoderms. nMf fraction is the non-magnetic fraction.

derm fauna. It should be noted that within the K-level interval the Llanvirn boundary can be recognised, which according to Lindström (1984) corresponds to a regressive sedimentation phase.

The samples were treated with acetic acid according to the method worked out by Jeppsson et al. (1985). During dissolution the Öl 97-samples were regularly examined for larger fragments (e.g. stems), which at the end of the dissolving period otherwise most likely would be disarticulated. After dissolution the samples were cleaned with water and sieved through a 0.063 mm-sieve. After this treatment the residue left was dried in an oven at 50 °C over night. The dried residue in some cases contained a lot of Fe-minerals (mostly glauconite). If this was the case the residue was sent through a magnetic separator working at a low "shaking rate" to minimise the risk of damaging the fragments. The samples thus treated were now ready for more thorough examination under a light microscope. Representative and interesting fragments

were picked out and examined and photographed in the S.E.M. using Polaroid film. Measurements were made directly on the S.E.M. photograph using a ruler.

Some residues were divided if their state of preservation were so poor that identification not was possible or if they did not seem to yield any echinoderm fragments at all. The samples that were divided are Öl 92-5, Öl 92-3, Öl 97-11, Öl 92-1 and Öl 97-10. The samples Öl 93-1, Öl 94-4, Öl 97-10, Öl 97-11, Öl 72-3, Öl 83-101, Öl 92-5, Öl 93-7, Öl 93-9, Öl 74-102, Öl 93-10A and Öl 83-109 did only contain less than 10 echinoderm fragments per sample. These samples are not included in the counting as the fragments in these also were undeterminable due to the poor preservation. For notes on this see the sample descriptions in Table 1.

The sample size was originally (before dissolution) approximately between 0.5 to 1.0 kg of rock. The observations done by A. Löfgren (1998) on conodont preservation are also summarized in Table 1. Her observations on

bad preservation of some particularly fragile conodonts (given as 0 in Table 1) also closely correlates with my observations on bad preservation of echinoderm fragments.

Preservation

Various authors (e.g. Schäfer 1972) have dealt with the taphonomy of echinoderms. To briefly summarise the discussion we can say that after the death of the animal, the decay and disarticulation are very fast processes. Within 15 hours the arms of some brittle stars begin to fall apart (Schäfer 1972). From this the conclusion can be drawn that for perfect preservation to occur, the animal must be buried very quickly.

Disarticulation can also precede death due to e.g. predation, storms and environmental stress (see e.g. Lewis 1980). Lewis (1980) also noted that small plates dissociate faster than big ones and that disarticulation also can be seen as a function of the "connective tissue joining the plates". Environmental stress is an ever accelerating process, that once started can be self inducing so that more and more animals die due to more and more organic contamination of the water (Schäfer 1972).

After disarticulation the processes of transportation and diagenetic alteration start. The first process which follows disarticulation is transportation. Due to the porous nature of the echinoderm stereom it will hydrodynamically act in the same way as a solid plate of calcite of much smaller size (Savarese et al. 1996). This means that echinoderm debris can be transported a very long distance away from the place of original disarticulation.

During transport extensive abrasion takes place and the topography of the fragment becomes less and less obvious. Llewellyn & Messing (1993) noted that abrasion of crinoid columnals can take place even in a deep-sea setting, wherever some topography on the sea bottom occurs. Seilacher (1973) suggested that prefossilization diagenesis before transportation of the stereom is necessary so that the effective density of the ossicle becomes greater, thus allowing abrasion and transport to take place. Meyer & Meyer (1986) on the other hand noted in their work on recent crinoid biostratinomy that prefossilization most likely is not "necessary for abrasion of crinoidal sedimentary grains". For an example of a heavily eroded columnal see e.g. Figs. 15C, 16H. Fig. 15C illustrates a heavily eroded columnal where even the articular facet has been greatly affected with differing articular facet height as a result of this.

Once they begin to settle, the fragments act as flakes moving back and forth in the horizontal plane (Savarese et al. 1996). When settled they can either be subjected to fur-

ther transportation or diagenetic alteration. Savarese et al. (1996) also noted that the spongy nature of the echinoderm stereom makes it an ideal place for nucleation and crystal growth. The originally different types of stereom will also most likely have varying potential as nucleation sites in a diagenetic environment (see further on for a fuller discussion).

When working with phosphatized cystoid stem columnals from the Middle Cambrian of Bornholm, Denmark, Berg-Madsen (1986) recognised 3 types of preservation. Of these only one is of interest to this essay, namely phosphatized calcite. The other two are calcitic preservation and casts in phosphoritic lumps. The lack of these preservation types in my material is probably mainly due to the type of sample preparation involving treatment with acetic acid. Some fragments have also been subjected to etching as a result from the use of acetic acid. For a short depictive description of the different stereom types as recognised by Smith (1980) see Fig. 8.

The preservation types distinguished in my material are:
Type 1. - This was designated phosphatized calcite by Berg-Madsen (1986); appearing as rinds of acid-resistant material around the calcitic trabeculae. This means that after treatment with acetic acid, the calcite is dissolved leaving a phosphatic rind. Berg-Madsen (1986) separated between rinds due to "phosphatization of the original trabecular calcite" (see Berg-Madsen 1986, fig. 7E-F and also e.g. Fig. 6C herein) and rinds precipitated as a thin coating in the stereom pores. In some cases the phosphate has also precipitated in the whole pore space (see e.g. Fig. 19D). Both these types give rise to excellent preservation of the stereom structure. The best preserved material is that where phosphate totally has replaced the original calcitic stereom mesh, building up a new meshwork, which is an exact replica of the original meshwork.

Fig. 6A shows an excellently preserved inner core of stereom and the outside is preserved as "sugary" (see below). Here phosphate has replaced calcite totally in the inner zone resulting in an excellent preservation. The blow-up (Fig. 6B) shows the perfectly preserved stereom. Some etching has occurred on the interconnecting swollen areas, most likely due to the treatment of the sample with acetic acid. The stereom can be called galleried following Macurda & Meyer (1975).

In my study I have added a number of new types, where both the type and site of phosphate precipitation are of great interest.

Type 2. - This type is that labelled "sugary" indicating the sugary appearance (white, shiny and almost hyaline) that the echinoderm fragment has when viewed through a light microscope. When viewed in S.E.M. it shows a
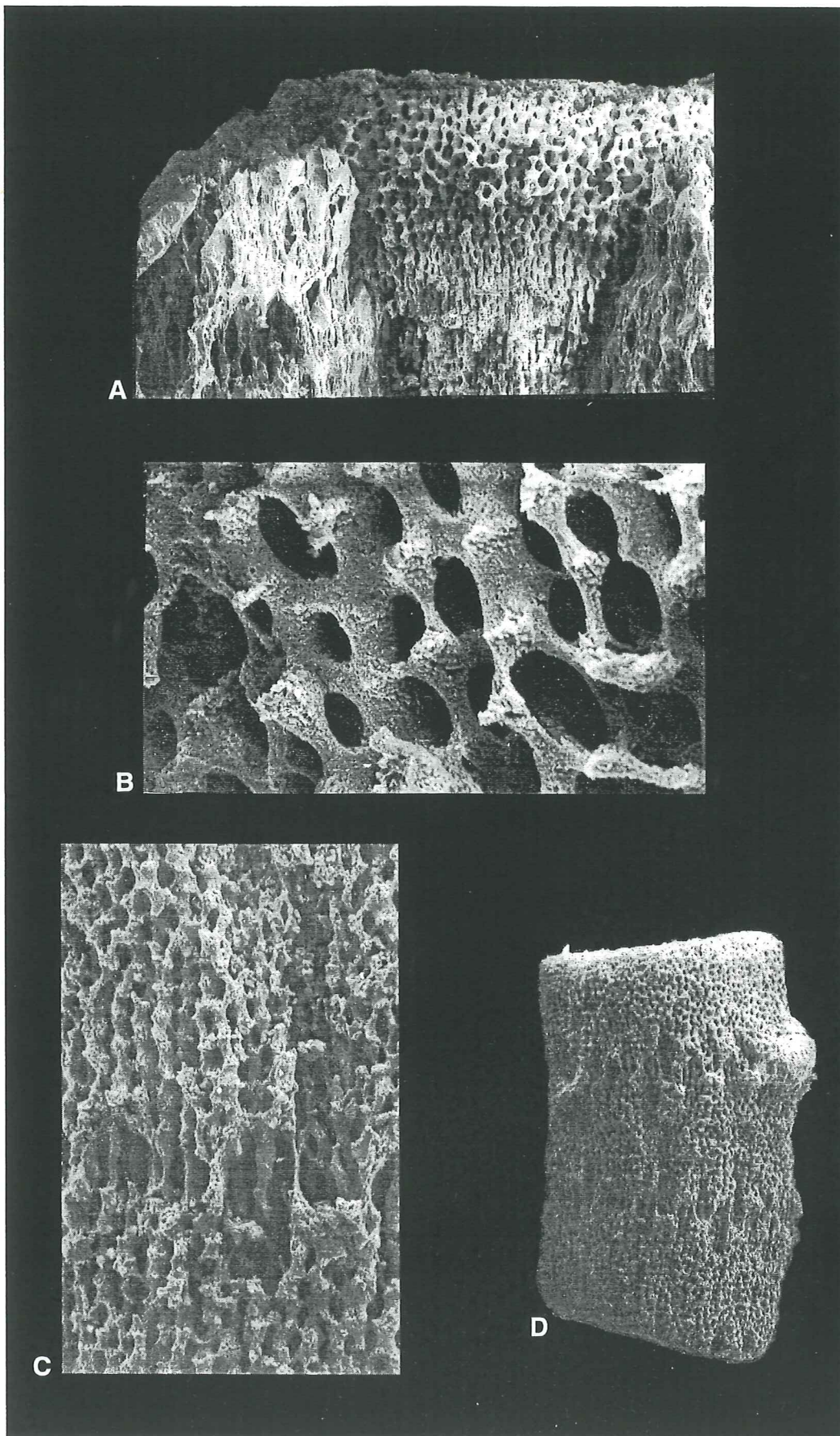
pattern of closely packed crystals giving the surface something best described as an icy coating. Lamboy (1987) noted in his work about the phosphatization of echinoderm fragments, that the outer surface of his fragments had a thin phosphatic film due to secondary diagenetic alteration which gave the fragments the shiny surface that usually can be observed in phosphatic grains. The shiny surface that he described closely resembles that called sugary in this paper. He further noted that the fragment also becomes better rounded due to this thin phosphatic film and that often two generations of phosphate occur, where the sugary one is the latest. This type of phosphatic preservation can involve a whole fragment or only the outer parts of it. The former type is the most common. This type often results in an almost totally closed pore system. Fig. 7A shows a columnal where this type of preservation occurs. The columnal illustrated is pentameric and circular with a well-developed areola with a probably pentagonal lumen. The outer parts show a sugary preservation with the typical shiny phosphatic film that occurs as a coating of these parts. The inner parts have a more rod-like preservation (see below). Fig. 7B illustrates a blow-up of the same columnal and here the shiny phosphatic film can be seen very clearly. The coating gives the columnal surface a more rounded outline (see above). In some places the coating is better developed, which results in a more complete shiny surface with a typical icy appearance. Note also how the coating rather efficiently fills up the pore-space. The coating consists of closely packed phosphate crystals with well-developed euhedral surfaces. The transition between "sugary" and rod-like preservation is sharp. The meric sutures do not seem to have been affected by the transition to a shiny phosphatic coating. Fig. 7E and 7F also depicts this kind of preservation but it differs somewhat to that described above. Fig. 7E shows a rather long and slender columnal, where the articulation is synostial. The outer parts are sugary with a thin phosphatic film made up by rather closely packed phosphate crystals (see Fig. 7F). The inner parts are preserved as substitution of the original calcitic structure with phosphate (see Fig. 7F). This means that the original structure is preserved. The transition between the different types is quite sharp with only a minor zone of mixing.

Fig. 6. **A-B.** Part of a long and slender rhombiferan columnal from Öl 93-12. A, blow-up of the upper parts of the columnal with an outer sugary preservation and an inner replacement preservation; x180. B, blow-up of the inner extremely well preserved zone of stereom; x1100. **C-D.** Three columnals which are still articulated from Öl 92-9. C, blow-up of the articulation area between two columnals; x430. D, overview of gently bent stem; x120.

The phosphate crystals of the outer zone are not as closely packed as in Fig. 7B but they have quite well-developed euhedral surfaces although not as well-developed as in Fig. 7B. They are also more extended along the columnal. An inner zone next to the outer one can be distinguished and it consists of phosphate crystals which are arranged in a more open structure so that they do not completely fill in the original stereom pores. This in combination with the former type gives the columnal surface a wavy outline, where one phosphate crystal often can be followed in the length direction of the columnal from one side to the other. Fig. 6A shows a part of a long and slender columnal with synostial articulation. The outer parts are preserved as sugary and the inner show a complete replacement of calcite with phosphate resulting in an excellent preservation. The sugary part shows a rather open frame-work in some places and the phosphate crystals are developed as long continuous sheets that run along the length of the columnal (also compare with Fig. 7E and 7F). The outer sugary surface of the columnal shows well-developed euhedral phosphate crystals. What is interesting to note in this columnal is that the very well preserved inner core of replacement is cone-shaped in outline. Looking at the whole columnal this zone is thinnest in the middle and then it widens outwards towards the columnal margins in the area of the articulating facets (see Fig. 6A). This means that this replacement zone seems to follow a very distinct path through the columnal (see below for discussion). Fig. 6B shows a blow-up of Fig. 6A with the excellently preserved original stereom structure. Also note the very small interconnecting stereom ribs that occur in some places. Only minor abrasion has occurred on the interconnecting knobs. Fig. 6D shows a very well preserved part of a stem consisting of three columnals, which are still fused together. The articulation of the columnals on which the articular facet can be seen is synostial. The articulation of the columnals which are still fused together most likely also is synostial. The stereom is preserved as complete replacement of calcite with phosphate, resulting in an excellent preservation. Also notice how the stereom attains a more open meshwork when passing over the articular facets of each columnal. Fig. 6C shows this area and it can clearly be seen that the stereom changes its outline when passing over the interconnecting area (the articular facet of each columnal) between two columnals. The whole stem is gently bent and each columnal has a wedge-shaped outline. Sugary preservation is present in the connection between the middle and topmost columnal. This preservation type has clearly invaded the more open meshwork of the interconnecting area between the two columnals. Possibly all of the columnals originally were coated with this thin phosphatic film (sugary preservation). See also discussion below. The stereom can be
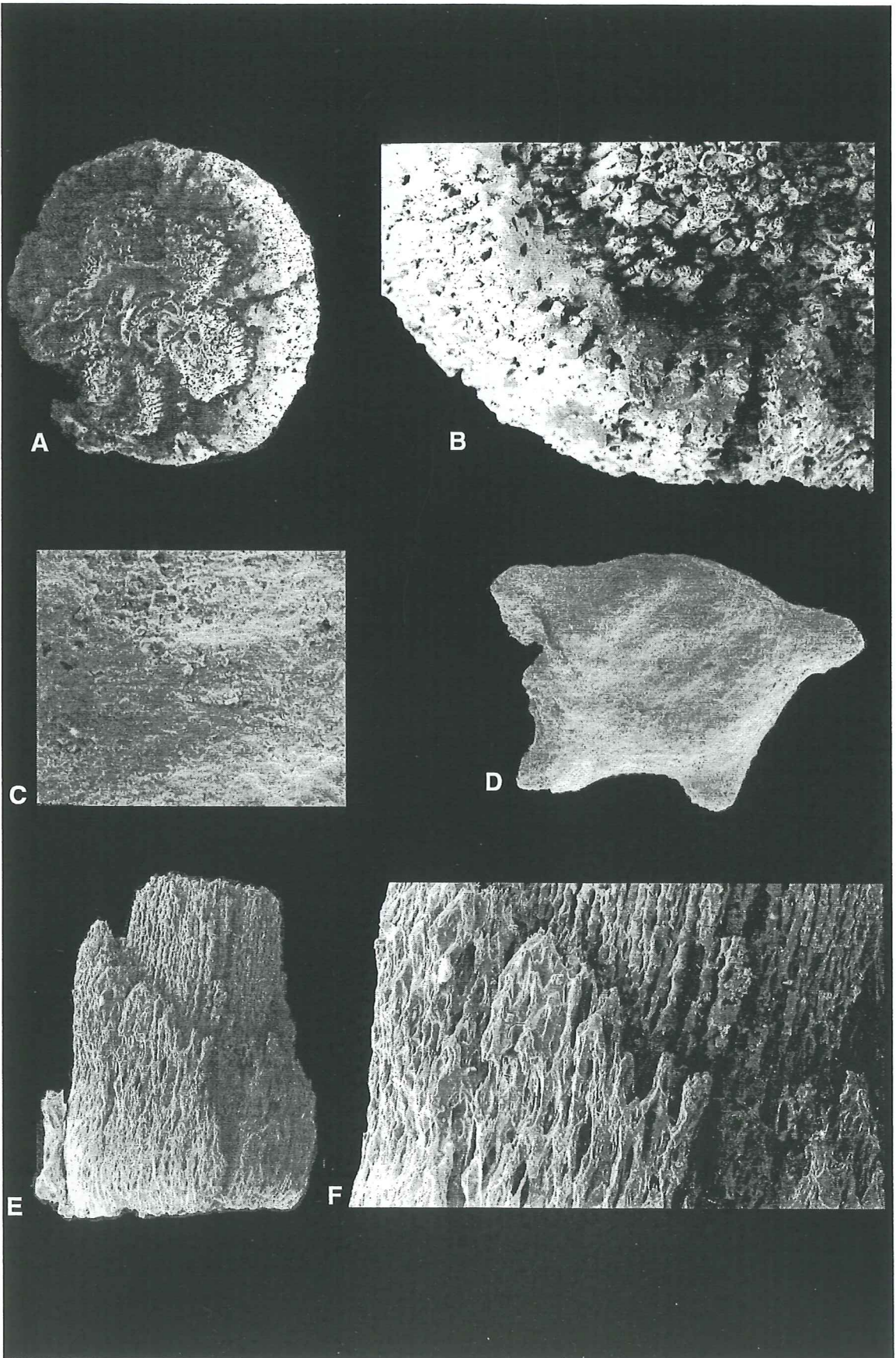
called galleried.

Type 3. - This type is called rod-like. The phosphate here occurs as long rods (radial fibrous) substituting much of the original stereom structure of the trabulae. The phosphate has filled up the open stereom pore space completely, so that now long rods of phosphate can be seen. Fig. 7B illustrates an example of rod-like preservation in an interconnecting area between sugary preservation and a preservation type that more resembles replacement of calcite with phosphate. This type is different from that where the phosphate replaces the original stereom structure resulting in excellent preservation (see above) and it also differs from that where a thin rind of phosphate has precipitated as a thin coating around the pore space. The rod-like preservation type possibly represents a further step, where the phosphate has precipitated in the whole pore-space and not only substituting for the original calcitic stereom structure or appearing as a thin rind around the original pore space. Most likely this type of preservation is very stereom type dependent (see discussion further on).

Type 4. - This type is intermediate between sugary, rod-like and total replacement of the original stereom structure with phosphate. These types often grade over into each other with a mixed zone in between. The sugary preservation is often restricted to the outer parts of the stereom and the rod-like in a zone next inside. In some fragments the rod-like zone can be seen passing over into an inner zone of phosphatized original calcitic trabecular. When this combination is present, there is also an outer zone of sugary preservation. Through an ordinary microscope the colour of the zones are as follows: white (outer zone, sugary) and then brown (inner zone - phosphatized original calcitic trabecular). This zonation also gives rise to varying preservation potential of the columnals as a whole. Some stratigraphic levels examined contain fragments that most likely are parted into two. This means that from an originally whole fragment there are now two,

one that is sugary (preservation of the outer parts of the stereom) and one that is phosphatized calcite (preservation of the inner parts of the stereom) appearing as replacement of the originally calcitic stereom. Fig. 7A and 7B illustrates examples of this with pictures of columnals, where these types of preservation appear fitted together as they were before parting occurred. One can clearly see that the outer parts are sugary and this zone gently passes over into a rod-like zone, which in turn passes over into a zone of what almost resembles phosphatized originally calcitic stereom. If this fragment became parted there would be one sugary (white) and one brown replacement structure (both containing phosphate). This has happened at many levels giving rise to some problematic systematic determinations.

Type 5. - The fifth type is coated with an unknown mineral possibly chamosite (no further studies have been carried out to investigate exactly which mineral it is). Chamosite is a ferrous mineral that is especially common at some levels of the section studied (see also Bohlin & Jaanusson 1955). Chamosite often precipitates as a coating on sand grains during early diagenesis. The echinoderm fragment is preserved with a thin coating of the mineral and in some places one can see through this coating (e.g. due to cracks in the coating) and get a glimpse of the stereom structure beneath. My observations indicate that beneath this crust, there is often a well-preserved stereom. When viewed through a light microscope the fragments have a light green colour (resembling that of chamosite) and it can clearly be seen that they have a coating. Fig. 7C and 7D shows this type of preservation. The coating clearly seen in Fig. 7D results in that the fragment obtains a more rounded shape in comparison with the original shape. Fig. 7C shows a blow-up of this.

Type 6. - This type is glauconitic. The glauconite also appears as a coating and sometimes it can be seen to have precipitated in the stereom pores. The colour is bright green. Sometimes a glauconitic grain has either precipitated or been trapped in the open lumen of a stem columnal. In some cases this grain has continued to grow and thereby cracked the stereom mesh-work wide open. Some fragments are half-glauconitic and half-phosphatized. It is well known that glauconite often occurs as an early diagenetic mineral.

Type 7. - The seventh type is pyritized. This type appears rarely, possibly due to the magnetic separation (see Material and methods), which has been performed on most of the samples.

Systematic palaeontology

Terminology. - The basic classification used herein is that suggested by Ubaghs (1978). More specialised classifica-

Fig. 7. **A-B.** A pentameric columnal showing transitional zones between the different types of preservation; from Öl 93-6. A, outer sugary preservation and inner rod-like preservation; x85. B, blow-up of A, showing the transition zone between sugary and rod-like preservation; x250. **C-D.** A holomeric spinose columnal showing that a coating of the original stereom has occurred; from Öl 93-8. C, blow-up of D showing a rather dense and homogeneous coating; x350. D, overview of C; x75. **E-F.** A long and slender columnal, possibly from a rhombiferan echinoderm, with two different preservational types; from Öl 93-6. E, the outer zone is preserved as sugary and the inner as total replacement of calcite with phosphate; x100. F, blow-up of E showing the sharp transition between the zones of sugary and replacement with calcite; x250.

tion systems have also been used (especially regarding class systematics). A combination of two systems has also been used in some cases and this is mostly due to the lack of compatible literature. Whenever some special type of systematics has been used this is mentioned in the text.

Stereom terminology follows that first suggested by Roux (1975) and then later modified and extended by Smith (1980). For an illustration of the different stereom types that Smith (1980) distinguished between, see Fig. 8. Indices, as first suggested by Moore et al. (1968) have not been used in this essay because of the impossibility to measure most of the columnals examined (the differentiation between lumen, crenulae and areola are in most cases hard to make out).

Whenever type (e.g. glyptocystoid columnal type a) is used, it refers to my own fabricated type classification. It has been used as a tool to separate between different types of fragments when I have not been able to assign a species name. The number of different ossicles and columnals counted in each sample is given in appendix A.

Measurements. - Measurements were made directly on the S.E.M Polaroid copy using a ruler with a mm-scale.

Occurrence. - The occurrence, amount and distribution of the different fragments are given in appendix A and in range-charts. Grouped together under this heading is also the first and last appearance within the samples examined. The letters used in given ranges are those given in Fig. 4. All fragments have not been counted in the samples (the fragment types that have been counted are listed in appendix A). The fragments that were not counted are those that were used as an illustration of preservation. Some columnals were also so poorly preserved that systematic determination was impossible. These are grouped together in appendix A as undetermined (e.g. undetermined columnals and pentagonal undetermined columnals).

Repositories. - Illustrated and cited specimens are stored at the Department of Geology, Lund University.

Subphylum Homalozoa Whitehouse, 1941
Class Stylophora Gill & Caster, 1960
Order Cornuta Jaekel, 1901

Terminology. - The terminology used in this class is that suggested by Ubaghs (1968). This also means that stylophorans are regarded as echinoderms and not as vertebrates as suggested by Jefferies (1968).

Stylocone spp.
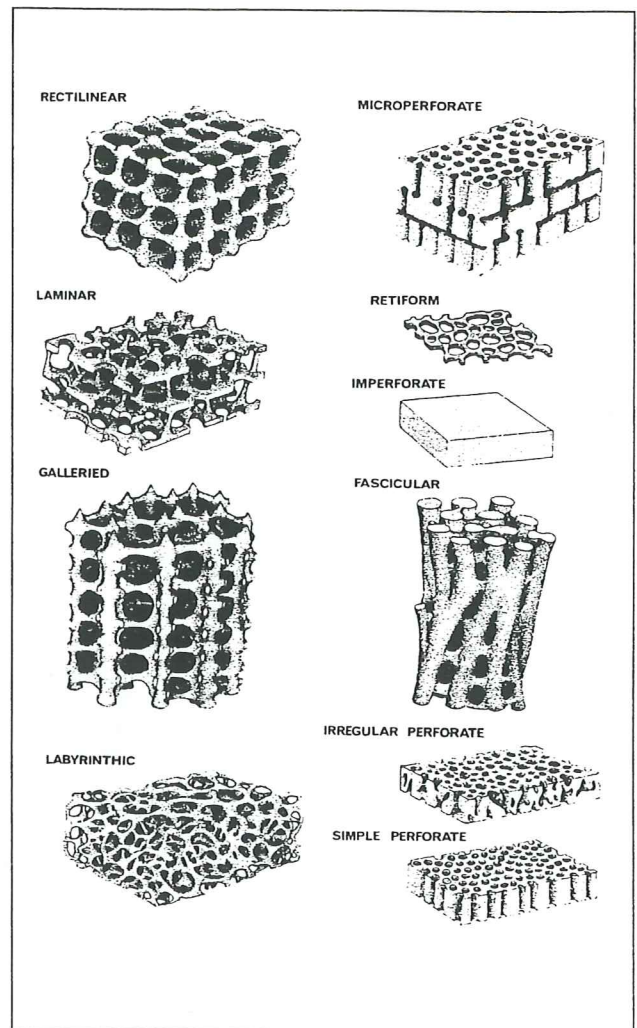
Fig. 8. Illustration of the stereom fabrics used herein and suggested by Smith (1980). Figure taken from Smith (1980).

Remarks. - Stylocones are rare, but specimens of varying size and shape have been found in some of the samples. The varying shapes are most likely family dependent or even genus dependent.

Stylocone type A
Fig. 9A (adoral view)

Description. - Short with a not so deep but rather broad proximal cavity that occupies most of the fragment. The distal face appears to be slightly abraded, which could suggest that it is the original shape that we are looking at now. Absence of median furrow and transverse channel might indicate that the stylocone has become broken after the death of the animal.

Occurrence. - Totally 3 specimens. Öl 97-12 to Öl 92-9; From just below Llanvirn boundary in K to top M.

Stylocone type B
Fig. 9B (adoral view)

Description. - The shape is long and slender with a rather deep and well-developed proximal cavity. The surface has been subjected to some weathering, because the transverse channels are just barely visible and the distal face is eroded. Preservation is replacement of original calcitic trabecular with phosphate. Length: 929 µm. Compare also e.g. with Ubaghs 1969, fig. 13.

Remarks. - Fig. 9D depicts a very poorly preserved stylocone?, where erosion has been severe but the main outline of the fragment can still be recognised. This fragment illustrates the heavy erosion that has occurred at some levels.

Occurrence. - Totally 5 specimens. Öl 93-6 to Öl 92-9; Basal K to top M.

Stylocone? type C
Fig. 9E

Description. - An ossicle with a well-developed median furrow and proximal cavity. Preservation is as coating of the original structure.

Remarks. - The strange shape of the distal region might indicate that this fragment may not be a stylocone ossicle.

Occurrence. - Totally 4 specimens. Öl 97-12 to Öl 92-6; mid K to topmost L.

Aulacophore

Remarks. - Aulacophore fragments are rather common in some samples. Their function is to build up the distal "tail" of cornutan echinoderms. See e.g. Ubaghs 1969, fig. 13:4 and fig. 14:3.

Aulacophore type A
Fig. 9C

Description. - Part of an aulacophore most likely from the more proximal region. Median furrow and transverse channels rather well developed though they are partly eroded.

Remarks. - Possibly this ossicle articulated directly against the stylocone. This suggestion is mainly based on the shape of the fragment, where the proximal face is wider than the distal face giving the fragment a cone like shape. The fact that this fragment type is rather rare within my material could also suggest that each animal just had one type A ossicle in its aulacophore.

Occurrence. - Totally 23 specimens. Öl 93-6 to Öl 92-6; K to topmost L.

Aulacophore type B
Fig. 9F

Description. - This type is part of the distal region of an aulacophore of a cornutan echinoderm. Median furrow is well developed and preserved. The lateral depressions that normally occur on the sides of the median furrow are not visible. Also note the concave articulation surfaces. Erosion of the fragment illustrated is also minor. Ornamentation on one side also occurs on some of the fragments. Length = 309µm and Width = 536µm (illustrated specimen). Compare also this ossicle with Ubaghs 1969, fig. 14.

Remarks. - It should also be noted that this type of distal aulacophore fragment is not genus dependent, so the same type can occur within many cornutan families. Naturally, the size of this type of fragment may vary greatly, depending on the original size of the animal from where it came. This type is also the most common remains from cornutan echinoderms in my material, as the aulacophore consists of many such fragments.

Occurrence. - Totally 22 specimens. Öl 94-6 to Öl 93-8; H to base of N.

Subphylum Echinozoa Haeckel in Zittel, 1895
Class Cyclocystoidea Miller & Gurley, 1895
Family Cyclocystoididae S. A. Miller, 1882

Terminology. - Descriptive terms follow those used by Smith & Paul (1982).

Remarks. - Berg-Madsen (1987) noted the occurrence of cyclocystoids when working with the section at Hälludden (upper Arenig). She described a new genus and the earliest known occurrence of this class ever. Numerous marginal ossicles have been found in my samples at various levels though most of them do not resemble those described by Berg-Madsen (1987). Two main types have been distinguished, although none of them has been given a generic name. Another type of marginal ossicle also occurs in some samples, but it is too poorly preserved to be described at all. It should be noted that the ossicles described here from Gillberga are restricted to upper Arenig beds.
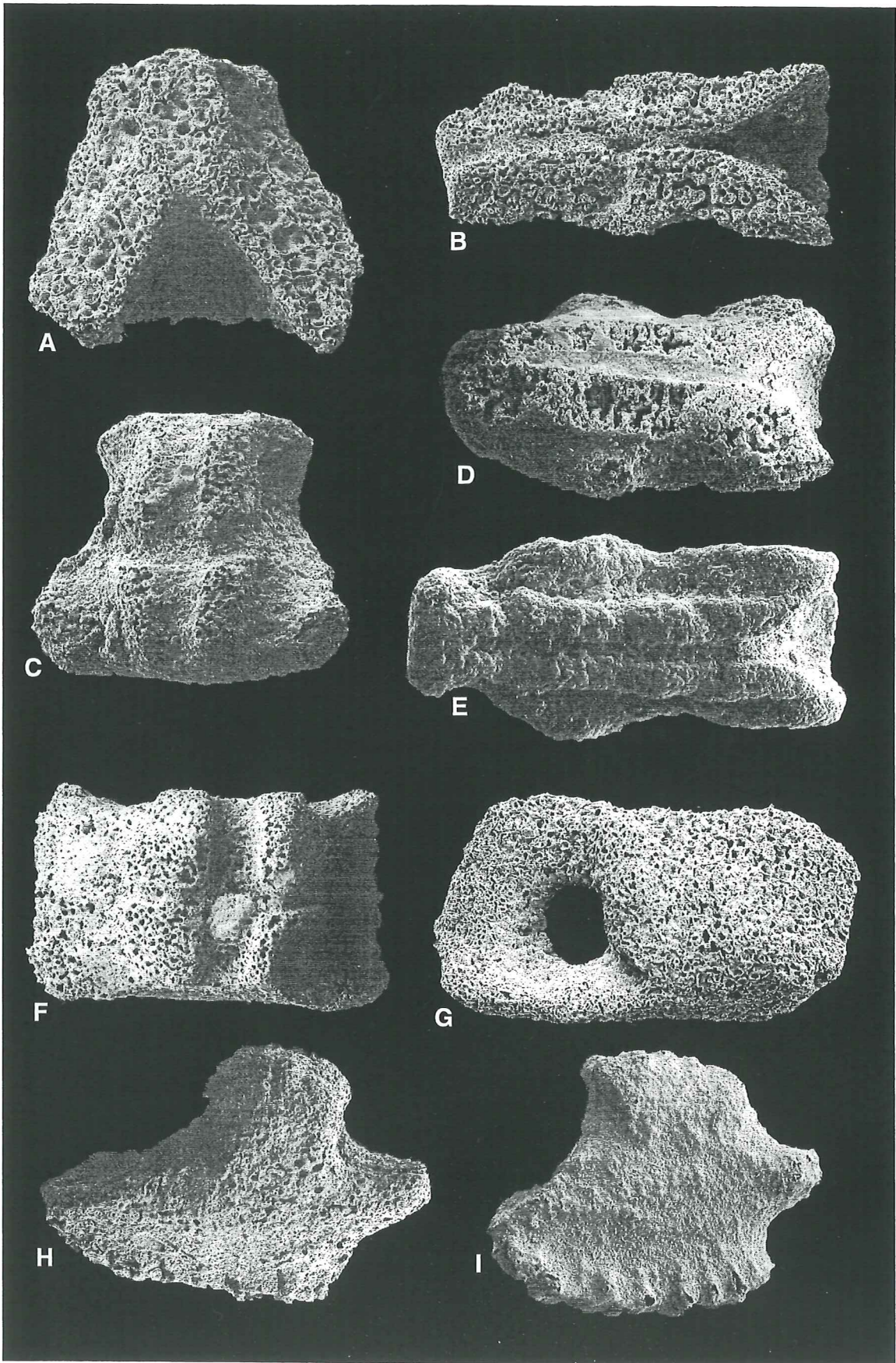
Cyclocystoididae type A (possibly *Monocycloides oelandicus* Berg-Madsen, 1987)
Fig. 9H (lateral view)

Description. - This ossicle shows similarities with *Monocycloides oelandicus*, which was described by Berg-Madsen (1987, plate 15, fig. 4 and plate 16, fig. 4). Crest is convex and shows no ornamentation (possibly because of the poor preservation). The crest is also broader than long and the width of the crest is less than the width of the ossicle. Radial facet well developed. Preservation is phosphatic without a coating.

Occurrence. - Totally 15 specimens. Öl 94-5 to Öl 97-12; H to middle K.

Cyclocystoididae type B
Fig. 9I (lateral view)

Description. - A marginal ossicle which is very compact in outline. Length almost coincides with height. The crest is almost as broad as half the height. The crest width almost coincides with crest length. Some pustules can be seen on the crest. Radial facet is rather well developed. Tubercles are not present, probably because of the poor preservation. Preservation is as a coating of the original ossicle structure. The crest is convex in shape and ornamented. Facets are less obvious due to the preservation. Width is almost equally along the length of the ossicle. The underside is heavily ornamented with ridges extending across it.

Occurrence. - Totally 6 specimens. Öl 92-3; middle K.

Subphylum Crinozoa Matsumoto, 1929

Remarks. - Descriptive columnal terms used herein are those advocated by Donovan (1986). For a short description of these see Fig. 10. Other terminology follows that suggested by Moore et al. (1968).

Class Rhombifera Zittel, 1879

Fig. 9. **A-B, D-E.** Stylocones. A, type A; from Öl 97-12, x190. B, type B; from Öl 93-6, x85. D, type A; from Öl 92-9, x140. E, Stylocone? type C; from Öl 92-6, x140. **C, F.** Aulacophores. C, type A; from Öl 93-6, x150. F, type B; from Öl 92-3, x95. **G.** Undet. Asteroz.? oss. type E; from Öl 97-12, x140. **H-I.** Cyclocystoid ossicles; from Öl 92-3. H, type A, x120. I, type B, x100.
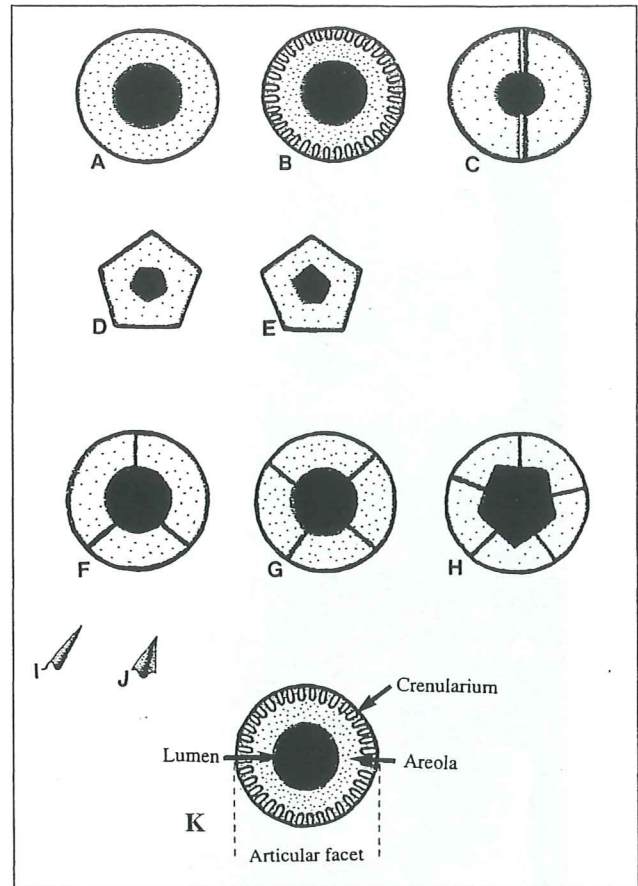
Fig. 10. Illustration of descriptive terms according to Donovan (1986), used when describing columnal morphology. **A-C.** Articulation types. A, synosty. B, symplexy. C, synarthry. **D-E.** Relationship between columnal and lumen angles. D, non-coincident. E, coincident. **A, F-H.** Meric relationships. A, holomeric. F, trimeric. G, tetrameric. H, pentameric. **I-K.** descriptive

Rhombiferan columnal type A
Fig. 11B

Description. - A small ribbed columnal with a small central cyclic lumen. Articulation is synostial. The articulation surface resembles a flower in outline. Compare e.g. with Pisera (1994, pl. 63, fig. 20-21).

Occurrence. - Totally 2 specimens, Öl 92-9 to Öl 93-10C; top M to middle P.

Rhombiferan? columnal type B
Fig. 11C

Description. - A circular columnal with a circular point sized lumen occurring in the middle. Latera of columnal is undulating. Articulation is synostial.
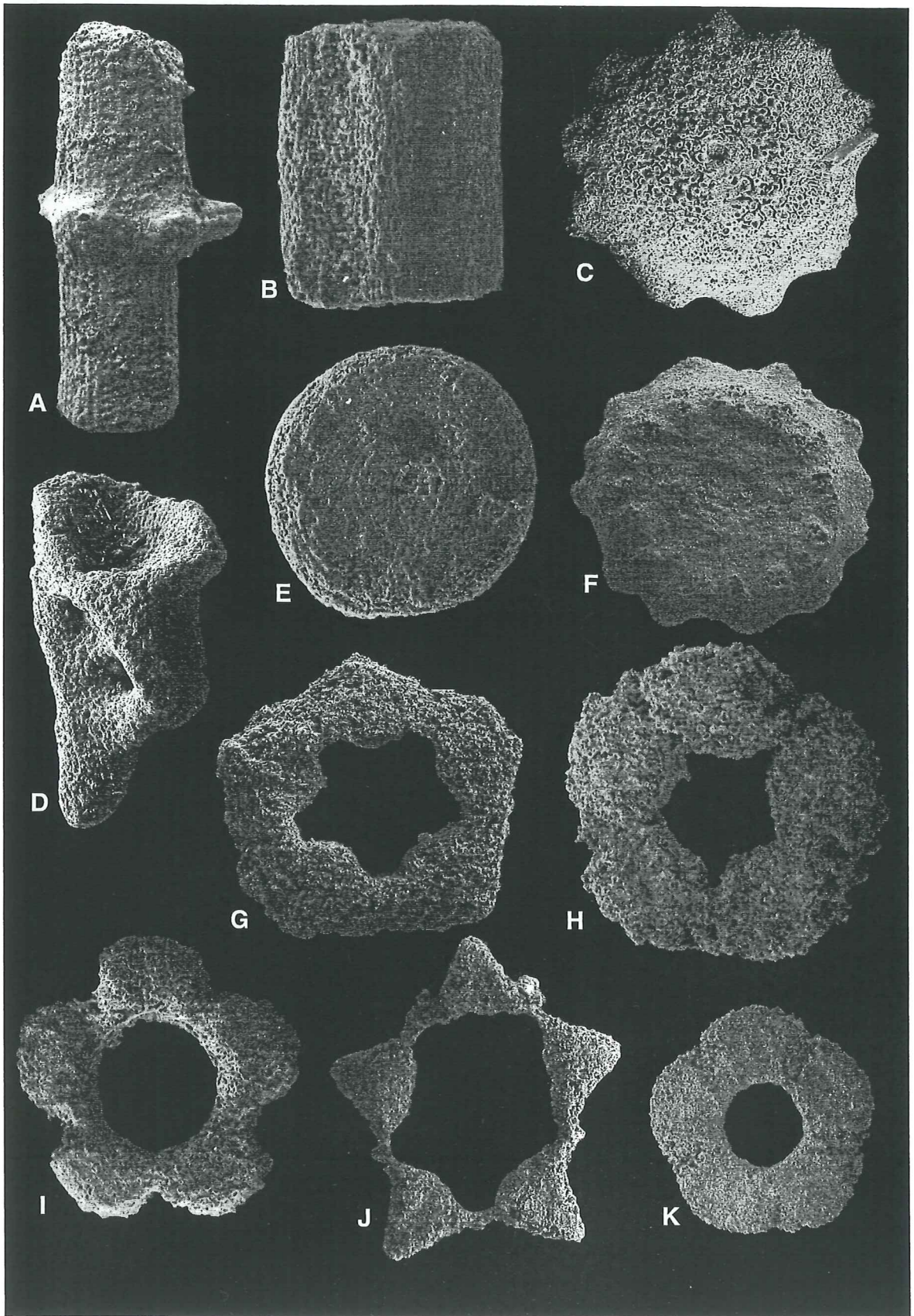
Remarks. - Most likely a rhombiferan cystoid columnal.

Occurrence. - Totally 5 specimens, Öl 93-6 to Öl 97-12; base K to mid K.

Rhombiferan? columnal type C
Fig. 11E

Description. - A circular holomeric columnal with synostial articulation. Lumen is hardly visible but appears to be point-sized and circular.

Remarks. - Most likely a proximal rhombiferan cystoid columnal. This columnal type is very common in many samples and it may vary somewhat in height, but otherwise the overall columnal outline is the same.

Occurrence. - Totally 34 specimens, Öl 97-12 to Öl 93-12; mid K to mid Q.

Rhombiferan columnal type D
Fig. 20A, B

Description. - A long and completely straight columnal with synostial articulation and a rather small lumen.

Remarks. - This type is extremely common at some levels and it may also vary greatly in height. Possibly these height differences may reflect different parts of the stem (distal and proximal), where the columnals with the greatest height represents more distal columnals. Another possibility is that the height mainly is genus dependent.

Occurrence. - Totally 577 specimens, Öl 94-6 to Öl 92-9; H to M.

Superfamily Glyptocystitida Bather, 1899

Glyptocystoid columnal type A
Fig. 11A

Fig. 11. **A.** Glyptocystoid col. type A; from Öl 92-3, x140. **B-C, E.** Rhombiferan columnals. B, Rhombiferan col. type A; from Öl 92-9, x190. C, Rhombiferan? col. type B; from Öl 93-6, x120. E, Rhombiferan? col. type C; from Öl 92-9, x150. **D.** Ambulacral oss. type F; from Öl 97-12, x100. **F.** Holomeric cyclic col. type A; from Öl 92-3, x100. **G.** *Bystrowicrinus* (col.) sp. A; from Öl 97-12, x150. **H.** *Sidericrinus*? (col.) sp. A; from Öl 93-11, x130. **I.** *Pentagonocyclopa*? (col.) sp. A; from Öl 93-11, x110. **J.** Holomeric col. five development. type A; from Öl 93-11, x110. **K.** *Baltocrinus*? (col.) sp. A; from Öl 93-11, x75.

Description. - A long and slender holomeric columnal with spiny projections in the middle section. The columnal also has a ribbed outer surface. Articulation is synostial with a small central round lumen. Most likely this fragment represents a distal glyptocystoid columnal. The illustrated specimen is abraded leaving spines that have almost rounded tips.

Remarks. - This type of columnal is rather common at some levels, but it is not as common as the other types of glyptocystoid columnals. Compare also with glyptocystoid columnal type C (Fig. 12D), which is of the same type but lacks the prominent spiny projections in the middle, which have been replaced by a more swollen area.

Occurrence. - Totally 21 specimens, Öl 92-3 to Öl 93-11; mid K to top P.

Glyptocystoid columnal type B
Fig. 20C

Description. - A double cone-shaped holomeric columnal from the distal parts of a glyptocystoid, showing almost perfectly preserved rectilinear stereom structure (illustrated specimen). Only minor etching of the stereom has occurred when treating the samples with acetic acid. Articulation is synostial and the lumen round. One of the most common types of glyptocystoid columnal in my material.

Occurrence. - Totally 87 specimens, Öl 94-6 to Öl 92-6; H to L.

Glyptocystoid columnal type C
Fig. 12C, D

Description. - A long and slender distal holomeric glyptocystoid columnal with a widening of the stereom occurring in the middle. Most likely rectilinear stereom (see blow-up Fig. 12C) and with a synostial articulation and circular lumen.

Remarks. - The stereom shows some etching on the interconnecting knobs, possibly due to the treatment with acetic acid. It seems as if the stereom is a negative imprint of the original structure.

Occurrence. - Totally 51 specimens, Öl 94-6 to Öl 92-8; H to mid M.

Glyptocystoid columnal type D
Fig. 13A

Description. - A holomeric round columnal with a round lumen. The surface of the ossicle is smooth with synostial articulation. Most likely a proximal glyptocystoid columnal.

Remarks. - Donovan (1989*a*) described some columnals (e.g. *Annulocolumnus*) resembling the one described here. He assigned these to crinoids based on the fact that in his samples nothing pointed to the presence of glyptocystoids. In my samples glyptocystoids are obviously present so therefore I regard this ossicle type as belonging to these.

Occurrence. - Totally 124 specimens, Öl 93-3 to Öl 94-201; upper I to top of section.

Glyptocystoid columnal type E
Fig. 13D

Description. - A holomeric round columnal with a rather small round lumen. Areola not present but a depressed circular area can be seen next to the lumen (areola or not?). This area extends outwards to the border of the ossicle where it has its highest position. This means that the area gently slopes towards the lumen from the neighbouring sides.

Remarks. - Possibly this fragment is a proximal glyptocystoid columnal (compare e.g. with Pisera, 1994 pl. 63, fig. 1).

Occurrence. - Totally 26 specimens, Öl 93-3 to Öl 94-201; upper I to top of section.

Glyptocystoid columnal type F
Fig. 13E

Description. - A round holomeric columnal with spines, which are part of the original stereom. Articulation is synostial with a small round lumen occurring in the middle. The areola seems to be somewhat depressed. Some abrasion has occurred and some of the spines have been broken off followed by erosion, leaving well-rounded spine tips.

Remarks. - This columnal is most likely from the proximal part of the stem. The stereom is preserved as an internal mould of the original structure.

Occurrence. - 1 specimen, Öl 97-12; mid K.

Class Crinoidea J.S Miller, 1821

Terminology. - Descriptive terms and systematic classification generally follow that used by Donovan (1986). In some cases descriptive terms and classification follow Stukalina (1988). Whenever her terms are used this is mentioned in the text. The systematic classification of crinoids has recently been reevaluated by Ausich (1998), but this classification has not been adopted herein.

Columnals with a 4-fold symmetry

Group Quadrilaterata Stukalina, 1966 (classification system according to Stukalina 1988)
Family Dwortsowaecrinidae Stukalina, 1980
Fig. 21E

Description. - A holomeric tetragonal columnal with a wide and tetragonal lumen, where lumen angles coincide with columnal corners. Articulation is symplectial.

Remarks. - Compare this type with e.g. that described by Stukalina 1988, text-fig. 21:2.

Occurrence. - Totally 2 specimens, Öl 94-201; top of section.

Subclass Inadunata Wachsmuth & Springer, 1881
Order Disparida Moore & Laudon, 1943
Family Ramseyocrinidae Donovan, 1984
Genus *Ramseyocrinus* Bates, 1968

Ramseyocrinus cambriensis (Hicks, 1873)
Fig. 14B

Description. - A poorly preserved specimen with tetragonal lumen, where angles coincide with the meric sutures. Lumen sides gently curve inwards (concave). Articulation is synostial.

Remarks. - Not very common probably due to the poor preservation potential of the columnal because of its fragile construction.

Occurrence. - Totally 4 specimens, Öl 92-9 to Öl 93-11; top M to top P.

Ramseyocrinus? sp. A
Fig. 14A

Description. - A holomeric tetragonal squarish columnal. Lumen outline too poorly preserved to be described.
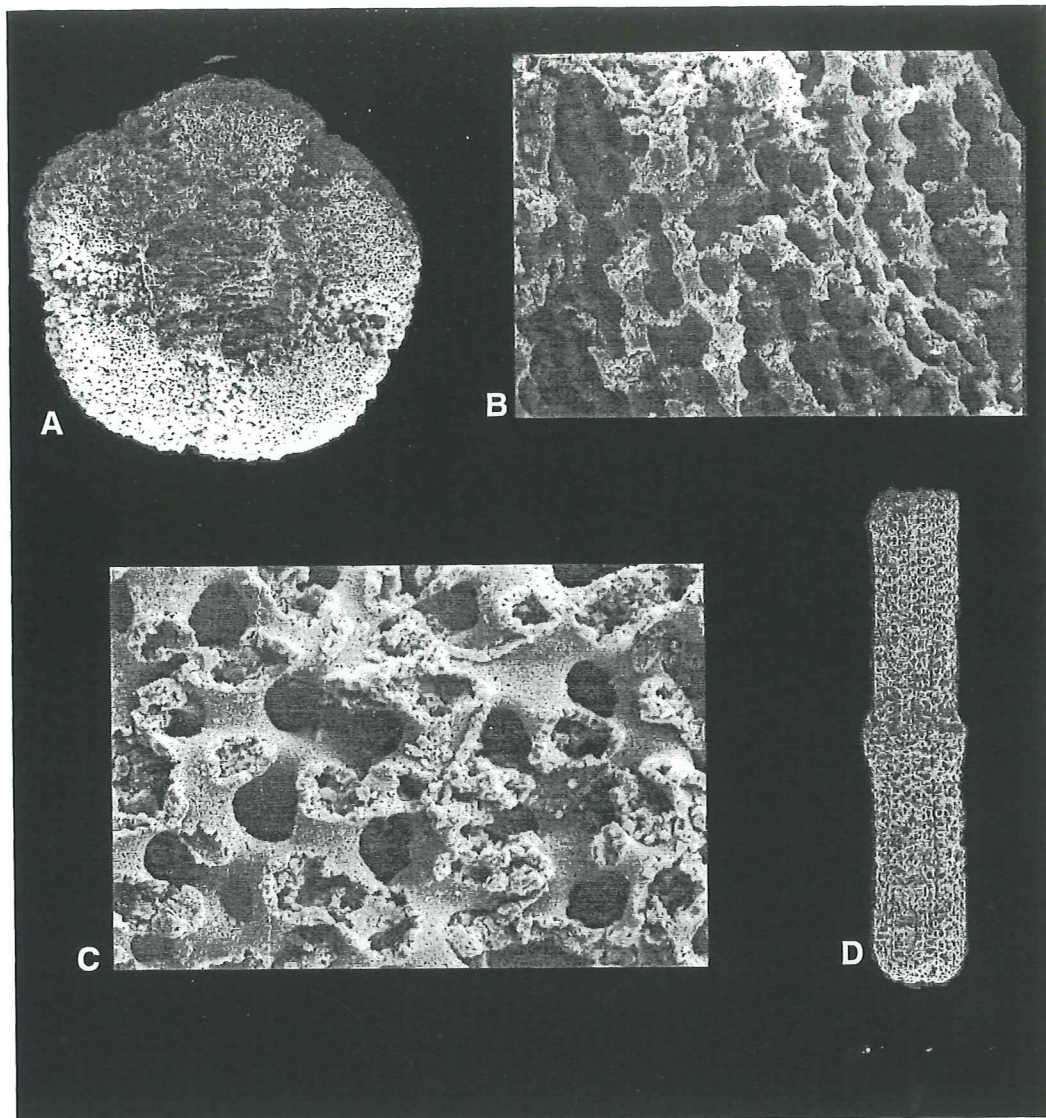
Fig. 12. **A-B.** Pentameric col. type A; from Öl 93-12. A, x90. B, blow-up of A, x600. **C-D.** Glyptocystoid col. type C; from Öl 97-12. C, blow-up of D, x1200. D, x130.

Columnal corners are well rounded. The overall preservation of the columnal is poor. Articulation possibly synostial.

Remarks. - Most likely this columnal type belongs within this genus due to the fact that *Ramseyocrinus* overall is the most common genus with tetragonal columnals within my samples and that this columnal type obviously also occurs in association with *Ramseyocrinus* columnals. Possibly the different types may reflect different parts of the stem (older evolutionary steps are retained in the more distal part of the stem). Donovan (1984a) discussed the occurrence of this genus in the British Isles during Ordovician time.

Occurrence. - Totally 3 specimens, Öl 92-1 to Öl 97-12;

mid J to mid K.

Ramseyocrinus? sp. B
Fig. 14C

Description. - A holomeric tetragonal columnal with a central small tetragonal lumen. Lumen angles are well rounded (almost tetrastellate) and coincide with columnal sides. Columnal corners seem to be somewhat outward pointing (compare with Fig. 14D). Articulation seems to be synostial.

Remarks. - Donovan (1986) noted that the distal stem of the genus *Ramseyocrinus* often has holomeric columnals. The overall lumen outline of the columnal described also best matches the lumen description for this genus (com

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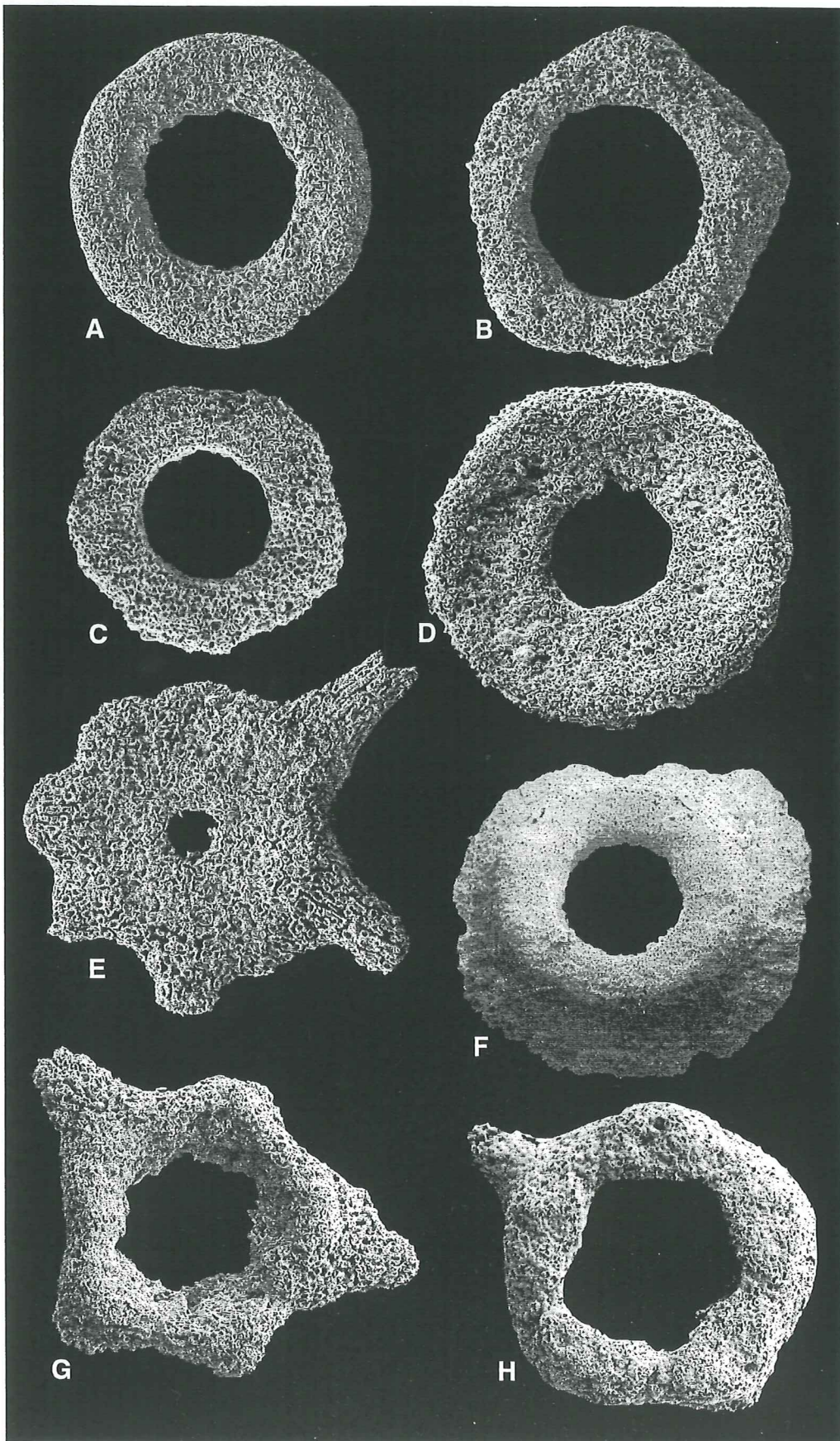
pare with e.g. Fig. 14B).

Occurrence. - Totally 14 specimens, Öl 97-12 to Öl 94-201; mid K to top of section.

Ramseyocrinus? sp. C
Fig. 21H

Description. - A tetrameric tetragonal squarish columnal with a tetrastellate lumen. Lumen angles are well rounded and they coincide with the meric sutures and the columnal sides. Articulation is synostial.

Remarks. - Most likely this columnal belongs within the genus *Ramseyocrinus* based on its overall outline.

Occurrence. - Totally 11 specimens, Öl 97-12.

Family Iocrinidae Moore & Laudon, 1943
Genus *Iocrinus* Hall, 1866
Iocrinus? sp. A
Fig. 21F

Description. - A holomeric pentagonal columnal with a central circular lumen. The areola is divided into five distinct pits, which coincide with the columnal angles. These pits are separated from each other by ribs, which coincide with the columnal sides. A small perilumen also exists.

Remarks. - This columnal type most likely belongs within the genus *Iocrinus* based on the description given by Donovan (1986). This genus also shows a perfect match in time based on the observation done by Donovan (1986).

Occurrence. - Totally 14 specimens, Öl 94-6 to Öl 93-12; H to upper Q.

Family Babanicrinidae Stukalina, 1969
Genus *Babanicrinus* Stukalina, 1969

Remarks. - Stukalina (1988) used a classification where this family was placed in her group *Pentamerata* and

within the order *Angulata*.

Babanicrinus? sp. A
Fig. 15A

Description. - A holomeric round columnal with a small central pentagonal lumen. Areola is divided into five distinct areola pits. The ridges between these correspond to the lumen angles. The pits are almost saddle-shaped and correspond to the lumen sides. A not so distinct perilumen also seems to occur around the lumen.

Remarks. - Pisera (1994, pl. 61, fig. 11) described an identical columnal. He also suggested that this columnal could belong to the genus *Babanicrinus*. It is likely that the areola pits in their original state had a different type of stereom in comparison with the rest of the columnal, though it is not possible to see this difference in its present state. Possibly a small tendency can be seen when comparing the overall stereom outline but no certain conclusions can be drawn regarding this.

Occurrence. - Totally 18 specimens, Öl 94-5 to Öl 93-11; top H to top P.

INCERTAE SEDIS

Genus *Tetragonocyclicus* (col.) Donovan, 1989*a* (*non* Yeltysheva, 1956)
Tetragonocyclicus? (col.) sp. A
Fig. 14D

Description. - A holomeric cyclic columnal with a tetrastellate lumen. Lumen angles coincide with columnal sides. Spiny outgrowths occur in a four-fold symmetry with the columnal sides. Articulation possibly symplectial from the beginning.

Remarks. - Possibly this columnal belongs to this morphogenus, which has a range of lower to upper Ordovician (Donovan 1989*a*).

Occurrence. - Totally 4 specimens, Öl 93-11; top P.

HOLOMERIC COLUMNALS WITH A CYCLIC SYMMETRY

Holomeric cyclic columnal type A
Fig. 11F

Description. - A holomeric cyclic columnal with a small central circular lumen. Articulation is symplectial with

Fig. 13. **A, D-E.** Glyptocystoid columnals. A, type D; from Öl 97-12, x170. D, type E; from Öl 93-6, x180. E, type F; from Öl 97-12, x160. **B, F.** Holomeric cyclic columnals. B, type B; from Öl 97-12, x150. F, type C; from Öl 93-6, x90. **C.** Pentameric? col. type G; from Öl 92-9, x120. **G-H.** Holomeric columnals five development. G, type B; from Öl 97-12, x180. H, type C; from Öl 92-3, x180.
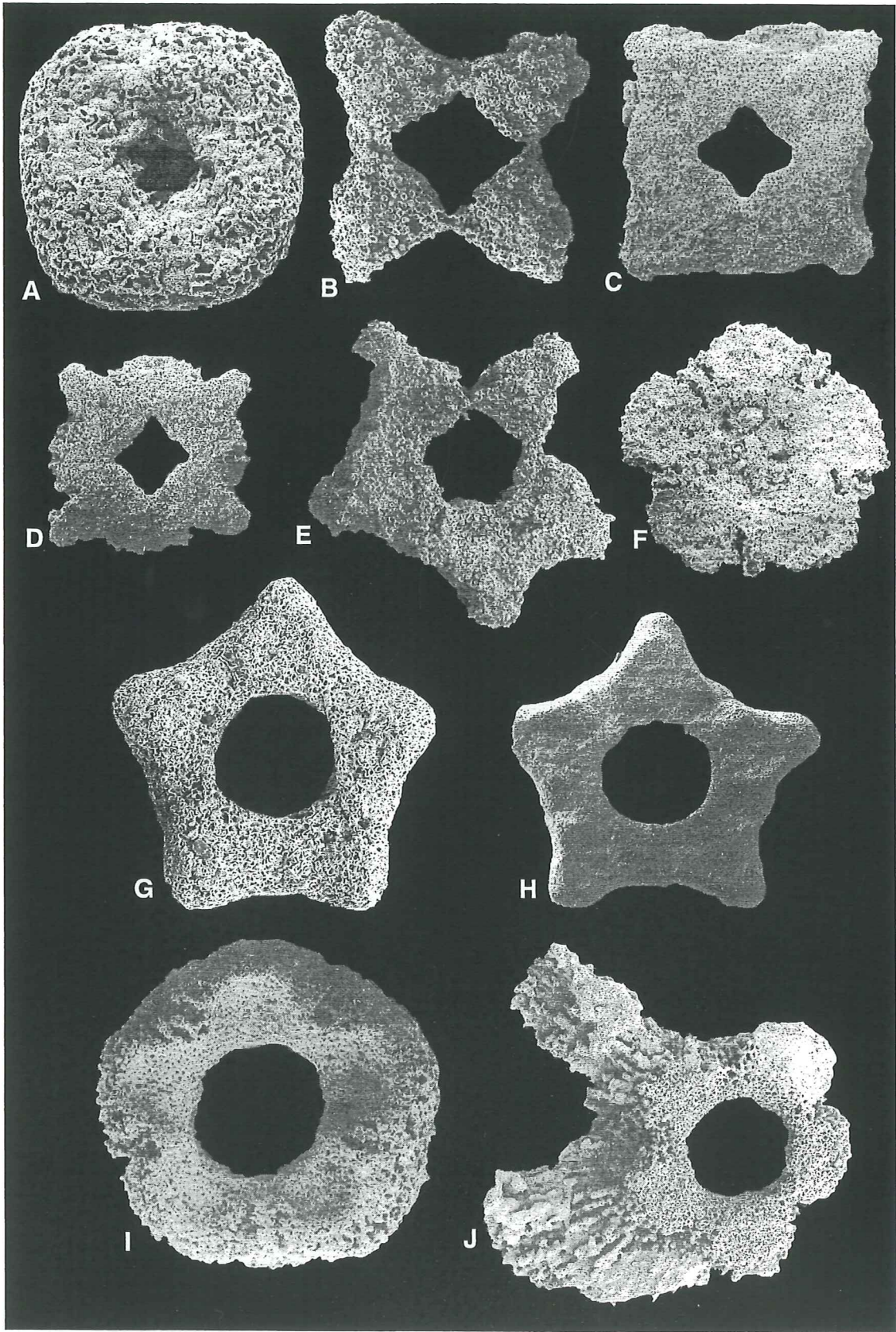
well-developed crenulae. Latera ornamented with outgrowths, giving it an undulating surface.

Remarks. - Possibly a cystoid columnal or possibly a crinoid columnal (nodal?).

Occurrence. - Totally 4 specimens, Öl 92-3; mid K.

Holomeric cyclic columnal type B
Fig. 13B

Description. - A holomeric, pentagonal columnal with a broad circular lumen. The pentagonal columnal angles are well rounded. Articulation seems to be synostial.

Remarks. - Possibly from a crinoid (compare also with Pisera, 1994, pl. 62, fig. 1).

Occurrence. - Totally 38 specimens, Öl 94-6 to Öl 92-9; basal H to top M.

Holomeric cyclic columnal type C
Fig. 13F

Description. - A very eroded holomeric columnal with a circular outline. Lumen circular and articulation seems to be synostial. Latera is convex, flange-like.

Occurrence. - Totally 3 specimens, Öl 93-6; base K.

Genus *Cyclocyclicus* (col.) Yeltysheva, 1955

Remarks. - The morphogenus *Cyclocyclicus* (col.) is the best represented morphogenus in many of my samples. The distinction between different species described is very small but here I have chosen to differentiate between columnal morphospecies that seem to differ consistently. Most columnals within this morphogenus have symplectial articulation and the main differences between species are based on the width of the areola and lumen. Several samples also contain a remarkable amount of heavily

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eroded columnals that share many similarities with *Cyclocyclicus* (col.). For a description on the genus *Cyclocyclicus* (col.) see Donovan (1989a).

Cyclocyclicus? (col.) sp. A
Fig. 15D

Description. - A holomeric cyclic columnal with a circular? lumen occurring in the columnal centre. Areola is depressed and dips towards the lumen. Symplectial articulation is well developed with crenulae, which taper towards the lumen.

Occurrence. - Totally 25 specimens, Öl 92-9 to Öl 94-201; top M to top of section.

Cyclocyclicus (col.) sp. B
Fig. 20D

Description. - A cyclic columnal with a central round lumen. Areola rather well developed. Articulation is symplectial.

Remarks. - The most common type of *Cyclocyclicus* (col.) amongst the samples examined.

Occurrence. - Totally 290 specimens, Öl 92-2 to Öl 94-201; basal K to top of section.

Cyclocyclicus (col.) sp. C
Fig. 15H (side view)

Description. - A holomeric circular columnal with a central round lumen. Areola well developed and articulation is symplectial. Crenulae taper towards the lumen. The overall columnal outline is wedge-shaped.
Remarks. - Wedge-shaped ossicles of this kind are very common in some samples (just one illustrated and counted most of them are though ascribed to *Cyclocyclicus* (col.) sp. B). The wedge-shaped outline is not genus-dependent, so this type of ossicle can occur within a stem in combination with normal (not wedge-shaped) columnals of the morphogenus *Cyclocyclicus*. The difference in shape reflects the adoption of another type of life-style than a different morphogenus (wedge-shaped columnals indicates a bent-over type of life-style).

Occurrence. - Totally 1 specimen, Öl 92-9; top M.

Cyclocyclicus (col.) sp. D
Fig. 20E

Description. - A circular holomeric columnal with a cir

Fig. 14. **A-C.** *Ramseyocrinus* spp. A, *Ramseyocrinus?* sp. A; from Öl 97-12, x300. B, *Ramseyocrinus cambriensis*; from Öl 93-11, x140. C, *Ramseyocrinus?* sp. B; from Öl 93-11, x85. **D.** *Tetragonocyclicus?* (col.) sp. A; from Öl 93-11, x80. **E, G-H.** Holomeric columnals five development. E, type D; from Öl 93-11, x120. G, type E; from Öl 97-12, x140. H, type F; from Öl 97-12, x55. **F.** *Baltocrinus?* (col.) sp. B; from Öl 93-11, x85. **I.** Pentameric col. type B; from Öl 93-11, x85. **J.** *Ramulicrinus?* (col.) sp. A; from Öl 93-6, x80.
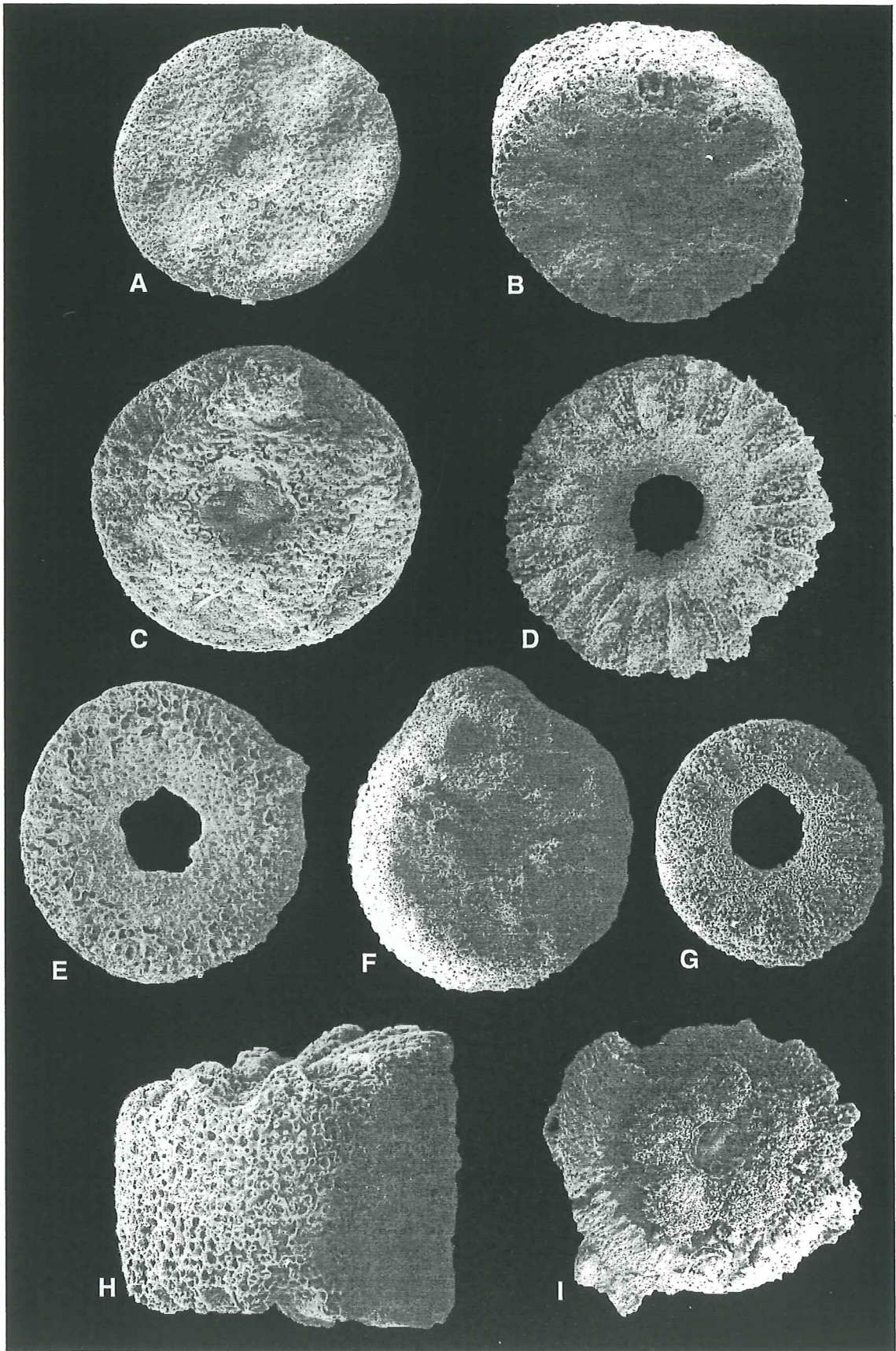
cular lumen. Areola is absent and crenulae wide and reach all the way to the lumen sides from the columnal sides. Articulation is symplectial and crenulae taper towards lumen.

Occurrence. - Totally 29 specimens, Öl 92-6 to Öl 94-201; top L to top of section.

Cyclocyclicus (col.) sp. E
Fig. 20F

Description. - A holomeric circular columnal with a very wide circular lumen. Areola is completely absent and articulation is symplectial.

Remarks. - This columnal shows some similarities with certain rhombiferan columnals but also with some crinoid columnals described by Donovan (1989*a*). Compare e.g. with Donovan 1989*a*, text-fig. 41B.

Occurrence. - Totally 19 specimens, Öl 92-9 to Öl 94-201; top M to top of section.

Genus *Pentagonoellipticus* (col.) Donovan, 1989*a* (non Yeltysheva, 1956)

Pentagonoellipticus? (col.) sp. A
Fig. 15B

Description. - A holomeric columnal with an elliptical outline. Lumen outline can not be seen. Marginal symplexy well developed, where crenulae almost extend to the area that is supposed to be that of the lumen. As seen from the side the columnal is wedge-shaped.

Remarks. - This columnal type is most likely not a product of deformation, so it should belong within the morphogenus *Pentagonoellipticus*. The wedge-shaped outline indicates a bent-over lifestyle of the animal.

Occurrence. - Totally 9 specimens, Öl 92-9; top M.

Fig. 15. **A.** *Babanicrinus*? sp. A; from Öl 93-11, x150. **B.** *Pentagonoellipticus*? (col.) sp. A; from Öl 92-9, x150. **C.** Heavily eroded columnal, possibly *Bystrowicrinus* (col.); from Öl 97-12, x250. **D, H.** *Cyclocyclicus* (col.). D, *Cyclocyclicus*? (col.) sp. A; from Öl 93-11, x95. H, *Cyclocyclicus* (col.) sp. C; from Öl 92-9, x190. **E, G.** *Pentagonocyclicus* (col.); from Öl 93-11. E, *Pentagonocyclicus* (col.) sp. A, x130. G, *Pentagonocyclicus* (col.) sp. B, x120. **F.** Pentameric columnal type C; from Öl 93-12, x130 **I.** *Ramulicrinus*? (col.) sp. C; from Öl 93-6, x70.

Genus *Pentagonocyclicus* (col.) Yeltysheva & Schewtschenko, 1960 (non Yeltysheva, 1955)

Remarks. - *Pentagonocyclicus* (col.) has been described by Donovan (1995).

Pentagonocyclicus (col.) sp. A
Fig. 15E

Description. - A holomeric circular columnal with a central pentagonal lumen. Lumen angles are well rounded. An areola seems to be developed with a denser stereom occurring as a coating of it. Articulation seems to be synostial, but it has probably been symplectial originally. The area where the crenulae were supposed to be also seems somewhat altered.

Occurrence. - Totally 3 specimens, Öl 93-11; top P.

Pentagonocyclicus (col.) sp. B
Fig. 15G

Description. - A holomeric circular columnal with a pentagonal lumen somewhat displaced from the centre of the columnal. A small areola occurs around the lumen. The areola gently slopes downwards against the lumen. A well-developed symplectial articulation can be seen. Crenulae taper towards the lumen.

Occurrence. - Totally 40 specimens, Öl 92-3 to Öl 94-201; lower K to top of section.

HOLOMERIC COLUMNALS WITH FIVE-FOLD SYMMETRY

Holomeric columnal with 5-fold development type A
Fig. 11J

Description. - A holomeric pentastellate columnal with a very broad pentastellate lumen. Lumen and columnal angles non-coincident. Lumen almost reaches the columnal border. Articulation seems to be synostial.

Remarks. - This columnal construction is regarded as very primitive (e.g. Stukalina 1988). The broad lumen was occupied by a very big axial connective commisure and articulation was very primitive. The overall construction of the columnal also naturally makes it extremely vulnerable to e.g. torsional movements.

Occurrence. - Totally 3 specimens, Öl 92-6 to Öl 93-11; top L to top P.

Holomeric columnal with 5-fold development type B
Fig. 13G

Description. - A holomeric spinose pentagonal columnal with a pentagonal broad lumen. Columnal outline is almost pentastellate. Lumen and columnal angles non-coincident. Columnal angles are rounded. Areola seems to be somewhat depressed. Articulation is synostial. Spines are developed from the columnals angles. Erosion of the fragment is severe.

Remarks. - There is some problem assigning this fragment type to any genus due to severe erosion of the material. Possibly a cystoid columnal.

Occurrence. - Totally 2 specimens, Öl 97-12 to Öl 94-201; mid K to top of section.

Holomeric columnal with 5-fold development type C
Fig. 13H

Description. - A holomeric spinose pentagonal columnal with a broad pentagonal lumen. Lumen and columnal angles non-coincident. Columnal angles are rounded. Some erosion has occurred. Most likely also synostial articulation from the beginning. A spine is developed from one of the columnal angles. Areola is absent. Lumen is wider than in type B (Fig. 13G).

Remarks. - A columnal which occurs rather rarely at most levels. Fairly primitive form with a broad pentagonal lumen.

Occurrence. - Totally 4 specimens, Öl 92-1 to Öl 92-4; mid J to top K.

Holomeric columnal with 5-fold development type D
Fig. 14E

Description. - A holomeric? pentastellate columnal with a pentagonal lumen. Lumen angles are well rounded, almost pentastellate in outline and non-coincident with the columnal angles.

Remarks. - Possibly this columnal was originally pentameric. It is also plausible that the overall columnal outline was different originally due to possible parting of the columnal.

Occurrence. - Totally 13 specimens, Öl 97-12 to Öl 93-12; mid K to mid Q.

Holomeric columnal with 5-fold development type E
Fig. 14G

Description. - A holomeric pentagonal columnal with a broad circular lumen. Columnal angles are well rounded. The articulation facet gives an undulating impression possibly due to the original facet outline of e.g. depressed areas. Abrasion has given rise to the well-rounded and smooth columnal outline.

Remarks. - Possibly this columnal could be placed within the columnal morphogenus *Cyclopentagonalis*.

Occurrence. - Totally 4 specimens, Öl 94-5 to Öl 97-12; topmost H to mid K.

Holomeric columnal with 5-fold development type F
Fig. 14H

Description. - A holomeric pentagonal, almost pentastellate, columnal with a central circular lumen. The overall outline of the columnal surface is smooth, which indicates that erosional processes have been at work. The articular facet has an "undulating" outline due to a distinct division of the surface by radiating ribs, which starts at the lumen and runs out to the columnal edge. This division depends on the fact that the articulation surface shows many depressed areas better known as areola pits, also known as a specialised kind of areola where ligamentary tissue adhere to. Ten distinct areas can be distinguished. Those occurring in the columnal angles are naturally bigger. The preservation shows a thin coating of the original stereom.

Remarks. - Most likely the same type of columnal as type E, but type F has a slightly different outline. I have separated between these just to show what a little erosion might do. It is also possible that these columnal types described (type E and F) belong to the same genus but are different species.

Occurrence. - Totally 4 specimens, Öl 92-3 to Öl 93-12; basal K to upper Q.

Holomeric columnal with 5-fold development type G
Fig. 16C

Description. - A holomeric pentagonal columnal with a pentastellate lumen. Lumen angles correspond to the columnal sides. Five areola pits, which coincide with the columnal angles, can be distinguished. These areola pits show a coating of a different type of stereom. The same type of columnal also occurs with spines (see Fig. 16D).

Remarks. - Possibly this columnal type belongs to the genus *Lobatocrinus* (see e.g. description given by Stukalina 1988). *Lobatocrinus* are often pentameric columnals, though this columnal could have been pentameric with meric sutures that correspond to the columnal sides and the lumen angles. In some parts of this columnal one can see a depressed linear area running from the lumen angle to the columnal side as an extension of the corresponding lumen angle. The areola pits are here clearly distinguished by the presence of what seems to be a different type of stereom. This is probably due to differences in the original type of stereom, but could be due to diagenetic alterations.

Occurrence. - Totally 9 specimens, Öl 93-6 to Öl 92-6 (if specimens like the one in Fig. 16D are included); basal K to upper L.

Holomeric columnal with 5-fold development type H
Fig. 16E

Description. - A holomeric pentagonal columnal with a central pentagonal lumen. Lumen and columnal angles are coincident. Areola divided into ten distinct pits with ridges in between them. Areola pits can clearly be distinguished due to their denser coating.

Remarks. - Compare this columnal type with Fig. 14G and 14H. The articulation seems to be the same but the overall columnal outline differs and the lumen outline is also different. In type H there is a distinct pentagonal lumen but in type E (Fig. 14G) and type F (Fig. 14H) there is a circular lumen.

Occurrence. - Totally 10 specimens, Öl 93-6 to Öl 93-12; base K to mid Q.

Holomeric columnal with 5-fold development type I
Fig. 16F

Description. - A holomeric pentagonal columnal with a rather wide circular lumen. This columnal has probably been subjected to intense abrasion and therefore the articular facet seems to be almost completely smooth.

Remarks. - Most likely the facet has been divided into distinct areola pits in its original state. The columnal sides have a wavy appearance most likely due to the above-described original facet outline. Even though the articulation facet of the columnal is heavily eroded, some resemblance exists with the genus *Pentagonocyclopa* (col.) as described by Donovan (1995). It is very likely that the columnal morphotype described here belongs to *Pen-tagonocyclopa* (col.) *hughesi* described by Donovan (1995). Compare e.g. with Donovan 1995, pl.18, fig. 8.

Occurrence. - Totally 4 specimens, Öl 94-6 to Öl 93-6; base H to base K.

Holomeric columnal with 5-fold development type J
Fig. 20G

Description. - A holomeric pentagonal columnal with a pentagonal lumen where lumen and columnal angles are non-coincident. Articulation seems to be synostial.

Occurrence. - Totally 18 specimens, Öl 94-5 to Öl 93-12; H to mid Q.

Holomeric columnal with 5-fold development type K
Fig. 20H

Description. - A holomeric pentagonal columnal with a pentagonal lumen where lumen and columnal angles are coincident. Lumen is much wider than in type J.

Occurrence. - Totally 18 specimens, Öl 92-3 to Öl 93-8, basal K to basal N.

Genus *Oanducystis* (col.) Stukalina *in* Stukalina & Hints, 1979

Remarks. - *Oanducystis* (col.) has been described by e.g. Donovan, 1995.

Oanducystis? (col.) sp. A
Fig. 21G

Description. - A holomeric pentagonal columnal with a pentastellate lumen. Lumen and columnal angles are coincident. Areola is rather narrow and outside this the area is uplifted above the areola, resulting in the areola being situated in a depressed area. The columnal is thus divided into two distinct areas: one outer, which is uplifted and one inner, which consists of the areola and which is depressed.

Remarks. - This columnal morphospecies differs from *Lanxocolumnus* (col.) (Donovan, 1995) in having the lumen and columnal angles coincident with each other (Donovan 1995).

Occurrence. - Totally 1 specimen, Öl 83-104; mid M.
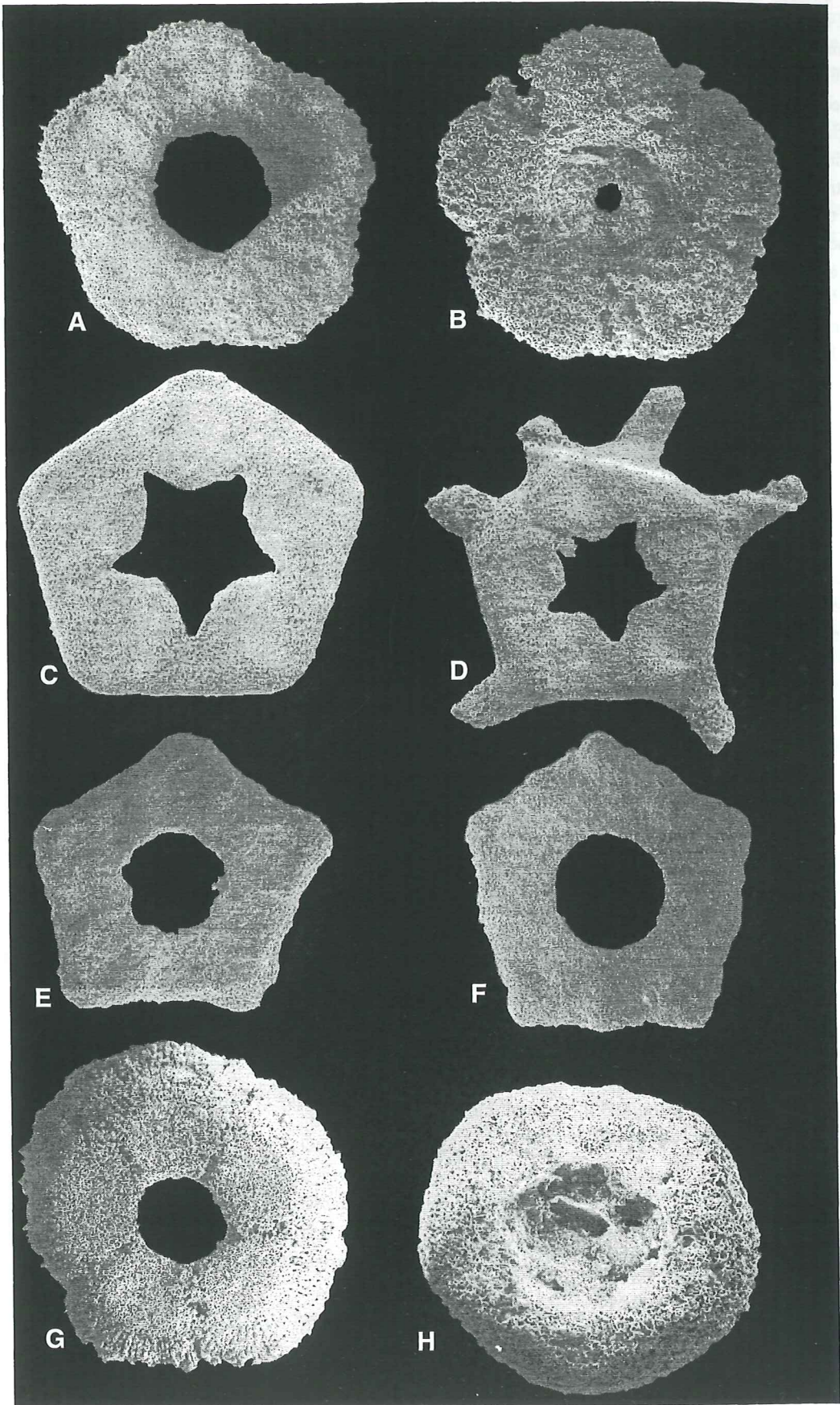
Genus *Bystrowicrinus* (col.) Yeltysheva *in* Yeltysheva & Stukalina, 1963

Remarks. - The genus *Bystrowicrinus* (col.) has been described by Stukalina (1988) and also by Donovan (1995). Based on the descriptions given by these authors the columnals described below are placed within the genus *Bystrowicrinus* (col.). In some cases this is, however, more insecure and these species have then been given a question-mark. Donovan (1995) described this columnal morphogenus as containing holomeric columnals with a pentastellate axial canal, "narrow centrally , but with five equally-spaced lumen rays pointing towards angles of columnal (if present); areola present or absent; articulation symplectial". He also noted that the columnal outline can be circular or pentagonal.

Bystrowicrinus? (col.) sp. A
Fig. 11G

Description. - A holomeric pentagonal columnal. Lumen has a pentastellate outline. Lumen angles and columnal angles are non-coincident, in contrast to the description issued by Donovan (1995). Columnal and lumen angles are well rounded. Most likely synostial articulation, but preservation is rather poor.

Remarks. - Most likely a *Bystrowicrinus* columnal (compare e.g. with Donovan 1995, text-fig 43H). Donovan (1995) described almost the same columnal type. He also noted that the articulation of his columnal most likely was not synostial from the beginning. Symplectial articulation is more likely. He also noted that in the genus *Bystrowicrinus* the lumen angles are coincident with the columnal angles, which is not the case in the present material. There are also some problems with the time span of this form. Donovan (1995) noted that this genus did not appear in the British Isles (South Faunal Province) until the Caradoc and became more common in the Ashgill as the Iapetus ocean closed, though Stukalina (1988) noted a somewhat different range of this taxon with older occurrences.

Occurrence. - Totally 14 specimens, Öl 93-6 to Öl 94-201; base K to top of section.

Bystrowicrinus? (col.) sp. B
Fig. 21A

Description. - A circular holomeric columnal with a pointed pentastellate lumen. Articulation type is not possible to decide.

Remarks. - See also above under *Bystrowicrinus*? (col.) type A.

Occurrence. - Totally 8 specimens, Öl 94-6 to Öl 93-12; H to mid Q.

Bystrowicrinus? (col.) sp. C
Fig. 21B
Description. - A pentagonal holomeric columnal with a pentastellate lumen. Lumen and columnal angles are coincident. Articulation type is not possible to make out.
Occurrence. - Totally 4 specimens, Öl 92-7 to Öl 93-8; M to basal N.

Bystrowicrinus? (col.) sp. D
Fig. 21C
Description. - A circular holomeric columnal with a rounded pentastellate lumen (in comparison with *Bystrowicrinus*? (col.) type B). Articulation type is not possible to decide.

Remarks. - See also above under *Bystrowicrinus*? (col.) type A.

Occurrence. - Totally 3 specimens, Öl 94-5 to Öl 92-3; H to mid K.

Genus *Pentagonocyclopa* (col.) Moore, 1939

Remarks. - The genus *Pentagonocyclopa* (col.) has also been described by Donovan (1995).

Genus *Pentagonocyclopa*? (col.) sp. A
Fig. 11I

Description. - A holomeric? pentalobate columnal with a rather wide circular lumen occurring in the centre.

Remarks. - This columnal does not agree in detail with the description for the columnal morphogenus *Pentagonocyclopa* as given by Donovan (1995). But, bearing in mind that parting of columnals has occurred at some levels, this might explain why this columnal looks the way it does in its present state. If erosion and parting have occurred it is

Fig. 16. **A.** *Ramulicrinus*? (col.) sp. B; from Öl 93-11, x100. **B, G.** Pentameric columnals. B, type D; from Öl 93-12, x95. G, type E; from Öl 92-9, x85. **C-F.** Holomeric columnals five development; from Öl 93-6. C, type G, x95. D, type G with spines, x100. E, type H, x100. F, type I, x85. **H.** Heavily eroded columnal, possibly *Bystrowicrinus* (col.); from Öl 92-9, x120.

29

very likely that this columnal belongs to the morphogenus *Pentagonocyclopa*. The overall diagnosis for *Pentagonocyclopa* as described by Donovan (1995) is: "Holomeric, pentagonal columnals with a small, circular lumen; areola absent or pentagonal to pentalobate; articulation symplectial, marginal, with crenulae arrayed perpendicular to the circumference of the articular facet". If an articulation area with e.g. crenulae was present outside the pentalobate area in the ossicle described above, this columnal most likely would be described as belonging to the morphogenus *Pentagonocyclopa*, Donovan 1995, text-fig. 44A. But it is also important to note that columnals with this original outline do occur in some species. So this columnal type is very difficult to assign to a particular genus or morphogenus, so the assignment to *Pentagonocyclopa* is very tentative.

Occurrence. - Totally 123 specimens, Öl 94-6 to Öl 93-12; H to mid Q.

PENTAMERIC COLUMNALS

Pentameric columnal type A
Fig. 12A

Description. - A pentameric pentagonal columnal with a pentagonal lumen. Lumen angles are coincident with the columnal angles. The meric sutures coincide with the lumen sides. Articulation seems to be synostial. The lumen is clearly infilled with stereom (see blow-up in Fig. 12B). The infill appears to have been growing from the lumen sides, but the direction and orientation of the stereom meshwork is clearly strange, possibly indicating trapping of a foreign particle of stereom. Stereom seems to be galleried or rectilinear.

Remarks. - It appears that the stereom infill was part of the original lumen structure. If this is the case it should be noted that infill of the lumen with stereom is known in some species but never to this extent. The normal thing is that the stereom grows into the lumen with only some minor branches and these never fill up the lumen completely thus allowing tissue to penetrate an almost open lumen. Macurda & Meyer (1975) noted in their work on *Endoxocrinus* that spike-like projections of the stereom projected into the lumen, penetrating 0.056 mm. into the lumen with a lumen diameter corresponding to 0.200 mm. These projections occurred just a short distance above and beneath the area of synostis. Also Donovan (1984b) noted the occurrence of "spike-like, labyrinthic stereom fingers" growing into the axial canal (see Donovan 1984b, pl. 74, fig. 3) in the same area as described above. He also noted that this would limit the amount of tissue in the

axial canal and that this original ingrowth of labyrinthic stereom fingers could possibly be an adaptation to autotomy, so that if breakage should occur along a synostial joint, the axial canal could rapidly be infilled by calcite growth (Donovan 1984b). But, in the columnal described here the infill does not resemble that described by Macurda & Meyer (1975) or Donovan (1984b). The stereom developed here is clearly organised into a complete meshwork and this might also indicate the trapping of a foreign stereom particle in the lumen.

Occurrence. - The occurrence of this columnal type is very scarce with totally 3 specimens. Öl 92-3 to Öl 93-12; K to mid Q.

Pentameric columnal type B
Fig. 14I

Description. - A pentameric pentagonal columnal with a central circular lumen. Columnal angles are well rounded. Areola divided into five distinct pits, which coincide with the columnal angles. Meric sutures coincide with the columnal sides.

Remarks. - Note especially the denser stereom occurring as a coating of the areola pits. This stereom seems to be composed of very unorganised pores and it also seems to be very thin and very dense. The interconnecting stereom-ribs are very thick. This clearly differs from the surrounding columnal stereom even though it is rather poorly preserved. This coating of stereom does not much resemble any of the usual types of stereom that would be expected in this area though it might represent a rather dense type of thin labyrinthic stereom. If this is due to alteration of the original stereom is hard to say. It might of course instead represent the original type of stereom.

Occurrence. - Totally 23 specimens, Öl 92-3 to Öl 94-201; K to top of section.

Pentameric columnal type C
Fig. 15F

Description. - A circular columnal, which at first glance seems to be trimeric, but most likely it was pentameric originally before alteration of the meric sutures occurred. Lumen seems to be circular. The meric sutures (not infilled ones) are well developed and each one of these is divided into two distinct open areas with a stereom chord occurring in between. The areola is divided into five distinct pits, which all except one seem to have a rather rounded outline. The pit with a more pointed outline, coincides with an outgrowth on the latera.

Remarks. - As described above this columnal most likely originally was pentameric. The later infilling of the meric sutures masks the original meric outline as described in a number of other columnals.

Occurrence. - Totally 1 specimen, Öl 93-12; Q.

Pentameric columnal type D
Fig. 16B

Description. - A pentagonal columnal with well-developed pentamerism. Meric sutures are clearly visible. Columnal angles are well rounded. Lumen is circular and divided into two distinct regions. One with stereom infilling and one point-sized circular area without any stereom infilling.

Remarks. - The distinct division of the lumen into two areas could represent one of the evolutionary steps that are common to pentameric pentagonal columnals. Stukalina (1988) noted that the evolution of pentameric pentagonal columnals proceeds towards a point-sized lumen and holomerism. Possibly this columnal could represent this step which has not yet been fully completed. Resorption and infilling of stereom are well known from other investigations (e.g. Donovan 1984b, Smith 1980). Only one specimen of this type has been found so far, but further investigations could possibly reveal interesting facts about the early evolution of pentameric pentagonal columnals. Most likely more columnals of this type and with better preservation will be revealed during further investigations.

Occurrence. - Totally 1 specimen, Öl 93-12; Q.

Pentameric columnal type E
Fig. 16G

Description. - A pentameric pentagonal? columnal with a central circular? lumen. Areola divided into five distinct pits with coating of a denser stereom.

Remarks. - As mentioned earlier the abrasion of some columnals often has resulted in the disappearance of the overall original columnal outline, only leaving some parts of the outer columnal stereom. This has probably happened to the columnal described here.

Occurrence. - Totally 1 specimen, Öl 92-9; top M.

Pentameric columnal type F
Fig. 21D

Description. - A pentameric pentagonal columnal with a pentagonal lumen. Lumen and columnal angles are non-coincident and the meric sutures correspond to the columnal sides. Articulation type is unknown.

Remarks. - Most likely, this columnal type belongs to a crinoid.

Occurrence. - Totally 4 specimens, Öl 92-9; top M.

Pentameric? columnal type G
Fig. 13C

Description. - A possibly pentameric columnal with a pentagonal outline. Lumen seems to be circular and articulation seems to have been synostial. Meric sutures seem to be present, coinciding with the columnal sides.

Remarks. - Most likely this columnal type belongs to a crinoid if it is pentameric, but if it should be holomeric it could possibly belong to a rhombiferan.

Occurrence. - Totally 5 specimens, Öl 92-3 to Öl 92-9; K to top M.

Genus *Ramulicrinus* (col.) Stukalina, 1968

Remarks. - This genus has also been described by Donovan (1995).

Ramulicrinus? (col.) sp. A
Fig. 14J

Description. - A holomeric?, possibly originally pentameric columnal. Lumen is pentagonal and the areola seems to be pentagonal with depressed areas (areola pits). Lumen angles are non-coincident with the areola angles. Lumen sides correspond to the areola pits. Two distinct outgrowths can be seen, which are most likely relicts of the original outer parts of the columnal which housed e.g. crenulae.

Remarks. - This columnal most likely belongs within this genus if taken in consideration that some parting has occurred (see also remarks on *Ramulicrinus*? (col.) sp. C). This preservation type is very common at some levels.

Occurrence. - Totally 3 specimens, Öl 93-6 to Öl 93-12; base K to mid Q.

Ramulicrinus? (col.) sp. B
Fig. 16A

Description. - A pentameric pentagonal columnal with a central pentagonal lumen. Columnal angles are well rounded and they are non-coincident with the lumen angles. Lumen angles are coincident with the meric sutures. Lumen sides correspond to the columnal angles. Articulation could have been symplectial originally. Five distinct areola pits can be distinguished. The stereom in these areas seems to be somewhat denser than in the other columnal areas.

Occurrence. - Totally 47 specimens, Öl 93-6 to Öl 94-201; base K to top of section.

Ramulicrinus? (col.) sp. C
Fig. 15I, 20I

Description. - A holomeric? or possibly pentameric columnal which appears to be almost circular in outline. Lumen is pentagonal and the areola is divided into five distinct well-rounded pits. Pits correspond to lumen sides and they are lifted up above the rest of the articular facet.

Remarks. - Donovan (1995) discussed the distinctions between *Ramulicrinus* (col.) and *Ranunculocolumnus* (col.) and his conclusions were that they are very similar but that *Ramulicrinus* (col.) differs in having the areola petals coincident with the lumen sides and not as in *Ranunculocolumnus* (col.) where they correspond to the lumen angles.

 This columnal also shows two types of preservation: one outer sugary of shiny phosphate and an inner of rather well preserved phosphatic replacement. After the diagenetic alterations some parting has possibly occurred, so that the columnal most likely had a slightly different original outline. For a possible reconstruction see Fig. 20I. It also seems that this columnal was not holomeric in its original state. It is more likely that it was pentameric. One suture can now be seen and if this is due to parting or the fact that it is an original part of a meric suture is impossible to tell. If the meric sutures were present in the original state they would most likely run between the areola pits and be coincident with the lumen angles. Compare also with Fig. 14J.

Occurrence. - Totally 127 specimens, Öl 93-6 to Öl 94-201; K to top of section.

Genus *Sidericrinus* (col.) Stukalina, 1968

Remarks. - This genus has also been described by Donovan (1986).

Sidericrinus? (col.) sp. A
Fig. 11H

Description. - A pentameric pentagonal columnal. Columnal angles are well rounded. Lumen large and pentastellate in outline. The lumen gently curves outwards into the meric sutures (possibly jugula). Meric sutures coincide with columnal sides. Articulation is synostial.

Remarks. - Donovan (1986) described a new columnal species, which he gave the name *Sidericrinus birtlei* (see Donovan 1986, pl. 4, fig. 4). This species somewhat resembles the columnal described above. The articulation of the columnal he described was synostial. The overall preservation is much poorer in the columnal described here. This columnal also shows a great deal of similiarities with the morphogenus *Fascicrinus* (col.) which has been described by for example Donovan (1986).

Occurrence. - Totally 8 specimens, Öl 94-5 to Öl 93-12; H to mid Q.

Family Baltocrinidae Stukalina, 1979
Genus *Baltocrinus* (col.)

Remarks. - This genus has been described by Stukalina (1988).

Baltocrinus? (col.) sp. A
Fig. 11K

Description. - A pentameric pentagonal columnal with a central circular lumen. Meres are well developed and they coincide with columnal sides. Articulation seems to be synostial. Erosion of this columnal is severe and possibly the articulation was of another type originally.

Remarks. - Stukalina (1988) noted that the family Baltocrinidae is a typical representative of pentapartial articulation. The term pentapartial was used by Stukalina (1988) to describe that the columnal is pentameric where "the articulation surface of the pentameres are covered by ligamentary relief pits, the outlines of which coincide with those of the pentameres". This description could very well be applied to the columnal described above if the fact that some erosion has occurred would be taken in consideration. Stukalina (1988) also noted that this family is a typical representative of the echinoderm fauna in the Middle Ordovician of the East European Platform.

Occurrence. - Totally 9 specimens, Öl 92-1 to Öl 94-201; J to top of section.

Baltocrinus? (col.) sp. B
Fig. 14F

Description. - A pentameric columnal with a well-rounded pentagonal outline. Lumen seems to be round. Meric sutures are well developed with two suture-lines occurring at every meric suture. The overall preservation of the columnal is very poor.

Remarks. - Possibly this columnal belongs within this genus but it is hard to say due to the poor preservation. This type of columnal and preservation are common at some levels. Preservation appears to be almost recrystallised where the phosphate fills up every stereom pore. Inward growth of phosphate has also occurred in the lumen.

Occurrence. - Totally 8 specimens, Öl 92-9 to Öl 93-12; top M to mid Q.

Subphylum Asterozoa Zittel, 1895
ClassStelleroideaLamarck,1816

Asterozoan? spines
Fig. 17C

Description. - The illustrated specimen is a broken spine with a well-developed articulation joint passing over into a slender spine with stereom running like long sheets along the extension of the fragment. The stereom meshwork is more open near the articulating joint. The spine extension has long parallel sheets of stereom, which is perforated in some places. It also shows a calcitic ultra-texture.

Remarks. - Spines are quite common in some samples and the overall shape of these resembles that described here although some minor differences may exist. Here they are all treated together. The illustrated spine shows some similarities with *Bothriocidaris* spines described by e.g. Nestler (1968), compare e.g. with his fig 1c, but it also resembles some asterozoan spines. Kolata (1975) also described some *Bothriocidaris* spines, which resemble some of those found in my samples (compare e.g. with his pl.14, fig. 4). Kolata (1975) also described some plates that resemble a plate (this plate is not illustrated in this essay) that was found in Öl 97-12 (see Kolata 1975, pl. 14, fig. 7). This spine type is rare in some samples. Most likely the spines found within my samples belong to asterozoans, based on the fact that most echinoderm fragments in the samples, where the spines are found, belong to asterozoans. Likewise, no direct evidence of the presence of e.g. *Bothriocidaris* (except for one plate) in the samples

has been found. Possibly though the earliest occurrences of spines (see appendix A) might represent *Bothriocidaris* spines.

Occurrence. - Totally 35 specimens, Öl 94-6 to Öl 92-9; H to top M.

Paxillar ossicle
Fig. 17I

Description. - A triangular ossicle carrying a small knob (compare e.g. with Blake 1973, plate 10, fig. 27 for an illustration of a paxillar ossicle). This is most likely a paxillar ossicle, which is common in some asterozoans. All sides and extensions are well rounded. Most likely an ossicle from an asteroid. Note also the different stereom structure occurring in the knob.

Remarks. - This ossicle type occurs on the aboral surface (extra axial skeleton) of some asterozoans and was not associated with the tube feet. The paxillae were equipped with small spinelets or granules, which had a respiratory, or sediment removing function. No detailed observations could be made regarding differences in stereom type due to the preservation of this ossicle, but some other paxillar ossicles in the samples clearly show stereom differentiation. Some other types of paxillar ossicles also occur in some of the samples (e.g. compare with Blake 1973, pl. 2, fig. 1 and pl. 4, fig. 2). All of these types have here been treated under the same heading, although they most likely represent different genera of asteroids. Note that paxillar ossicles are also present in somasteroids.

Occurrence. - Totally 19 specimens, Öl 94-5 to Öl 92-9; H to top M.

Spine attachment ossicle type A
Fig. 18G

Description. - An ossicle with two distinct articulating knobs. Length of photographed specimen 588 µm and width approximately 500 µm. Length of knobs approximately 125 µm and width approximately 100 µm. Most likely an asterozoan or possibly an echinoid spine attachment ossicle.

Remarks. - Note the denser stereom occurring around the base of the knobs as an overlay. This stereom type shows no pores at all and therefore it possibly can be called imperforate. But it is also possible that this area has been subjected to later diagenetic infilling of an original fine-meshed stereom network. Smith (1980) noted that in spine muscle fibres attachment areas of some echinoids a
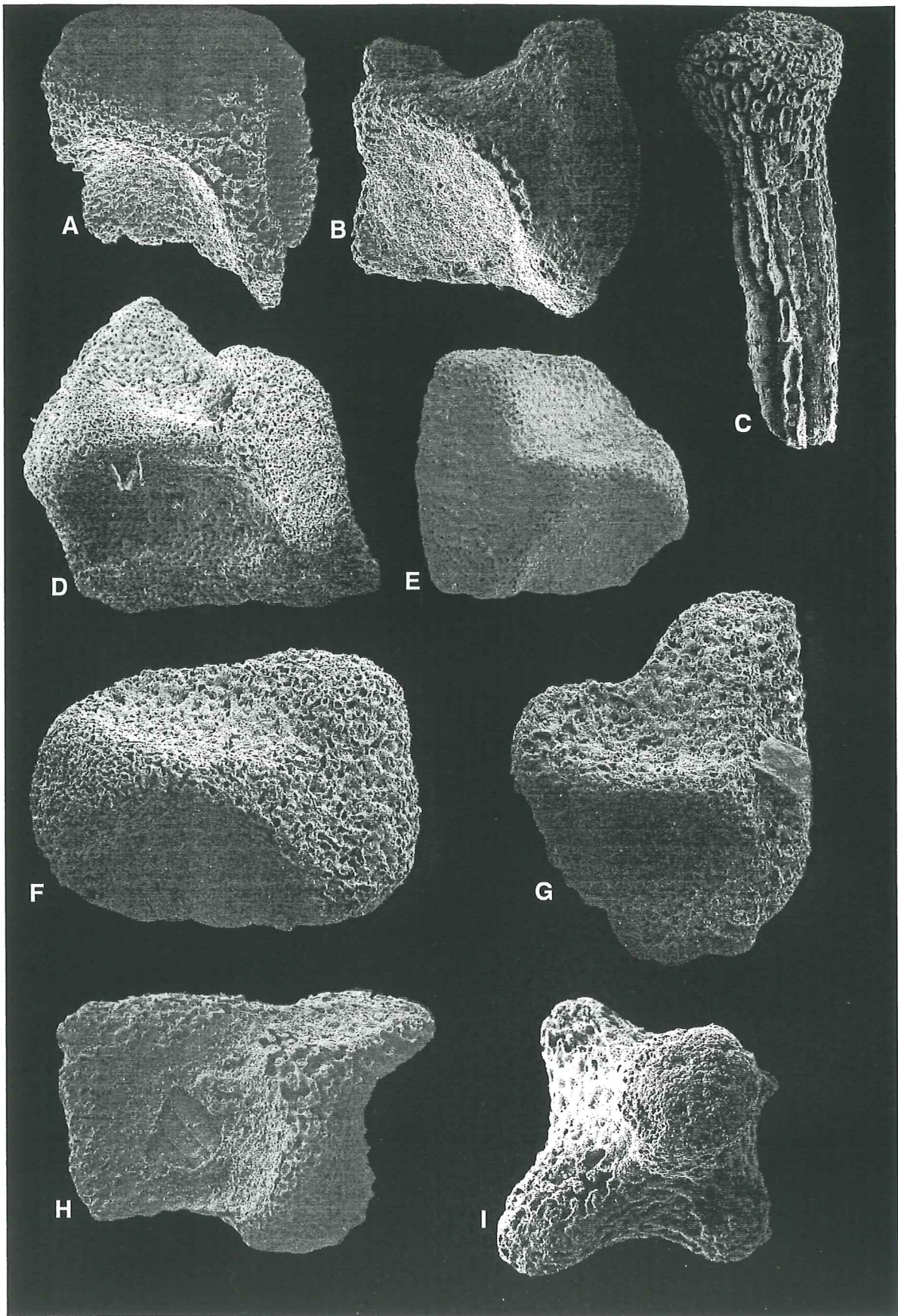
thin coating of more dense labyrinthic stereom occurs (see e.g. Smith, 1980 pl. 22, fig. 4). He also noted that imperforate stereom "is found at articular surfaces of larger tubercles and spines" and it provides a "strong and smooth surface which is minimally resistant to sliding movements of the spine". No traces of infilled labyrinthic stereom produced during growth of the plate can be seen in this fragment. Note also the more open stereom meshwork of the knobs (articulation and attachment area of spine). This stereom shows no internal arrangement between pores and the overall outline of it is rather irregular. Most likely it represents a very open type of labyrinthic stereom. Smith (1980) noted that a labyrinthic stereom often can be found in the core of tubercles of echinoids. Further he described that a quick removal of the spine from the tubercle might result in an increased surface porosity (conclusions drawn by Smith from other authors´ observations on the fact that the tubercles change their appearance from glassy to opaque after a quick spine removal) and due to this observation he suggested that "following spine loss a more open stereom takes the place of the more usual compact, perforate stereom layer of the mamelon" (Smith 1980). The area outside the coating shows rather good pore-alignment and possibly this area represents a rectilinear stereom, though it is hard to say due to the fact that no cross-section has been examined and it might as well represent galleried stereom. Many different types of spine attachment ossicles have been found. Most of them resemble the one described here in shape and only the tubercles may vary in shape and size. The number of tubercles present in one ossicle also varies.

Occurrence. - Totally 19 specimens, Öl 94-5 to Öl 92-9; H to top M.

Marginal ossicle
Fig. 18I (side view) and Fig. 18J (crest)

Description. - A marginal ossicle lacking ornamentation (compare e.g. with Blake 1973, pl. 14, fig. 9, which illustrates one marginal ossicle from an asteroid; Rasmussen 1972, pl. 3, fig. 19a; Rasmussen 1950, pl. 1, fig. 7-9 and

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Fig. 17. **A-B, F, H.** Ambulacral ossicles. A, type B; from Öl 93-6, x190. B, type C; from Öl 93-6, x190. F, type D; from Öl 93-6, x180. H, type E; from Öl 93-11, x200. **C.** Asterozoan? spine; from Öl 93-6, x160. **D.** Adambulacral? ossicle type A; from Öl 93-6, x110. **E, G.** Undetermined asterozoan ossicles. E, type F; from Öl 93-6, x110. G, type A; from Öl 93-11, x160. **I.** Paxillar ossicle; from Öl 97-12, x170.

Smith & Jell 1990, fig. 50A, which illustrates a marginal ossicle from a somasteroid). This type of ossicle supported the margins of certain asteroids and also some somasteroids. Two different types of marginal ossicles can be distinguished among asteroids, namely inferomarginals and superomarginals (descriptive terms from Blake 1973). The marginal ossicles found in my samples can not be assigned to any of these types with certainty.

Remarks. - Nichols (1969), amongst others, discussed the evolution of asteroids and he described the transformation of virgalia to marginal ossicles as an early evolutionary step. The second row of marginals on the aboral side he termed supramarginals and the first and earliest row inframarginals. He also stated that the evolution of supramarginals from virgalia happened after inframarginals had already evolved.

Occurrence. - Totally 11 specimens, Öl 92-2 to Öl 92-9; base K to top M.

Asterozoan ambulacra

Ambulacral? ossicle type A
Fig. 18A

Description. - Most likely an asterozoan ambulacral ossicle with a well-developed podial basin as support for the tube feet. A denser stereom occurs as a thin coating of the podial basin. The overall shape of the ossicle is well developed to fit in the ambulacral system. No other stereom specialisation can be seen.

Remarks. - This ossicle type occurs abundantly at some levels. It resembles some asterozoan ambulacral and abactinals.

Occurrence. - Totally 14 specimens, Öl 93-3 to Öl 92-9; top I to top M.

Ambulacral ossicle type B
Fig. 17A

Description. - A triangular ridge extends across this ossicle, separating it into two distinct regions of articulating basins, where one basin is more prominent than the other. Note also the denser stereom occurring as a coating of the basins. The ridge is highest and most prominent in the middle. The outline of the ossicle is squarish with distinct and sharp angles. Erosion of this ossicle is minor. An open stereom meshwork occurs on top of the ridge.

Remarks. - Smith (1980) noticed that in echinoids the area
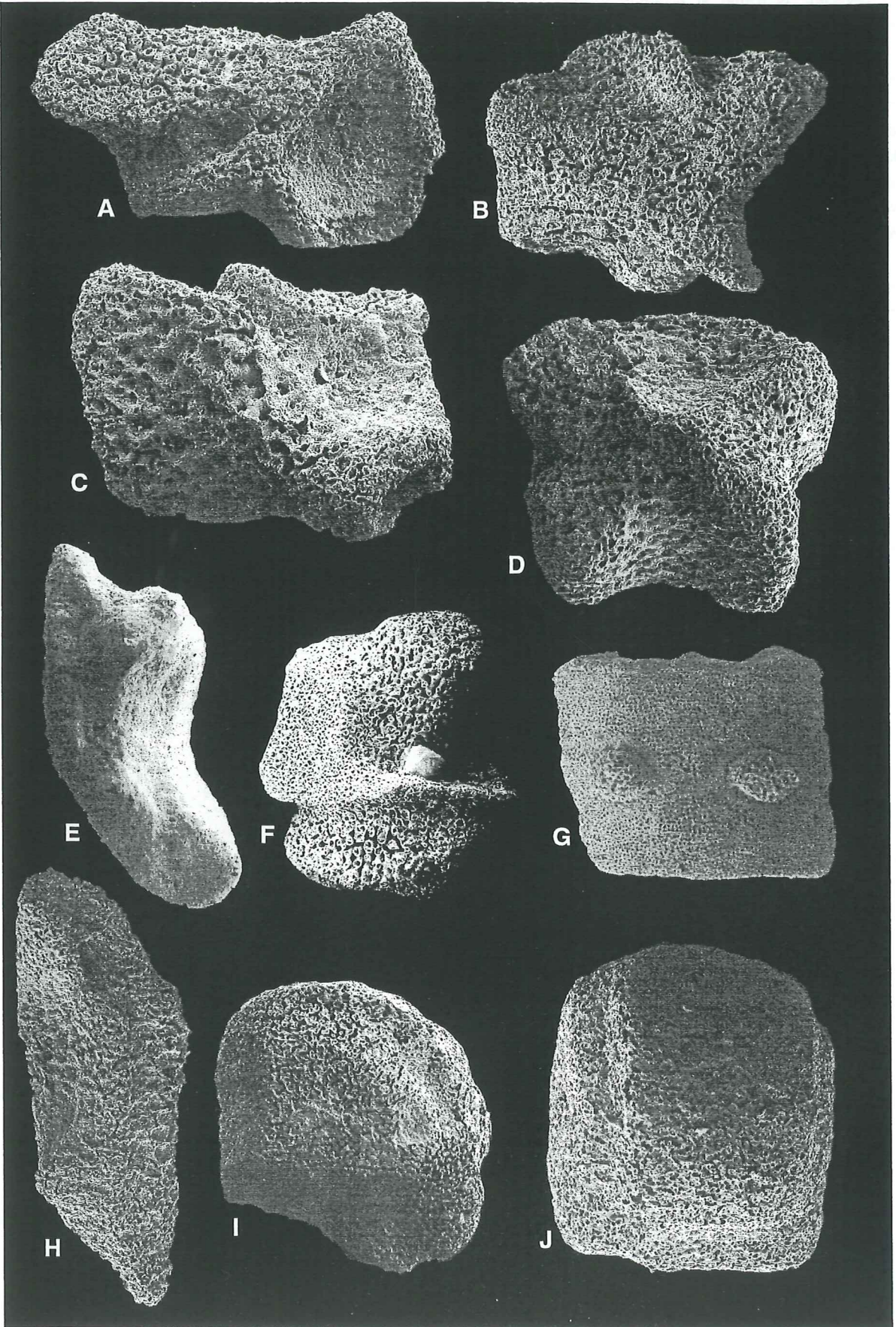
that acts as a support for the tube foot shows a thin coating of labyrinthic stereom, similar to that seen here (see also illustration of labyrinthic stereom in Fig. 8). This ossicle shows great resemblance with ambulacral plates occurring in the arms of some ophiuroids. A long row of these were fitted together so that two ossicles together build up one distinct podial basin (see the two articulating basins on the ossicle described). One tube foot basin was thus shared between two ambulacral ossicles. Also note that the basins in this ossicle type differ in size. As the evolution of vertebrae ossicles (the same as ambulacral plates) in ophiuroids proceeded the basins became more and more different in size and at last only one basin supports most of the tube foot (Spencer & Wright 1966). This means that as the last evolutionary step only one well-developed basin exists as support for the tube foot in each ambulacral ossicle, while the other basin becomes less and less obvious. The conclusion drawn from this discussion is that the ossicle described here almost has reached the last evolutionary step.   This ambulacral ossicle type is the most common asterozoan plate type at many levels, presumably because numerous ossicles build up one arm. Most likely all of these ossicles belong to ophiuroids (vertebral ossicles) but some also show similarities with certain starfish adambulacral plates. See Fig. 22C for an illustration how this ossicle type could have functioned as part of an ophiuroid arm.

Occurrence. - Totally 101 specimens, Öl 94-6 to Öl 92-9; H to top M.

Ambulacral ossicle type C
Fig. 17B

Description. - An ambulacral ossicle which shows great resemblance to ambulacral ossicle type B. This ossicle type is better rounded though and shows overall a much poorer preservation than type B.

Remarks. - Most likely an ophiuroid vertebrae ossicle.

Occurrence. - Totally 2 specimens, Öl 93-6; K.

Fig. 18. **A, E, H.** Ambulacral? ossicles. A, type A; from Öl 92-3, x160. E, type G; from Öl 92-9, x100. H, type G; from Öl 97-12, x170. **B.** Adambulacral? ossicle type B; from Öl 92-3, x140. **C-D, F.** Undetermined asterozoan ossicles. C, type B; from Öl 93-11, x180. D, type C; from Öl 92-3, x190. F, type D; from Öl 93-6, x85. **G.** Spine attachment ossicle type A; from Öl 93-6, x90. **I-J.** Marginal ossicles. I, side view of specimen; from Öl 93-6, x110. J, crest view of specimen; from Öl 92-3, x140.

Ambulacral? ossicle type D
Fig. 17F

Description. - A well-rounded ossicle which bears some resemblance to an ambulacral plate as described above. A ridge extends across the ossicle separating it into two distinct regions. Shape of ridge is concave with a straight outline. The ridge is highest in the middle. The two basins are coated with denser stereom. The margins of the ossicle are well rounded with no distinct angles. The ossicle outline is ellipsoidal.

Remarks. - This ossicle can not be assigned with certainty to any special asterozoan; it might even be an asterozoan adambulacral ossicle.

Occurrence. - Totally 34 specimens, Öl 92-1 to Öl 92-9; mid J to top M.

Ambulacral ossicle type E
Fig. 17H

Description. - An ambulacral plate with a ridge occurring at one side of the fragment. The ridge is highest in the middle and is L-shaped. One distinct flat and smooth basin is developed over most of the fragment. This basin appears to have a more dense stereom coating, though it is hard to tell if this is the original stereom type. The shape of the ossicle is quadratic on one side and with a more distinct and well-rounded outline on the other side. Preservation is poorer than in the ossicles described above.

Remarks. - Most likely an ambulacral ossicle from an ophiuroid. Note especially that only one wide-spread basin occurs in this ossicle, a more advanced shape than in the older ossicles (see remarks above).

Occurrence. - Totally 4 specimens, Öl 93-11; top P.

Ambulacral ossicle type F
Fig. 11D

Description. - A long and slender ossicle where the length is more than twice the width. One end has a distinct podial basin, which is coated with denser stereom. In direct connection with the podial basin there is a distinct ridge, which runs obliquely to the narrowest sides of the fragment. The ridge is penetrated by two holes, which run from the podial basin to one of the ossicle sides. On the opposite side of the podial basin the ossicle is pointed.

Remarks. - The holes most likely represent channels for

the water-vascular system. Most likely this ossicle represents a vertebral ossicle from an ophiuroid (compare e.g. with Rasmussen 1972, pl. 10, fig. 14a). Blake & Guensburg (1993) however noted that edrioasteroids developed pores between ambulacral ossicles and that these resemble those developed by certain late-Palaeozoic stelleroids. Some other types of asterozoans also possessed this type of penetrating holes in their ambulacral plates.

Occurrence. - Totally 3 specimens, Öl 97-12 to Öl 92-9; K to top M.

Ambulacral? ossicle type G
Fig. 18E, H

Description. - A long and slender ellipsoidal ossicle with indications of articulation areas at the ends (Fig. 18H). The ossicle in Fig. 18E is regarded as the same type as that in Fig. 18H, but most likely belonging to another species. The ossicle illustrated in Fig. 18E is also heavily eroded and the surface is almost completely smooth.

Remarks. - This ossicle could also be an inferomarginal plate or an adambulacral ossicle. Another possibility is that it represents an actinal ossicle from an asteroid (compare e.g. with Rasmussen 1950, pl. 4, fig. 5f). If this ossicle type belongs to an ophiuroid or an asteroid is difficult to say, but judging from its shape, the ossicle most likely belongs to an asteroid.

Occurrence. - Totally 21 specimens, Öl 93-6 to Öl 97-12; bottom half of K.

Asterozoan adambulacra

Adambulacral? ossicle type A
Fig. 17D

Description. - An ossicle with a triangular ridge extending across it (compare ambulacral type B in Fig. 17A). Ridge smooth, probably due to erosion of the fragment. Ridge thinner in the middle. Basins more prominent and well developed than in type B and they coincide in size with each other. The basins also have a better rounded and smoother outline. Angles and sides of the ossicle are moderately rounded. A denser stereom occurs as a coating of the basins.

Remarks. - This ossicle could also be an ambulacral plate. See also remarks on type B ambulacral ossicle, but note that the basins in this ossicle almost coincide in size with each other. Most likely, however, this ossicle is an asteroid adambulacral plate (compare e.g. Blake & Guensburg

1988, fig. 2A).

Occurrence. - Totally 19 specimens, Öl 92-1 to Öl 92-9; mid J to top M.

Adambulacral? ossicle type B
Fig. 18B

Description. - A distinctive and thin ossicle with what seems to be an articulating area at one side (to the right in the picture). Some minor ridges also extend across the ossicle.

Remarks. - Most likely this fragment is an adambulacral ossicle from an asterozoan. What points in this direction is that the overall outline of the ossicle is shaped as to protect something and that the ossicle has something that looks like an articulating area. Ossicles of this type could alternatively represent virgalia or ambulacral ossicles.

Occurrence. - Totally 48 specimens, Öl 93-6 to Öl 97-12; bottom half of K.

Undetermined asterozoan ossicles

Remarks. - Most asterozoan ossicles remain undetermined and here I have just chosen to illustrate some of the most common types. The rest of the undetermined asterozoan ossicles have been accounted for together (see range charts).

Undetermined asterozoan ossicle type A
Fig. 17G

Description. - A triangular ossicle with a ridge separating it into two distinct regions. The sides are well rounded with no distinct angles except for one side where the ossicle border shows a sharp and distinct angle (top of Fig. 17G).

Remarks. - This ossicle resembles some ophiuroid ambulacral plates and some asterozoan adambulacral plates.

Occurrence. - Totally 6 specimens, Öl 92-3 to Öl 93-11; bottom half of K to upper P.

Undetermined asterozoan ossicle type B
Fig. 18C

Description. - A rather flat ossicle with two ridges extending across it. The biggest depressed area (to the left in Fig. 18C) gently slopes outwards against the margin of the ossicle from one of the ridges. This part of the ossicle is

paddle-shaped. The highest ridge is in the centre of the ossicle and extends from one corner to an other. The shape of the ridge is like a drawn out Z. This ridge ends in a swollen knob-like area in one of the corners (lower right in Fig. 18C). This corner seems to be an articulation area. The other ridge occurs along the margin of one of the sides and it is much lower. Between the two ridges there is a depressed channel.

Remarks. - This fragment could be an adambulacral or an ambulacral ossicle. It might also represent a virgalium ossicle.

Occurrence. - Totally 3 specimens, Öl 92-3; bottom half of K.

Undetermined asterozoan? ossicle type C
Fig. 18D

Description. - An almost rectangular ossicle with distinct ridges across it, resembling an X.

Remarks. - This fragment does not have any distinct articulating area, indicating that it possibly had the function of covering.

Occurrence. - Totally 7 specimens, Öl 93-6 to Öl 92-8; bottom half of K to mid M.

Undetermined asterozoan? ossicle type D
Fig. 18F

Description. - A rather well rounded ossicle without sharp angles. Several distinct articulating areas can be seen. No stereom specialisation can be seen.

Remarks. - This ossicle could be part of an asterozoan, but it might just as well be part of some other echinoderm. The distinct outline suggests that the main function of this ossicle was that of articulation.

Occurrence. - Totally 10 specimens, Öl 92-1 to Öl 92-9; mid J to top M.

Undetermined asterozoan? ossicle type E
Fig. 9G

Description. - A fragment with a rectangular outline. Corners are well rounded. One side is clearly depressed and gently dips inwards towards an almost circular opening, which penetrates the fragment. The other side of the fragment is slightly upraised compared with that with the hole.

Remarks. - Echinoderm fragments with holes penetrating through the whole fragment occur in some samples. These holes could indicate that some kind of vessel (most likely vessels from the water-vascular system) penetrated these areas. It is very possible that this kind of fragment belonged to an asterozoan echinoderm but it could also represent an ossicle from an edrioasteroid. Compare also with e.g. Rasmussen 1950, pl. 16, fig. 5, which illustrates vertebral ossicles from ophiuroids.

Occurrence. - Totally 23 specimens, Öl 93-6 to Öl 92-4; bottom half of K to top half of K.

Undetermined asterozoan ossicle type F
Fig. 17E

Description. - A smooth ossicle with a squarish outline and a triangular ridge extending across the upper parts of the ossicle.

Remarks. - Most likely this ossicle belongs to an asterozoan. This is just an example of the many different types of undetermined asterozoan ossicles that exist within the samples.

Occurrence. - Totally 2 specimens, Öl 93-6 to Öl 97-12; K.

Other echinoderm fragments of uncertain origin

Fragment type A of uncertain origin
Fig. 19A

Description. - A well-rounded and smooth fragment with a ridge across. Possibly this ridge could represent an articulating ridge. Depressed areas can be seen on both sides of the ridge. One side of the fragment has a semi-circular outline with a raised border occurring at the margin. On the other side the outline is irregular. The ridge connects to a raised border on this side.

Remarks. - Possibly a brachial.

Occurrence. - Totally 1 specimen, Öl 92-3; bottom half of K.

Fragment type B of uncertain origin
Fig. 19E

Description. - A rectangular fragment with a ridge occurring in the middle, running parallel with the longest side of the fragment. The ridge separates two distinct regions
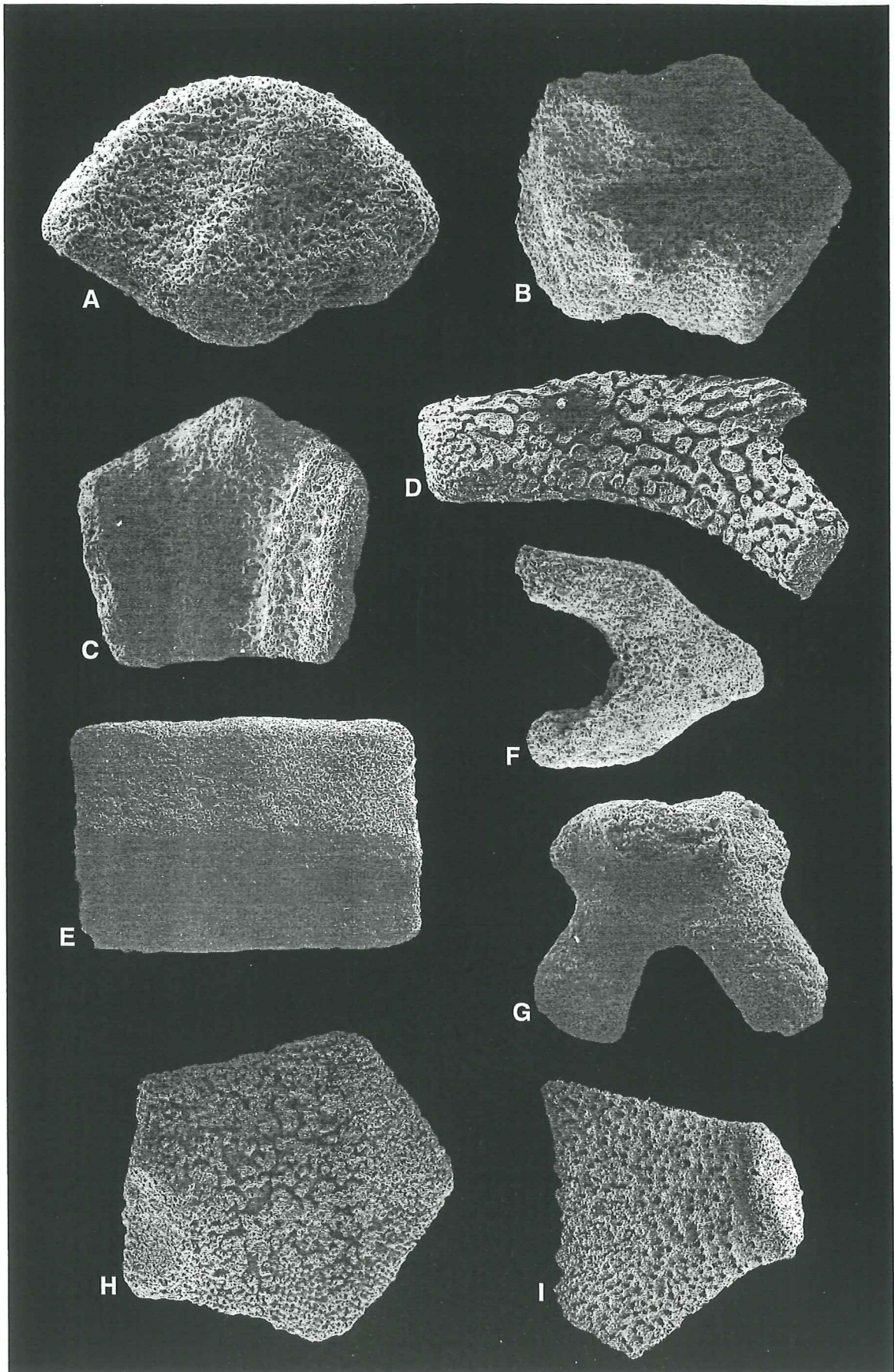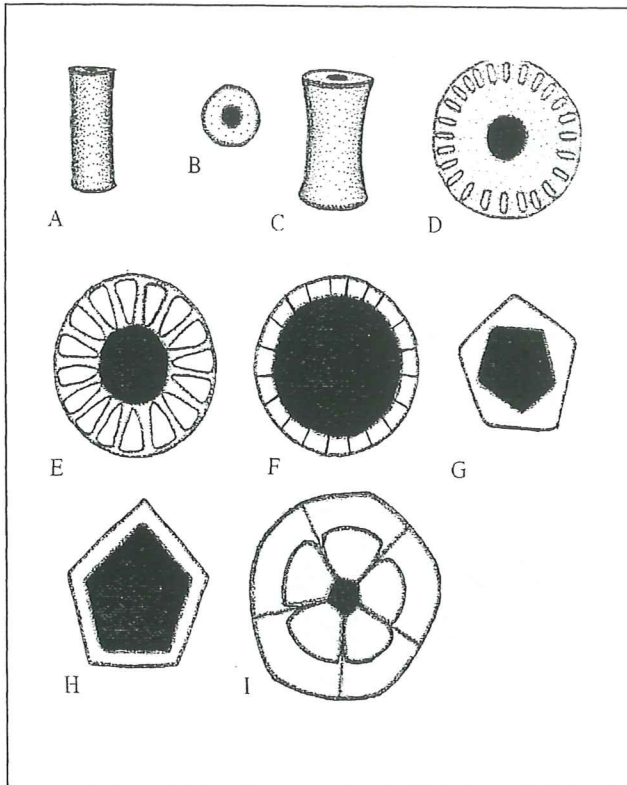
Fig. 20. Drawings of columnals. **A-B.** Rhombiferan col. type D from Öl 97-12. A, Side-view. B, Top-view. **C.** Glyptocystoid col. type B; from Öl 97-12. **D-F.** *Cyclocyclicus* (col.) spp; from Öl 97-12. D, *Cyclocyclicus* (col.) sp. B. E, *Cyclocyclicus* (col.) sp. D. F, *Cyclocyclicus* (col.) sp. E. **G-H.** Holomeric col. five development from Öl 97-12. G, type J. H, type K. **I.** Possible reconstruction of *Ramulicrinus*? (col.) sp. C.

Fig. 21. Drawings of columnal cross-sections. **A-C.** *Bystrowicrinus* (col.). A, *Bystrowicrinus* (col.) sp. B from Öl 94-6. B, *Bystrowicrinus* (col.) sp. C from Öl 92-7. C, *Bystrowicrinus* (col.) sp. D from Öl 94-5. **D.** Pentameric col. type F from Öl 92-9. **E.** Dwortsonaecrinidae from Öl 94-201. **F.** *Iocrinus*? sp. A from ÖL 94-6. **G.** *Oanducystis*? (col.) sp. A from ÖL 83-104. **H.** *Ramseyocrinus*? sp. C from Öl 97-12.

where one is more upraised than the other. When the ridge passes from the highest side to the lowest, it gently curves inwards against the highest part of the ossicle. The stereom also changes its outline passing from the highest part of the ossicle to the lowest. On the highest part, the stereom is finer with more stereom pores occurring per unit of area in comparison with the lowest side, where the stereom pores are broader. This stereom distinction is clearest just beneath the ridge on the lowest side of the ossicle.

Remarks. - This type of ossicle is common in many samples. Especially interesting to note are the stereom differences. Most likely the ridge represents some kind of articulating area and therefore this ossicle type most likely fills the function of articulation.

Occurrence. - Totally 265 specimens, Öl 94-6 to Öl 94-201; H to top of section.

Fragment type C of uncertain origin
Fig. 19G

Description. - A fragment with two distinct and well-rounded outgrowths. The area from where these originate is flat and lens-shaped.

Remarks. - Several different types of ossicles with strange shapes exist within the samples and most of them still remain undetermined.

Occurrence. - Totally 1 specimen, Öl 92-9; top M.

Fig. 19. **A, E, G.** Fragments of uncertain origin. A, Fragment type A; from Öl 92-3, x160. E, Fragment type B; from Öl 93-6, x95. G, Fragment type C; from Öl 92-9, x150. **B.** Brachial type A; from Öl 92-3, x190. **C-D, F.** Pinnular. C, Pinnular type A; from Öl 97-12, x140. D, Pinnular type B; from Öl 92-9, x70. F, Pinnular type C; from Öl 92-9, x120. **H-I.** Echinoderm plates. H, specimen from Öl 97-12, x120. I, specimen from Öl 93-6, x75.

Brachials and pinnules of uncertain origin

Brachial type A
Fig. 19B

Description. - A brachial with a rather smooth surface. A groove extends from one side to the other, penetrating most of the ossicle. One of the sides is pointed and one looks more like an articulating area with two depressed semi-circular areas occurring next to the groove. The articulating surface is almost vertical. In the middle the ossicle is cone-shaped. No specialised stereom can be seen.

Remarks. - Compare this brachial type with that described e.g. by Macurda & Meyer 1975, pl. 14, fig. 6.

Occurrence. - Totally 5 specimens, Öl 94-5 to Öl 97-12; H to mid K.

Pinnule type A
Fig. 19C

Description. - A fragment, which at one end is rectangular with slightly outward curving sides and at the other end has a triangular outline. The surface of the ossicle is divided into distinct steps with a flat channel surface at the bottom. These steps follow the somewhat gently outward curving sides. The channel surface is widest at the triangular end and also splits into two separate sections near this end. The stereom surface of the channel and the steps has a coating of what seems to be denser stereom. The other side (the one not depicted here) of this ossicle is smooth and bulges gently outwards.

Remarks. - The denser stereom occurring at the bottom of the channel might indicate a stereom specialisation due to the tissue present. Macurda & Meyer (1975) noted that in pinnules, the area of the muscular fossae often shows labyrinthic stereom. This is most likely also the case with this ossicle. Also note that the denser stereom only occurs in the area where the vessels from the water-vascular system are supposed to lie.   Here I have chosen only to depict some different types of pinnules but many other types are present within my samples. Some only have one channel that is not bifurcated and some show a different overall outline e.g. they are broader, they do not posses a triangular side, the length may vary and so on. The distribution of most pinnules is also clearly size-dependent, meaning that smaller sample-fractions (nano-fractions) contain more pinnules than coarser ones. This type described here is the overall most common type.
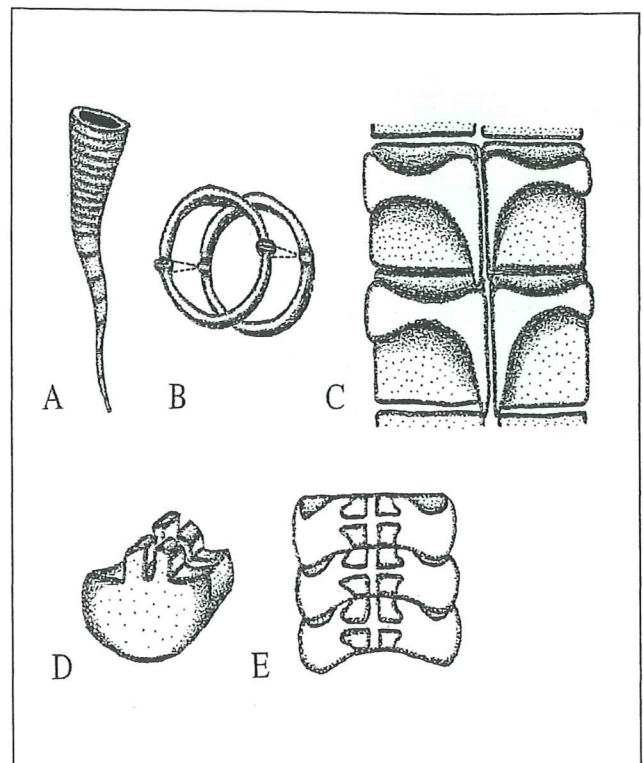
Fig. 22. **A.** A rather typical glyptocystoid stem, which tapers distally. **B.** Stem articulation in rhombiferans; interlocking ribs are guided in place by either muscular or ligamentary tissue. **C.** Illustration of how the ambulacral ossicles type B could have worked as part of an ophiuroid arm. **D-E.** Aulacophore ossicles. D, One ossicle viewed from the side. E, Ossicles acting together, making the distal parts of the animal movable.

Occurrence. - Totally 320 specimens, Öl 93-6 to Öl 94-201; base K to top of section.

Pinnule type B
Fig. 19D

Description. - A long and slender pinnule, which bifurcates at one end. Some abrasion has occurred and this resulted in the break-off of the bifurcated parts.

Remarks. - The delicate structure of this fragment would most likely result in breakdown during postmortem transport. This might explain that only one specimen was found in the samples.

Occurrence. - Totally 1 specimen, Öl 92-9; top M.

Pinnule type C
Fig. 19F

Description. - A very short and delicate crinoid pinnule. The overall outline is horse-shoe like. The surface is very

smooth (most likely due to erosion) and the corners are rather well rounded.

Remarks. - Pisera (1994) described exactly the same type of pinnule. See Pisera 1994, pl. 60, fig. 2. See also remarks above under type B.

Occurrence. - Totally 3 specimens, Öl 92-9; top M.

Echinoderm plates
Fig. 19H, 19I

Description. - Fig. 19H shows a pentagonal plate of unknown affinity. One side has a depressed area with what seems to be denser stereom.
Fig. 19I shows another type of plate which is almost triangular. One side has a raised area resembling some kind of articulation area.

Remarks. - Many different types of plates have been found in the samples and those depicted here are not representative for all of these. The aim of showing these here is more to give the reader a general idea of what these plates can look like. The depressed area in the fragment shown on Fig. 19H may represent an articulating joint, but it may also represent a broken-off area.

Occurrence. - Totally 22 specimens, Öl 93-6 to Öl 92-9; base K to top M.

Discussion and results

Species and implications for different types of columnal morphology. - The establishment of columnal morphogenera is a necessary first step to bring some order among the multitude of different forms. The overall lack of knowledge to which natural groups these different types belong, makes it quite hard to interpret the palaeoecology. Some observations can be made, however, as the columnal outline often reflects the life-style (e.g. wedge-shaped ossicles indicate a bent over lifestyle). The distribution of different types of articulation could also be interesting to note. In some cases it is, however, not possible to determine if a columnal is derived from a cystoid or a crinoid. In these cases conclusions could be drawn judging from the non-presence or presence of other types of columnals which with certainty can be ascribed to either cystoids or crinoids. Other parameters that can be used in this distinction between these classes are the columnal articulation types. In this study, though, the differentiation between these classes have in most cases been clear and distinct.

Samples	Sum Stylophora	Sum Cyclocystoididae	Sum Rhombifera	Sum Asterozoa	Sum Crinoidea
Öl 94-201	0	0	3	0	32
Öl 93-12	0	0	11	0	182
Öl 93-11	0	0	18	5	258
Öl 83-107	0	0	0	0	3
Öl 93-10C	0	0	1	0	1
Öl 93-10B	0	0	0	0	2
Öl 93-8	1	0	2	0	8
Öl 92-9	13	0	34	59	302
Öl 92-8	0	0	19	4	6
Öl 83-104	0	0	0	0	1
Öl 92-7	0	0	13	0	3
Öl 92-6	8	0	18	19	19
Öl 72-5	1	0	36	10	5
Öl 92-4	0	0	38	1	2
Öl 97-12	17	12	150	203	53
Öl 92-3	9	8	143	121	65
Öl 93-6	5	0	14	96	40
Öl 92-2	1	0	0	2	1
Öl 92-1	0	0	39	13	16
Öl 93-4	1	0	0	0	0
Öl 93-3	0	0	204	4	0
Öl 94-5	0	1	33	2	17
Öl 94-6	1	0	152	5	14

Table 2. The table summarizes the values used in the chart in Fig. 23. See under Fig. 23 for notes on the summation of each class.

The number of columnals varies between different species, so that some species and classes will produce more fragments than others. An example of this is extremely thin or low columnal ossicles of which there are many per length unit. Glyptocystoids often have a stem that tapers away distally, so that columnals often decrease in diameter distally, but they can also often increase in height distally (see Fig. 22A for an illustration of a glyptocystoid stem).

The overall most common type of articulation is symplexy. Some levels, however, show a dominance of columnals with synostial articulation. In my samples synostial articulation is almost exclusively found in columnals which most likely belong to rhombiferans. These columnals are either extremely thin or at least of quite equal height. It is also important to remember that articulation in rhombiferan stems functions quite differently from that adapted by crinoids. See e.g. Paul (1984) for a discussion dealing with cystoid articulation. Fig.

22B illustrates schematically how articulation in rhombiferans works, so generally one can distinguish between synostial and symplectial columnals.

Holomeric columnals are the most common type while pentameric ones are rarer. The evolution of columnals clearly goes in the direction of holomerism (e.g. Stukalina 1988; Donovan 1990). Donovan (1990) suggested that the meric sutures obviously provided the necessary flexibility for the stem so that a special articulation type was not necessary at an early stage. He suggested that it had been a disadvantage to evolve another kind of articulation at this stage, but also noted that "with the evolution of the holomeric columnal, an alternative to synostial articulation was essential to preserve stem flexibility". At an even later stage ligamentary articulation based on ligaments situated in distinct pits (ligamentary pits or areola pits) on the articular facet was introduced (see e.g. Stukalina 1988). Fig. 23 summarizes the class distribution through time. Table 2 summarizes the values used to produce the chart in Fig. 23 clearly illustrating that the early samples are dominated by rhombiferans. Figs. 24, 25 and 26 are range charts for each specimen identified. Fig. 25 illustrates that holomeric columnals with a five-fold development are introduced at a rather early stage (Öl 94-6, base of H). Likewise are holomeric columnals with a cyclic symmetry introduced at this stage. Interesting to note is that the genus *Cyclocyclicus* (col.) does not occur in my samples until Öl 92-2 at the J/K boundary and this is also the first occurrence of symplectial articulation in my samples. This genus does not become very common until it clearly dominates the sample Öl 92-9
at the top of M (see Appendix A).

Pentameric columnals are rather uncommon in comparison with other crinoid columnals at the stratigraphically earliest stages in my samples but they are represented from Öl 94-5 (top H) and upwards. At an even later stage (Öl 93-11; top P, and upward) ligamentary articulation, based in areola pits on the articulation facet (e.g. *Ramulicrinus*), becomes more common (see Appendix A). At some levels it even dominates over other types of articulation (e.g. Öl 93-11; top P). It should be emphasized that the Figs. 23, 24 and 25 and Appendix A only illustrate phosphatized fragments, so that some gaps in the distributional record exists, where phosphatization did not happen.

Rhombiferan columnals dominate the samples from Öl 94-6 (basal H) to Öl 92-9 (top M). See Appendix A for the amount of this class in this interval. In the sample Öl 92-9 the columnal domination is taken over by the genus *Cyclocyclicus* (col.) (see Appendix A). In the interval represented by the samples between Öl 92-9 and Öl 93-11 (top P) the number of species is very low and some of the samples do not even contain columnal ossicles. So the data in this interval is of very low statistical importance in comparison with the samples Öl 92-9 and Öl 93-11. Something happens, however, in this interval as the columnal articulation type that dominates Öl 93-11 is ligamentary attachment based in areola pits (for example *Ramulicrinus* (col.)). This interval also represents a heavy decline in the number of *Cyclocyclicus* (col.) columnals, while other types of columnal articulation types retain their relative low contribution to the total number of columnals in the samples. Appendix A indicates that the only change that happens in this interval is that the percentage of *Cyclocyclicus* (col.) columnals declines and the percentage of *Ramulicrinus* (col.) columnals increases. Possibly then the shift of dominational articulation type within this interval could be explained by the fact that ligamentary articulation based in areola pits is better adapted to the life-environment as represented by this interval. It is, though, here clearly indicated that domination within crinoids seems to closely follow the known evolution of articulational types (see below for discussion of this evolution).

In Fig. 23 the link and connection with the distribution of the different subphyla and classes is demonstrated. Appendix A also illustrates that pentameric columnals are rather uncommon in all the samples examined and that true pentameric crinoid columnals first occur at Gillberga at a rather late stage. At this stage most of the other morphological columnal types had already been introduced in the stratigraphic record, as represented by the section at Gillberga. Individuals with pentameric columnals probably lived in an environment that first is represented a bit up in the Gillberga section.

The columnals recognized as most likely belonging to crinoids in the stratigraphically earliest samples also show a domination of a rather wide and complex lumen outline (see for example Fig. 21B). The lumen width amongst columnals examined mostly shows the same size. Some "extreme" cases are those where the lumen is point-sized or very wide. The columnals having a very wide lumen

Fig. 23. Distribution of stylophorans, cyclocystoids, asterozoans, crinoids and rhombiferans with time. Each bar represents stacked values of fragments for each sample. Total sums for each class can be found in appendix A. The total sum of crinoid columnals is based on all columnals that have not been ascribed in the text to the class Rhombifera. Note also that the stratigraphic boundaries illustrated at the bottom of the diagram are only approximate (only the samples that have been examined are illustrated). Pinnules, brachials, plates and other types of indeterminable echinoderm fragments have not been used in the summation. See fig. 4 for the complete biozonation of the section studied.
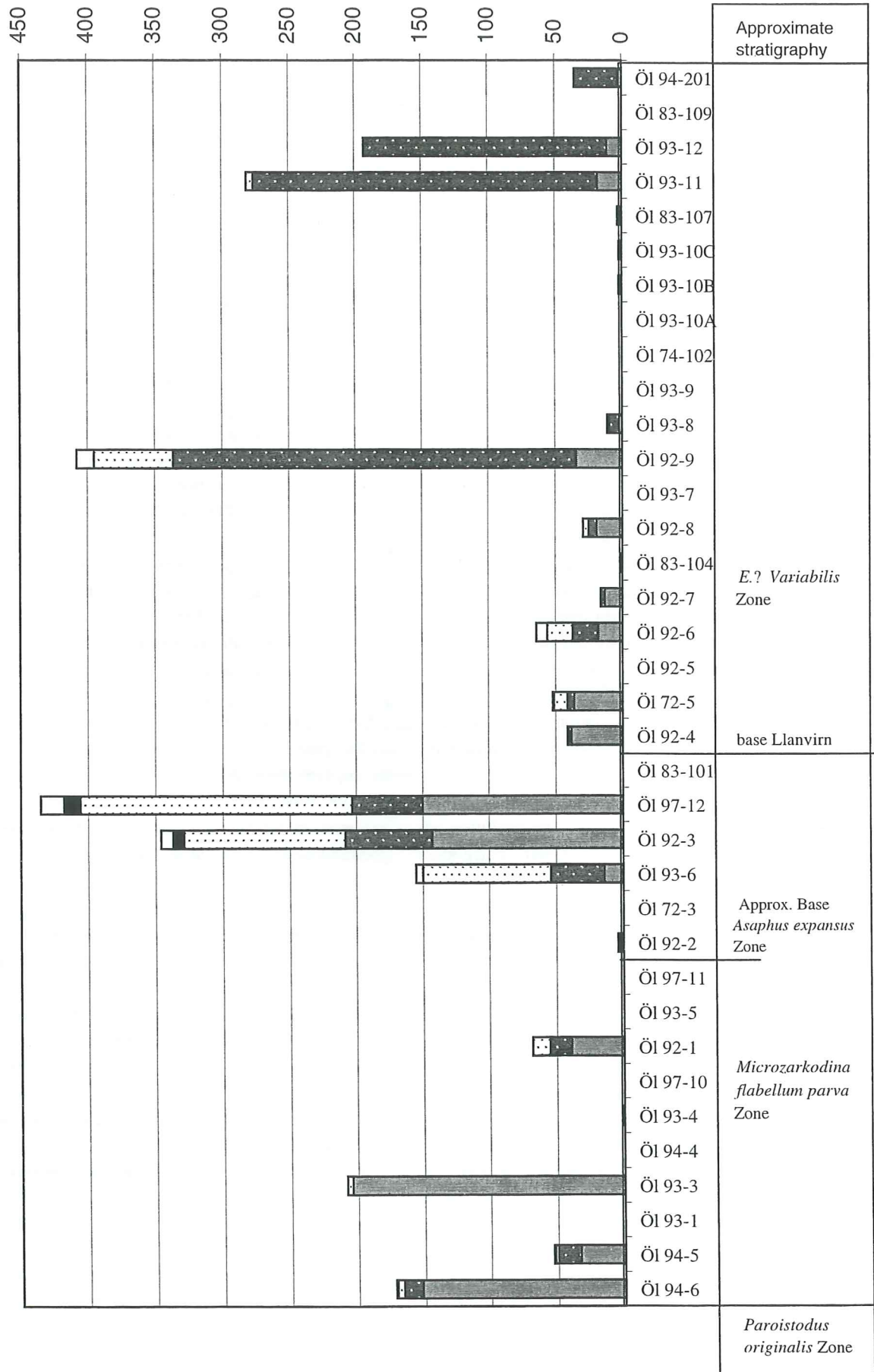
and only a very small articulation surface indicate a rather primitive early evolutionary form of columnal morphology (Stukalina 1988). The evolution of columnals with time goes towards a point-sized lumen with a successively wider articulation surface (Stukalina 1988). Stukalina (1988) also noted that the next step then in most cases goes in the direction of a specialisation of the articulation surface e.g. with the development of special areas for ligamentary attachment (areola pits) or with the evolution of another kind of articulation. She also concluded that a wider articulation surface naturally is achieved by constriction of the axial canal and consequently also a restriction of the axial canal connective tissue. This means that the axial canal connective tissue more and more loses its function of binding columnals together. Stukalina (1988) also concluded that there are two main types of trends in the constriction of the axial canal, one where a gradual decrease in axial canal size is associated with the formation of lobes, which are directed towards the columnal angles (e.g. *Bystrowicrinus*) and the other where the initial shape of the axial canal is retained even though its size decreases. It is also important to note that early evolutionary morphology of columnals often is retained in the more distal parts of the stem so that one complete stem can show many different types of evolutionary steps (Stukalina 1988). Donovan (1990) concluded that the evolution of different articulation types went from synostial to symplectial. The columnals with a point-sized lumen mostly show synostial articulation in my samples and is recognized as belonging to mostly rhombiferans in this investigation.

Extremely low ("leaf-thin") ossicles are present in some species. Stukalina (1988) concluded that the evolution of a point-sized lumen in some species clearly correlates with a decrease in columnal height. This decrease in columnal height, she concluded, could account for the change in tensional forces acting on the axial canal connective commisure as the result of the size-reduction of the axial canal. This evolution of extremely thin columnals resulted in an increasing number of columnals in the stem, which could "have favoured large tilt amplitudes of stems with small divergence angles of the columnals" (Stukalina 1988). The distribution and amount of extremely thin ossicles and / or columnals with a point-sized lumen clearly correlates with the distribution of rhombiferans within the samples examined (see Fig. 23 for the distribution and amount of each class-subphylum ossicle/columnal within the samples). As discussed earlier the amount of thin ossicles is clearly linked to the presence or non-presence of rhombiferans and each individual provides more ossicles per unit length of stem to the sediment than e.g. crinoids with "normal" ossicle height. This means that the amounts illustrated in Fig. 23 can not

directly be interpreted as proportional to number of individuals.

Some species also clearly show stereom specialisation due to the nature of the investing tissue. This is most clear amongst fragments from asterozoans, probably because the number of different types of investing tissue is greater in them than in pelmatozoans. See also below under stereom.

Preservation. - The different types of preservation as described above mostly occur at different levels. Some levels clearly show a mixture between different types of preservation. This in combination with the fact that especially some levels show heavily abraded columnals indicate that transport of debris sometimes has been very active. Sorting processes have also been very active at some levels. Some levels are also so diagenetically altered or show so heavily eroded columnals that systematic determination is impossible and only overall columnal outline could be described.

The diagenetic alteration of the material has not been investigated by the use of thin-sections but some diagenetic observations have been made. No traces of bacterial communities trapped in the stereom have been found. Lamboy (1990) noted that bacterial activity is very important in the phosphatization processes. Many other authors have also stressed the role of microbial mediation in phosphatogenesis (e.g. Soudry & Lewy 1988; Prévôt & Lucas 1986). Lamboy (1990) also noted long threads occurring in the phosphatized echinoderm stereom. These threads he suggested were remains of algal filaments. No such remains have been found in my material. A possible explanation for the absence is that they have not been phosphatized. All the samples examined were treated with acetic acid as noted before, so no "original" samples have been examined. Nordlund (1989a) also suggested that the role of algae was important in the phosphatization processes that might have been at work in generating phosphatic hard grounds in the Ordovician of northern Öland. If the same alteration process was responsible for the phosphatization of the echinoderm stereom in the material examined is hard to say without further diagenetic investigations, but most likely bacterial activity played an important role during phosphatogenesis of the material examined.

Most of the taxa described show an abundance peak in the samples Öl 93-6 to Öl 97-12 (lower half of division K) and the species diversity is also greatest at this time (see appendix A). These samples roughly correspond to the time just before the Arenig-Llanvirn boundary. As noted earlier the Llanvirn boundary is known to represent a regressive phase. The peak in diversity and abundance could be linked to extensive phosphatization of particles

Figure 24 (range-chart). Row labels (top to bottom):

- Undeterm. columnals
- Pentagonal col. undeterm.
- *Oanducystis?* (col.) sp. A (Fig. 21G)
- *Dwortsonaecrinidae* (Fig. 21E)
- *Tetragonocyclicus?* (col.) sp. A (Fig. 14D)
- *Ramseyocrinus?* sp. C (Fig. 21H)
- *Ramseyocrinus?* sp. B (Fig. 14C)
- *Ramseyocrinus?* sp. A (Fig. 14A)
- *Ramseyocrinus cambriensis* (Fig. 14B)
- Pentameric? col. type G (Fig. 13C)
- Pentameric col. type F (Fig. 21D)
- Pentameric col. type E (Fig. 16G)
- Pentameric col. type D (Fig. 16B)
- Pentameric col. type C (Fig. 15F)
- Pentameric col. type B (Fig. 14I)
- Pentameric col. type A (Fig. 12A)
- Rhomb. col. type D (Fig. 20A)
- Rhomb.? col. type C (Fig. 9E)
- Rhomb.? col. type B (Fig. 11C)
- Rhomb. col. type A (Fig. 11B)
- Glypto. col. type F (Fig. 13E)
- Glypto. col. type E (Fig. 13D)
- Glypto. col. type D (Fig. 13A)
- Glypto. col. type C (Fig. 12D)
- Glypto. col. type B (Fig. 20C)
- Glypto. col. type A (Fig. 11A)
- Cyclocystoididae type B (Fig. 9I)
- Cyclocystoididae type A (Fig. 9H)
- Aulacophore type B (Fig. 9F)
- Aulacophore type A (Fig. 9C)
- Stylocone? type C (Fig. 9E)
- Stylocone type B (Fig. 9B)
- Stylocone type A (Fig. 9D)
- Stylocone type A (Fig. 9A)

Conodont biozones (bottom): *E. ? variabilis* Zone; Llanvirn boundary; Base *Asaphus expansus* Zone; *Microzarkodina flabellum parva* Zone; *Paroistodus originalis* Zone.

Fig. 24. Range-chart for stylophoran fragments, rhombiferans, pentameric columnals, *Ramseyocrinus*, *Tetragonocyclicus* (col.), *Oanducystis* (col.), undetermined pentagonal columnals and undetermined columnals. Note also that every sample is represented even though not every one has yielded echinoderm fragments. Solid rectangles represent proven occurrences of that particular species or type.

in connection with sea level low-stands. The samples do, however, most likely reflect a "true" diversity peak, in this interval, as noted by several other authors (see discus-

sion further on).

What is interesting to note is that in some fragments, where there is both sugary and total replacement of calcite

Range chart of crinoid columnal taxa against samples and conodont biozones:

Taxa (top to bottom):

- Iocrinus? sp. A (Fig. 21F)
- Ramulicrinus? (col.) sp. C (Fig. 15I)
- Ramulicrinus? (col.) sp. B (Fig. 16A)
- Ramulicrinus? (col.) sp. A (Fig. 14J)
- Sidericrinus? (col.) sp. A (Fig. 11H)
- Bystrowicrinus (col.) sp. D (Fig. 21C)
- Bystrowicrinus (col.) sp. C (Fig. 21B)
- Bystrowicrinus (col.) sp. B (Fig. 21A)
- Bystrowicrinus (col.) type A (Fig. 11G)
- Babanicrinus? sp. A (Fig. 15A)
- Baltocrinus? (col.) sp. B (Fig. 14F)
- Baltocrinus? (col.) sp. A (Fig. 11K)
- Pentagonocyclicus (col.) undeterm.
- Pentagonocyclicus (col.) sp. B (Fig. 15G)
- Pentagonocyclicus (col.) sp. A (Fig. 15E)
- Pentagonoellipticus? (col.) sp. A (Fig. 15B)
- Pentagonocyclopa? (col.) sp. A (Fig. 11I)
- Cyclocyclicus? (col.) sp. E (Fig. 20F)
- Cyclocyclicus (col.) sp. D (Fig. 20E)
- Cyclocyclicus (col.) sp. C (Fig. 15H)
- Cyclocyclicus (col.) sp. B (Fig. 20D)
- Cyclocyclicus? (col.) sp. A (Fig. 15D)
- Circular col. undeterm.
- Hol. cycl. col. type C (Fig. 13F)
- Hol. cycl. col. type B (Fig. 13B)
- Hol. cycl. col. type A (Fig. 11F)
- Hol. col. five dev. type K (Fig. 20H)
- Hol. col. five dev. type J (Fig. 20G)
- Hol. col. five dev. type I (Fig. 16F)
- Hol. col. five dev. type H (Fig. 16E)
- Hol. col. five dev. type G with spines (Fig. 16D)
- Hol. col. five dev. type G (Fig. 16C)
- Hol. col. five. dev. type F (Fig. 14H)
- Hol. col. five. dev. type E (Fig. 14G)
- Hol. col. five. dev. type D (Fig. 14E)
- Hol. col. five. dev. type C (Fig. 13H)
- Hol. col. five. dev. type B (Fig. 13G)
- Hol. col. five. dev. type A (Fig. 11J)

Sample (left to right):

Ol94-201, Ol83-112, Ol83-111, Ol87-6, Ol87-5, Ol87-4, Ol74-100, Ol83-110, Ol72-8, Ol83-109, Ol93-12, Ol74-101, Ol83-108, Ol93-11, Ol93-10C, Ol93-10B, Ol93-10A, Ol74-102, Ol93-9, Ol83-106, Ol87-3, Ol87-2, Ol93-8, Ol72-7+Ol83-105, Ol92-9, Ol93-7, Ol92-8, Ol83-104, Ol92-7, Ol72-6, Ol83-103, Ol92-6, Ol87-1, Ol92-5, Ol72-5, Ol83-102, Ol92-4, Ol83-101, Ol97-12, Ol92-3, Ol93-6, Ol72-3, Ol72-4, Ol92-2, Ol72-2, Ol83-100, Ol97-11, Ol93-5, Ol92-1, Ol97-10, Ol93-4, Ol88-6, Ol72-1, Ol94-4, Ol93-3, Ol88-5, Ol93-1, Ol94-5, Ol88-4, Ol94-6, Ol94-7, Ol88-3

Column groups: S, R, Q, P, O, N, M, L, K, J, I, H

Conodont biozones:
- E. ? Variabilis Zone
- Llanvirn boundary
- Base Asaphus expansus Zone
- Microzarkodina flabellum parva Zone
- Paroistodus originalis Zone

48

with phosphate, the alteration zones can clearly be seen to follow distinct paths within the stereom structure. If this is due to the original stereom meshwork structure or to different phosphatization penetration depths, possibly of algal mycel or some other agent is hard to say. The zones available for phosphatization also depend on cementation with other minerals. Most likely, though, is that the phosphatization happened at a rather early stage. Lamboy (1987) noted in his work about the phosphatization of echinoderm debris that a first generation of phosphate precipitates in the intrastereomic pores, resulting in a phosphatic network. The calcite is then dissolved, allowing a second generation of phosphate to be precipitated. He further described the development of a thin phosphatic film on the surface of the fragment (see also above under preservation) which gives the fragment an outline that closely resembles that of a phosphatic grain (the surface becomes smooth and shiny). He also demonstrated that this transformation occurs within the sediment. Another important aspect that he noted is that "at each stage, the skeletal remain corresponds to a permeable framework constituting a semi-confined micro-environment". Prévôt & Lucas (1986) noted in their work on the microstructure of apatite replacing carbonate that "apatite preferentially replaces structural elements, but it also occupies voids".

In some fragments the replacement of calcite with phosphate have resulted in distinct zones with a special type of preservation. In e.g. Fig. 7B there is a clear distinction between the preservation zones as described before. The outer zone is sugary and the inner rod-like. The rod-like zone most likely represents an original galleried stereom structure, where the phosphate has precipitated in the stereom pores resulting in the rods described. There are no interconnecting pores between rods. This is as could be expected if the original stereom structure was galleried, because galleried stereom as described by Smith (1980) appears as "long parallel galleries running in one direction only and shows no pore alignment perpendicular to this direction". Galleried stereom is usually associated with areas where the investing tissue runs like long fibres interconnecting e.g. different columnals (see e.g. Macurda & Meyer 1975). In Fig. 7B, the rod-like preservation occurs

in what probably once was the areola pits of the columnal (also see above under preservation). Areola pits are sites of attachment and articulation between columnals. Donovan (1984b) noted in his work on recent crinoids that the stereom structure in the petaloid zones of the columnals he examined was rectilinear. Rectilinear stereom as described by Smith (1980) shows good pore alignment in three directions. If the original stereom had been rectilinear in the fragment in Fig. 7B, there most likely would have been some interconnecting pores of phosphate between the rods. So probably the rod-like preservation represents originally galleried stereom.

In Fig. 6A there is an outer zone of sugary preservation as described earlier. Inside this we still have sugary preservation, but with a more open phosphatic framework. Pore space is here still available. If this is the result of some kind of limiting phosphate precipitation factor is hard to say due to the fact that no thin-sections have been examined. This pore space most likely was filled with calcite prior to the treatment of the sample with acetic acid. The amount of precipitated secondary phosphate clearly varies between the samples and also within some samples. What the controlling factor has been in the precipitation of the secondary generation of phosphate is hard to say without proper diagenetic investigations. Lamboy (1993) for instance noted that necessary chemical elements for apatite crystallisation are: PO_4^{3-}, Ca^{2+} and CO_3^{2-} ions. The phosphate ions could be released "from organic matter by the action of alkaline phosphatase and other enzymes" and the Ca^{2+} and CO_3^{2-} ions from "calcium carbonate through the production of organic acids that dissolve the carbonate and result in extracellular apatite precipitation" (Lamboy 1993). Still it is very interesting to find out what the controlling factor of secondary phosphate precipitation has been, particularly as secondary phosphate often occurs in very special zones. One might suspect that the original stereom pore geometry and structure could be important but also the fact that the sugary preservation in most cases is restricted to the outer parts of the columnal is of great interest. Possibly the phosphatization process has halted before reaching all the way through all of the stereom meshwork. The main problem arises when a fragment is preserved as sugary all through the stereom meshwork. This could then possibly be regarded as a complete secondary phosphate precipitation.

Some stereom types show a more restricted pore system in comparison with others. Rectilinear stereom shows, as described earlier, good pore alignment in three directions in a lattice-like structure while galleried stereom shows very long and open interconnecting pores in one direction (see also Fig. 8). This results in permeability within one fragment most likely varying between different stereom

Fig. 25. Range-chart for holomeric columnals with five-fold development, holomeric cyclic columnals, *Cyclocyclicus* (col.), *Pentagonocyclopa* (col.), *Pentagonoellipticus* (col.), *Pentagonocyclicus* (col.), *Baltocrinus* (col.), *Babanicrinus, Bystrowicrinus* (col.), *Sidericrinus* (col.), *Ramulicrinus* (col.) and *Iocrinus*. Note also that every sample is represented even though not every one has yielded echinoderm fragments. Solid rectangles represent proven occurrences of that particular species or type.
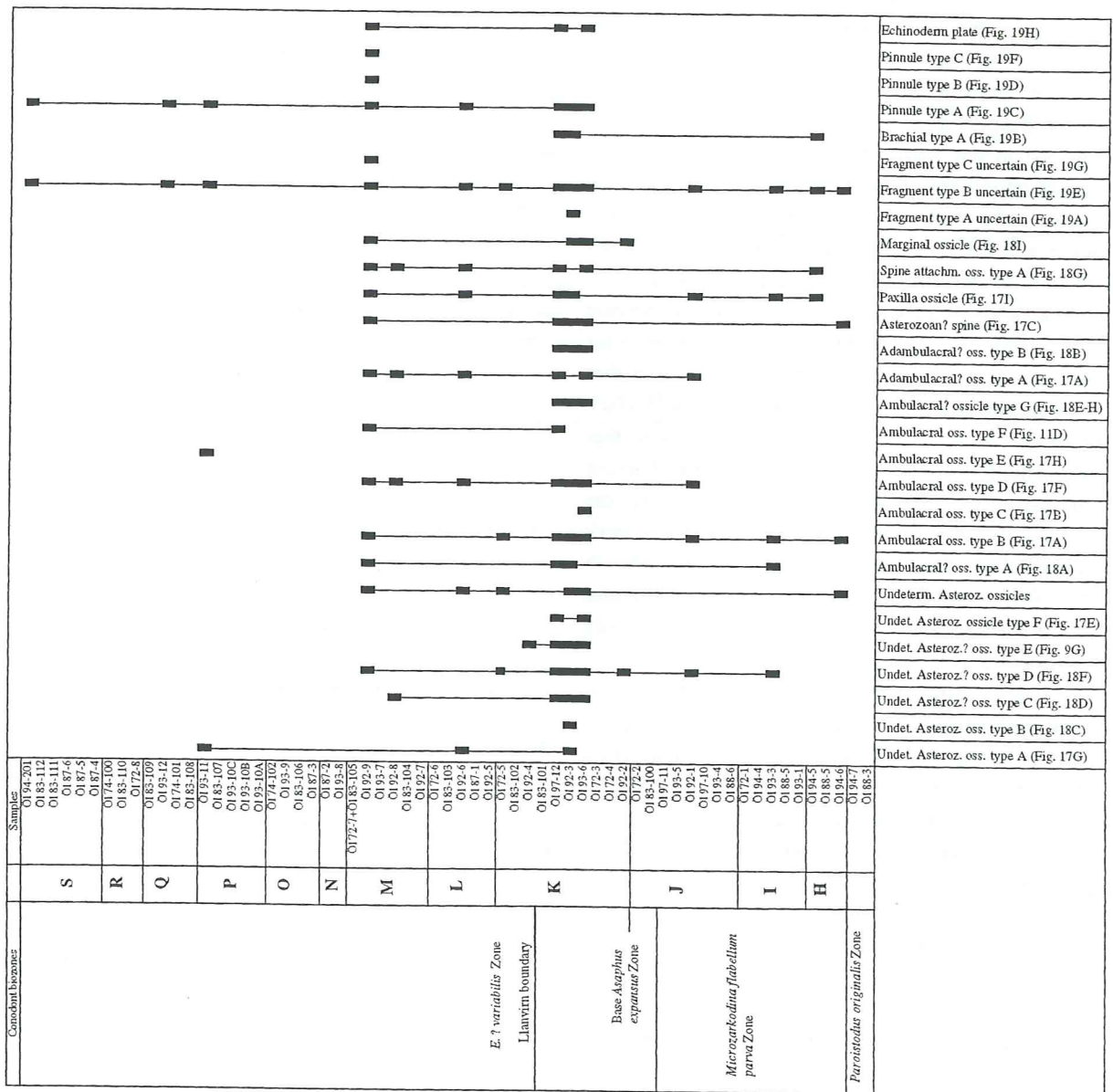
Fig. 26. Range-chart for asterozoan fragments, brachials, pinnular, fragments of uncertain origin and echinoderm plates. Note also that every sample is represented even though not every one has yielded echinoderm fragments. Solid rectangles represent proven occurrences of that particular species or type.

zones. Further investigations within this area could result in interesting diagenetic observations. Clearly several limiting factors of phosphate precipitation have been important in the sequence at Gillberga. The amount of phosphate also varies between different levels there. Some levels show no phosphatization at all and this is probably due to the nature of the depositional environment.

If fragments with sugary and rod-like preservation occur together in one sample but are separated between fragments one might expect that some parting of fragments during sample preparation have occurred. This is true if

the sugary preservation is a function of precipitation of secondary phosphate within the sediment as suggested by Lamboy (1987). If this process happens within the sediment it is hard to think that some kind of syndepositional sorting process is responsible for the occurrence of these different types of preservation within one sample. It should naturally also be noted that one sample might have been taken across two different preservational zones. Also note that within some samples many different types of preservation occur and this then might indicate some kind of sorting process. In some cases sugary and rod-like preservation occur within the same fragment (e.g. some fragments in Öl 93-10C) and this could then been seen as a function of gentler sample preparation so that no parting has occurred during this process.

Occasionally the sugary preservation has replaced a whole fragment, a phenomenon occurring at many different levels. What the controlling factors for precipitation and halting of the process have been in these cases has yet to be determined.

The coated preservation only occurs rather scarcely at some levels. In some cases the surface of the coating has a rather flaky appearance. This coating most likely has happened after the preservation of stereom structure because the coating seems to appear on a perfectly preserved stereom. As previously mentioned this coating results in a more rounded and smoother outline of the fragment and that it increasingly resembles a very abraded fragment. When this type of preservation occurs within a sample one should therefore be very careful before determing the erosional level of the fragments. It is difficult to tell which kind of mineral that builds up this coating without proper investigations but some resemblance exists with chamosite. It should be noted, however, that Sturesson (1986) in his work on Lower Ordovician ooids from northern Öland, expressed that "Ooids with varying amounts of chamosite has been found at all localities, except for Gillberga".

Glauconitic preservation also occurs at some levels. As mentioned earlier this preservation can occur within the stereom or as a filling of the lumen. The last type often has as a result that the stereom meshwork has cracked wide open due to continued growth of the glauconite grain. This naturally implies continued growth within the sediment either of detrital glauconite grains or diagenetic grains.

The occurrence of pyritic preservation is hard to work out because of the magnetic separation of some samples. This type of preservation is though most likely not that common (less than 10 fragments with this type of preservation have been found in the samples examined).

The best overall preservation of stereom structure is naturally when phosphate has replaced calcite totally, result-

ing in an exact replica of the original stereom meshwork. The surface of such fragments appears white and glossy with an almost grainy texture.

Stereom organisation and relationship to investing tissue. - The relationship between stereom organisation and investing tissue in echinoderms has been discussed by various authors. Smith (1980) made the most detailed compilation in his work on the stereom structure of echinoids. He also noted that the conclusions drawn in his work most likely also applies to other groups of echinoderms. Various authors have also noted that during growth the stereom can adjust to new types of investing tissue leaving only a remnant of the old stereom organisation (see e.g. Donovan 1984b; Smith 1980). Thus, during growth of the animal, distinct stereom centres with specialised functions related to investing tissue, move along the plate as growth continues, leaving only an old remnant of the original stereom type, which often can be recognised (see e.g. Smith 1980, pl. 22, fig. 4, 6). This means that resorption and reprecipitation of stereom are ongoing processes that can be affected not only by growth but also e.g. by changing life-environments. The stereom organisation is affected by the life-habitat of the animal so that e.g. echinoids that live in a near-shore environment have a denser stereom building up a thicker calcitic test, that is able to resist the high wave-energies that it is subjected to (Smith 1980). He also noted that stereom growth-lines often can be distinguished, where more fast-growing and open stereom meshworks can be related to a change in the life-environment of the animal (e.g. better conditions for calcite precipitation).

The main question regarding stereom organisation in crinoids is if the crinoid column has muscular tissue or not. Donovan (1989b) discussed the improbability of a muscular crinoid column and he also came to the conclusion that muscular tissue had not been present in fossil crinoid columnals. The fact that recent crinoid columnals do not have muscular tissue also supports these conclusions drawn by Donovan. It should be noted though that muscular tissue can be present in e.g. cirri. Donovan also concluded that glyptocystoids have muscular tissue present in their columnals, as the articulation function of their column clearly is not the same as in the crinoid column (see Fig. 22B for an illustration of how the glyptocystoid articulation works). The columnals of glyptocystoids are often smooth and unornamented and the interlocking function between separate columnals is controlled by muscular tissue which often is guided in place by interlocking ribs at the edge of the columnal (see Paul 1984 and also Fig. 22B herein). The axial canal in several different types of early glyptocystoids often occupies most of the columnal diameter and this results in lack

of space for the eventual evolution of more sophisticated articulation methods. The crinoids solved this problem by restricting the axial canal to point-size. Many other types of rhombiferans though show a point-sized lumen with a synostial articulation. This is probably mainly due to the fact that rhombiferans mostly have a completely different mode of life in comparison to crinoids (see e.g. Paul 1984 and discussion further on). These facts also imply that different stereom types as a function of investing tissue in rhombiferans are of a minor importance.

Muscular tissue is clearly present in other echinoderm classes as e.g. sea stars and in these cases it can also be linked to the stereom plate organisation (see also under remarks above).

Ranges, class distribution and introduction of species. - Smith (1988) adressed some of the problems associated with the early diversification of echinoderms and he also discussed more in detail problems associated with the distribution of species on a class level in the stratigraphic record. The main problems which he noted with establishing taxonomic diversity patterns amongst early echinoderms were: (1) the poor knowledge of the Cambrian echinoderm fauna, (2) Sampling, preservation and Lagerstätten and (3) taxonomic artefacts (for example extinctions and pseudoextinctions). Furthermore he also made a cladistic analysis of the early history of echinoderms ranging from the start of the Cambrian to the Arenig.

As discussed earlier, rhombiferans clearly dominate the stratigraphically earliest samples while later samples are dominated by crinoids (see Figs. 23, 24, 25 and appendix A). If this should be linked to the fact that crinoids are generally rather uncommon in the stratigraphic record before the Llanvirn (see e.g. Ausich et al. 1998) or to the fact that rhombiferans and crinoids often show different habitat preferences and modes of life will be discussed in greater detail further on. Most crinoid and crinoid columnal morphospecies described here, however, show an early first appearance in the stratigraphic record in comparison with those described by Donovan (1986, 1989*a* and 1995) but they more closely correlate in time with those described by Stukalina (1988). Some of the taxa are also clearly different from those described by these authors. Also note that some taxa described based on columnals are not that common in most of the samples (see appendix A), so their ranges and first appearances are yet preliminary. This is also linked to the fact that only phosphatized fragments have been examined. Another aspect of this is whether or not the columnals examined come from juvenile specimens or not. It is a well-known fact that many early adult crinoids were extremely small. If the columnals examined mostly come from juvenile specimens, one can possibly expect that the sample preparation with sieving has acted as an unwanted form of sorting process, which only has left smaller adult and juvenile specimens in the samples. This could have resulted in a false reflection of species domination and distribution within the samples. This is not true if the smaller specimens of crinoids and rhombiferans in the samples in fact represent the true species domination as most likely is the case in Gillberga.

The richness of pinnules and brachials in some samples could largely be correlated with the sample preparation, where everything below a certain size fraction has been sieved away (see Table 1 for the sample data). Smaller sample fractions clearly yield more pinnules. The absence of larger echinoderm plates is most likely not a result of the sample preparation as the coarser fractions examined yielded almost no echinoderm plates at all. No bigger plates were found either during observations done during the dissolution period of the samples Öl 97-10, Öl 97-11 and Öl 97-12. Larger echinoderm plates could be lacking because they act differently as nucleation sites during phosphatization in comparison with smaller fragments. During diagenesis, though, it is a well known fact that there is a tendency for coarser grains to grow on the expense of smaller grains (e.g. during quartz growth). The processes of phosphatization of echinoderm fragments do not follow the same rules as the echinoderm stereom represents an open framework (see discussion above) in comparison with e.g. a quartz grain. Another aspect of this could possibly be that these types (plates, pinnules and brachials) have different hydrodynamic behaviour in an agitating postmortem environment. The great number of pinnules that occur in later samples (e.g. Öl 93-12) could possibly be explained by the fact that more crinoids successively evolved pinnules later on in the stratigraphic record (see e.g. Guensburg & Sprinkle 1992).

Interesting to note is also that most of the rarer species occurring in the samples clearly show a greater columnal size in comparison with the "normal" size distribution for the sample in question. Fig. 25 illustrates the distribution and ranges of some crinoids and undetermined columnals.

A diversity and species number peak in the samples that roughly corresponds to the time just before the Arenig-Llanvirn boundary (Öl 93-6 to Öl 97-12) is clearly evident, as is a faunal shift across this border. Rhombiferans and stelleroids (see Fig. 23) dominate the samples representing the interval just below the boundary. Crinoids dominate samples above this boundary and the number of rhombiferan and stelleroid fragments also decreases in these samples. Most likely these observations represent a true faunal shift. The main problem is to locate this in time, due to the fact that only phosphatized fragments have been examined. The time represented by the samples just before the boundary could represent a true abundance

peak or a peak related to the regressive phase, which is linked to the phosphatization process. The faunal shift could alternatively have happened in the interval represented by the samples Öl 83-101 to Öl 72-7 + Öl 83-105 as these samples mostly show no phosphatization at all. These samples roughly correspond to about 3.6 meters in the section. Whether the faunal shift is related to a new environment (e.g. different depth-conditions) or to the introduction of species that are more effective (e.g. better articulation) in the old environment, is hard to tell. Introduction of more successful articulation types appears to have happened, though. It is more likely, however, that this shift possibly is based on changing substrates as a regressive phase (as discussed earlier) resulted in the formation of hardgrounds. It is also most likely that the articulational type has mainly controlled the species domination amongst the crinoids. Sprinkle (1991) noted in his work on the Fillmore Formation in North America, that rhombiferans and mitrates "were vagile on soft, fine-grained substrates". He also noted that "Early Ordovician attached, hard substrate echinoderms were largely limited to shallow-water near-shore environments, in contrast to vagile, soft substrate echinoderms that inhabited a wide range of water depths". Further he noted that crinoids later on in the Middle Ordovician, starting approximately at the lower Llanvirn boundary, developed rootlike holdfasts (earlier holdfasts were discoidal) and thus they were able to move onto soft substrates, which naturally resulted in the expansion of their ecological range. He concluded that "This ability to exploit a wide range of substrates was a major factor in the rise to dominance of Paleozoic crinoids". This could then be linked to the fact that later crinoids were able to exploit almost all substrate types resulting in the clear dominance of crinoids that can be seen in my younger samples. Conclusions that can be drawn from Sprinkle´s (1991) investigation indicates that the decline in rhombiferans in my samples most likely is due to changing bottom substrate hardness as this class is known to preferentially exploit soft-bottoms. The investigations on columnal articulation shows that amongst the crinoids the main factor that has controlled species domination is the evolution of better articulational types.

Guensburg & Sprinkle (1992) noted that early crinoids "were overwhelmingly large-food-groove suspension feeders with relatively open filtration fans attached by small discs to hardground surfaces in shallow water". They also noted that crinoids "were preadapted for this life mode". They also argued "for an extrinsic environmental control (substrate availability)" for the echinoderm distribution that they observed. Their samples from the Ninemile Shale of central Nevada also showed a clear dominance of rhombiferans. This section they noted is composed of "limestones that were deposited on the outer

shelf to upper slope in deeper, less agitated water and more stable conditions". The amount of mitrate stylophorans is also high in the Ninemile Shale in comparison with the other sites that they investigated.

At a later stage in my samples, symplectial articulation becomes less important as articulation based on areola pits becomes more important (see Appendix A).

Stylophorans have been found from the oldest sample investigated (Öl 94-6) and the fragmentary remains of the class are dominated by aulacophore ossicles (for the ranges of the different types of stylophoran ossicles see Fig. 24). This domination is linked to the fact that each animal possesses more than one aulacophore ossicle and just one stylocone (see also Figs. 22D-E for an illustration of how aulacophore ossicles acted together). The absence of stylophoran central plates in all the samples could possibly be explained by these plates acting hydrodynamically differently in comparison with the other fragments from the animal. Another possibility is that just sample residues below a certain fraction have been examined so that these fragments have been removed during sample preparation as most of the samples originally were prepared for conodont-studies. This possibility is less likely, though. More reasonable is that different types of stereom have different preservation potential (e.g. a plate is more sensitive to transport as the stereom meshwork in a plate is different from that in columnals). A three-dimensional network of stereom with many interconnecting ribs (e.g. rectilinear) has the ability to withstand greater forces than e.g. thin laminar stereom as found in an echinoderm plate. This then makes a plate more vulnerable to transport. The combination of tranportational forces and sorting forces could then explain the absence of stylophoran central plates in my samples as in the case with other echinoderm plates (see discussion above). The last appearance of the class in the samples examined is in Öl 93-8 (base of N).

The appearance of the class Cyclocystoidea in the stratigraphic record of Öland has earlier been discussed by Berg-Madsen (1987) and the species found in my samples closely correlate in time with those described by her. The class is scarce in all samples where present, restricted to the Arenig part; first appearance is in Öl 94-5 (in H) and its last is in Öl 97-12 (mid K). See also Fig. 24.

The early phylogeny of the subphylum Asterozoa has been discussed by various authors (see e.g. Blake & Guensburg 1993). The Ophiuroidea though clearly dominates (see appendix A) within the samples where this subphylum is present. No arm-plates at all from ophiuroids have strangely enough been found. This could possibly be linked to the sample preparation or to a different hydrodynamic behaviour of these plates in a sorting environment or to different diagenetic behaviour of arm-plates in comparison with e.g. columnals. Fig. 26 illustrates the strati-

graphic ranges of asterozoan ossicles found within the samples examined. The first appearance of asteroid fragments could possibly be equal to the first appearance of paxillae and marginal ossicles, which probably belong to an asteroid. If this is true, the first appearance is in Öl 94-5 (in H), but this observation is only based on the finding of one paxillar ossicle. The main problem is that the Somasteroidea also is present at this time in the stratigraphic record. Blake & Guensburg (1993) noted though that "somasteroids are known only from rare and usually incomplete Palaeozoic fossils". This class closely resembles starfishes in plate morphology. It is most likely, though, that most of these ossicles represent fragments from asteroids. Some edrioasteroidean marginal plates also closely resemble the marginal plates of both Somasteroidea and Asteroidea (Blake & Guensburg 1993). The main problem here is that the distinction between these is mostly based on finds of almost complete specimens (distinction is more based on whole morphology than single plate morphology). Nothing, though, points in the direction of that these marginal plates should represent remnants from edrioasteroids in my samples (no other fragments from edrioasteroids have been found). So therefore I regard these marginal ossicles as belonging to either Somasteroidea or Asteroidea. The greatest possibility is that they belong to Asteroidea based on the known relative scarceness of somasteroids at the time, represented by the sequence in Gillberga. Smith (1988) also discussed some of the problems associated with eocrinoids and edrioasteroids. Interesting to note is also that asterozoan ossicles occur in great numbers in some samples (Öl 93-6 to Öl 97-12; bottom half of K to mid K) and that the number of these ossicles diminishes higher up in the section (from Öl 93-8; base N, and up). Öl 93-6 (bottom half of K) also represents a more certain and definitive occurrence of asteroid fragments. It should also be noted that a great number of asterozoan ossicles remain undetermined (see appendix A and Fig. 26). Some of these fragments could also possibly belong to edrioasteroids.

The great number of different shapes of the same type of ossicle (e.g. paxillar ossicles and spines) at some levels most likely reflects the occurrence of several different species of asterozoans. Some spines, especially the earliest ones, could possibly belong to *Bothriocidaris*. Blake & Guensburg (1988) also came to the conclusion that "as early as the middle and late Ordovician, modes of life of asteroids broadly paralleled those seen today". This could most likely be linked to the scarcity of asterozoan ossicles in the later samples (Öl 93-8; base N, and further on) seen as a function of changing substrate.

Conclusions

The section at Gillberga has yielded a lot of different types of echinoderm fragments, some of which are completely new to Öland and some that have previously been found at other localities in Öland.

The columnals investigated show close morphological relationship with those described by Donovan (1986, 1989*a* and 1995) and Stukalina (1988). The systematics of most of these columnals are mainly based on morphology (morphospecies). The early introduction of most columnal morphospecies at Gillberga is an interesting fact, possibly linked to an early expansion of crinozoans. It is also shown that the Asterozoa plays a more important role as a constituent of the echinoderm fauna of the region at this time than recognised before. Ophiuroids are particularly common at some levels. A rather early first appearance of fragments that closely resemble those from asteroids has also been shown. Some of these fragments might come from edrioasteroids and/or somasteroids. Both these taxa are generally considered uncommon, so most of the fragments (recognised as belonging to the Asterozoa) more likely represent remains from ophiuroids and asteroids.

Other groups that are represented in the samples are stylophorans, cyclocystoids, rhombiferans and crinoids. The rhombiferans are clearly important contributors to the early echinoderm fauna. Some of these classes span the whole stratigraphic record at Gillberga.

Interesting to note is also what seems to be a major faunal shift occuring just around the Arenig-Llanvirn boundary (see fig. 23). This is interpreted to represent a faunal shift that is due to the introduction of species that are better adapted to exploit hard bottoms. This would then explain the scarceness of rhombiferans and stylophorans later on in the samples. The early dominance of rhombiferans could also be linked to prevailance of soft bottoms and their decreasing amount in later samples could then be linked to increasing competition from crinoids in combination with changing substrate hardness. Another possibility is that this faunal change is a function of more particles on the bottom to attach to. Note, though, that other echinoderm classes also change their occurrence across this boundary, e.g. the amount of asterozoans decreases and the cyclocystoids diminish. Environmental factors have thus mainly controlled the distribution of echinoderms within the samples examined. Sedimentological parameters such as e.g. particle size may have affected the amount and distribution of echinoderms that attach themself to these kind of particles. It is thus stressed in this investigation that the faunal shift that occurs around Llanvirn boundary mainly is due to changing bottom substrate hardness.

The types of crinoids that have dominated the samples through time have also shifted. These different domination stages seem to be closely linked to the evolution of new and better-adapted articulation types. This evolution has earlier been described by various authors and what they suggested also seems to be applicable to the section at Gillberga. The echinoderm diversity has also changed with time and it is highest around the Llanvirn border.

This study has also pointed out the occurrence of extremely well preserved echinoderm fragments. These fragments are in many cases so well preserved that they closely resemble recent material. The stereom organisation and its relationship to investing tissue in most cases clearly follows the work by Smith (1980) on recent echinoids. In some cases it seems that the original stereom structure determines what preservational type is observed after diagenetic alteration of the fragments. The most well preserved echinoderm fragments clearly come from the K-level. Further investigations are here clearly needed and these would reveal new interesting facts about the stereom organisation of early echinoderms and how the echinoderm stereom works in a diagenetic environment. It should also be noted that only a minor part of the fragments found have been illustrated.

Diagenetic studies would also reveal if the faunal shift described is a function of sedimentological parameters or not. Further investigations from other localities in Öland would also reveal interesting facts about the echinoderm fauna of this time. Phosphatized horizons are also known from Västergötland and some samples from this area have also been briefly examined. These samples also showed a rich and diverse echinoderm fauna and further investigations in this area would most reveal interesting facts about the environmental control on echinoderm distribution as this area represents deeper water conditions.

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Appendix A

All of the samples examined yielded echinoderm fragments. Counting, though, has not been carried out with some samples (Öl 93-1, Öl 94-4, Öl 97-10, Öl 97-11, Öl 72-3, Öl 83-101, Öl 92-5, Öl 93-7, Öl 93-9, Öl 74-102, Öl 93-10A and Öl 83-109). These samples contained less than 10 echinoderm fragments per sample and the fragments were also so poorly preserved that any systematic description was impossible. The sum of each type of echinoderm fragment within each sample has been calculated and a total sum for all of the samples is also given. The echinoderm fragments that are used as illustrations of preservational types have not been included in the counting. Otherwise all illustrated echinoderm fragments are included in the counting. Some columnals were impossible to give a systematic description so they were grouped together as undeterminable (e.g. undetermined columnals and pentagonal undetermined columnals) based on the overall columnal outline if this was possible to make out. This also applies to some asterozoan fragments. The total sum of fragments of some of the bigger groups (e.g. *Cyclocyclicus* (col.) and stylophorans) are also given. If this is not given as is the case for e.g. *Tetragonocyclicus* (col.), this means that only one species type of this fragment has been found and therefore the total sum for this type is also the total sum for this group within all of the samples. If for example the term common is used this is related to the amount of this certain type of echinoderm fragment in comparison to the total amount within the echinoderm class to which this particular fragment has been ascribed.

	Total sums	Öl 94-201	Öl 83-109	Öl 93-12	Öl 93-11	Öl 83-107	Öl 93-10C	Öl 93-10B	Öl 93-10A	Öl 74-102	Öl 93-9	Öl 93-8	Öl 92-9	Öl 93-7	Öl 92-8	Öl 83-104	Öl 92-7	Öl 92-6	Öl 92-5	Öl 72-5	Öl 92-4	Öl 83-101	Öl 97-12	Öl 92-3	Öl 93-6	Öl 72-3	Öl 92-2	Öl 97-11	Öl 93-5	Öl 92-1	Öl 97-10	Öl 93-4	Öl 94-4	Öl 93-3	Öl 93-1	Öl 94-5	Öl 94-6
Sum Cyclocystoididae	21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	18	2	0	0	0	0	0	0	0	0	0	1	0	0	0
Sum Stylophora	57	0	0	0	0	0	0	0	0	0	1	0	13	0	0	0	0	8	0	0	1	0	17	9	5	0	1	0	0	0	0	0	0	0	1	0	1
Pentagonal col.undetermined	94	13											56				12						13														
Undetermined columnals	100			12							66						11												11								
Oanducystis? (col.) sp. A (Fig. 21G)	1																1																				
Dwortsonaecrinidae (Fig. 21E)	2	2																																			
Tetragonocyclicus? (col.) sp. A (Fig. 14D)	4			4																																	
Ramseyocrinus? sp. C (Fig. 21H)	11																						11														
Ramseyocrinus? sp. B (Fig. 14C)	14	3		2					1				1										7														
Ramseyocrinus? sp. A (Fig. 14A)	3																						1									2					
Ramseyocrinus cambriensis (Fig. 14B)	4				1	1							2																								
Pentameric? col. type G (Fig. 13C)	5												3										2														
Pentameric col. type F (Fig. 21D)	4												4																								
Pentameric col. type E (Fig. 16G)	1												1																								
Pentameric col. type D (Fig. 16B)	1			1																																	
Pentameric col. type C (Fig. 15F)	1			1																																	
Pentameric col. type B (Fig. 14I)	23	1		15	4								1										2														
Pentameric col. type A (Fig. 12A)	3	1											1										1														
Rhomb. col. type D (Fig. 20A)	577												6		14		12	2			34	32	20	109	5					35				158	15		135
Rhomb.? col. type C (Fig. 9E)	34		11	13									1		2						3		1	3													
Rhomb.? col. type B (Fig. 11C)	5																						1	4													
Rhomb. col. type A (Fig. 11B)	2								1				1																								
Glypto. col. type F (Fig. 13E)	1																						1														
Glypto. col. type E (Fig. 13D)	26	2											2					2					17	1	1									1			
Glypto. col. type D (Fig. 13A)	124	1											26		2		1	7			1		57	13										16			
Glypto. col. type C (Fig. 12D)	51														1			2	1				32	1										5	4		5
Glypto. col. type B (Fig. 20C)	87																		2	1	4		19	4	3					4				24	14		12
Glypto. col. type A (Fig. 11A)	21			5																			16														
Cyclocystoididae type B (Fig. 9I)	6																						6														
Cyclocystoididae type A (Fig. 9H)	15																						12	2										1			
Aulacophore type B (Fig. 9F)	22										1		9					2					6	1			1								1		1
Aulacophore type A (Fig. 9C)	23																	3	1				14	3	2												
Stylocone? type C (Fig. 9E)	4																	2					2														
Stylocone type B (Fig. 9B)	5												2								1									2							
Stylocone type A (Fig. 9D)	2												2																								
Stylocone type A (Fig. 9A)	1																						1														

58

	Total sums	Öl 94-201	Öl 83-109	Öl 93-12	Öl 93-11	Öl 83-107	Öl 93-10C	Öl 93-10B	Öl 93-10A	Öl 74-102	Öl 93-9	Öl 93-8	Öl 92-9	Öl 93-7	Öl 92-8	Öl 83-104	Öl 92-7	Öl 92-6	Öl 92-5	Öl 72-5	Öl 92-4	Öl 83-101	Öl 97-12	Öl 92-3	Öl 93-6	Öl 72-3	Öl 92-2	Öl 97-11	Öl 93-5	Öl 92-1	Öl 97-10	Öl 93-4	Öl 94-4	Öl 93-3	Öl 93-1	Öl 94-5	Öl 94-6
Sum Brachial + Pinnule type A-C	329	11	0	89	18	0	0	0	0	0	0	0	37	0	0	0	0	6	0	0	0	0	101	38	28	0	0	0	0	0	0	0	0	0	0	1	0
Sum Fragment type A-C uncertain	267	6	0	1	3	0	0	0	0	0	0	0	5	0	0	0	0	10	0	5	0	0	75	63	54	0	0	0	0	4	0	0	0	1	0	23	17
Sum Adambulacral oss. type A-B	67	0	0	0	0	0	0	0	0	0	0	0	11	0	1	0	0	2	0	0	0	0	39	10	3	0	0	0	0	0	0	1	0	0	0	0	0
Sum Ambulacral oss. type A-G	179	0	0	0	4	0	0	0	0	0	0	0	11	0	1	0	0	5	0	2	0	0	113	24	5	0	0	0	0	10	0	0	0	3	0	0	1
Sum Undetermined Asteroz. oss.	214	0	0	0	1	0	0	0	0	0	0	0	30	0	1	0	0	10	0	8	1	0	25	58	76	0	1	0	0	1	0	0	0	0	0	0	2
Echinoderm plate (Fig. 19H)	22												4										13		5												
Pinnule type C (Fig. 19F)	3												3																								
Pinnule type B (Fig. 19D)	1												1																								
Pinnule type A (Fig. 19C)	320	11		89	18								33					6					99	36	28												
Brachial type A (Fig. 19B)	5																						2	2												1	
Fragment type C uncertain (Fig. 19G)	1												1																								
Fragment type B uncertain (Fig. 19E)	265	6		1	3								4					10		5			75	62	54					4				1		23	17
Fragment type A uncertain (Fig. 19A)	1																							1													
Marginal ossicle (Fig. 18I)	11												1										4	5	1												
Spine attachm. oss. type A (Fig. 18G)	19												3		1			1					7		6										1		
Paxillar ossicle (Fig. 17I)	19												1					1					3	11						1				1	1		
Adambulacral? oss. type B (Fig. 18B)	48																						37	10	1												
Adambulacral? oss. type A (Fig. 17A)	19												11		1			2					2		2							1					
Asterozoan? spine (Fig. 17C)	35												2										16	14	1												2
Ambulacral? ossicle type G (Fig. 18E, H)	21																						19	1	1												
Ambulacral oss. type F (Fig. 11D)	3												1										2														
Ambulacral oss. type E (Fig. 17H)	4				4																																
Ambulacral oss. type D (Fig. 17F)	34												4		1			5					13	9	1					1							
Ambulacral oss. type C (Fig. 17B)	2																								2												
Ambulacral oss. type B (Fig. 17A)	101												5								2		70	12	1					9				1			1
Ambulacral? oss. type A (Fig. 18A)	14												1										9	2										2			
Undetermined Asterozoan oss.	163												28					9		6				46	72												2
Undet. Asteroz. ossicle type F (Fig. 17E)	2																							1	1												
Undet. Asteroz.? oss. type E (Fig. 9G)	23																			1		19	2	1													
Undet. Asteroz.? oss. type D (Fig. 18F)	10												2							2			2	1	1		1			1							
Undet. Asteroz.? oss. type C (Fig. 18D)	7														1								3	2	1												
Undet. Asteroz. oss. type B (Fig. 18C)	3																						3														
Undet. Asteroz. oss. type A (Fig. 17G)	6				1													1					4														

59

Table (rows = taxa, columns = sample numbers; blank cells = no specimens). The following abbreviated column headers are used, in order: Total sums, O194-201, O183-109, O193-12, O193-11, O183-107, O193-10C, O193-10B, O193-10A, O174-102, O193-9, O193-8, O192-9, O192-8, O192-7, O183-104, O192-6, O192-5, O172-5, O192-4, O183-101, O197-12, O192-3, O193-6, O172-3, O197-11, O193-5, O192-2, O192-1, O197-10, O193-4, O194-4, O193-3, O193-1, O194-5, O194-6.

Taxon	Total sums	O194-201	O183-109	O193-12	O193-11	O183-107	O193-10C	O193-10B	O193-10A	O174-102	O193-9	O193-8	O192-9	O192-8	O192-7	O183-104	O192-6	O192-5	O172-5	O192-4	O183-101	O197-12	O192-3	O193-6	O172-3	O197-11	O193-5	O192-2	O192-1	O197-10	O193-4	O194-4	O193-3	O193-1	O194-5	O194-6
Sum *Ramulicrinus* (col.) sp. A-C	177	2		36	128	1						4					1						2	3												
Sum *Bystrowicrinus* (col.) sp. A-D	29	2		4							2					2						6	7	3												3
Sum *Baltocrinus* (col.) sp. A-B	17	2		5	2							6	1												1											
Sum *Pentagonocyclicus* (col.) sp. A-B	65	2		20								25					4	1					2			11										
Sum *Cyclocyclicus* (col.) sp. A-E	364	17		82	11							230	5				8		4	1			4	1		1										
Sum Hol. cycl. col. type A-C	45											1										12	5	11											7	9
Sum Hol. col. five devl. type A-K	89	1		8	6	2	1				5	8				6				1		14	27										2			8
Iocrinus? sp. A (Fig. 21F)	14			3							1	4										1	2	2												1
Ramulicrinus? (col.) sp. C (Fig. 15I)	127	1		24	99							1											1	1												
Ramulicrinus? (col.) sp. B (Fig. 16A)	47	1		10	29	1						3					1						1	1												
Ramulicrinus? (col.) sp. A (Fig. 14J)	3			2																			1													
Sidericrinus? (col.) sp. A (Fig. 11H)	8			1	2																	1	3													1
Bystrowicrinus (col.) sp. D (Fig. 21C)	3																						2													1
Bystrowicrinus (col.) sp. C (Fig. 21B)	4										2					2																				
Bystrowicrinus (col.) sp. B (Fig. 21A)	8			2																		4														2
Bystrowicrinus (col.) sp. A (Fig. 11G)	14	2		2																		2	5	3												
Babanicrinus? sp. A (Fig. 15A)	18			2								2					1					8	4													1
Baltocrinus? (col.) sp. B (Fig. 14F)	8			5	1							2																								
Baltocrinus? (col.) sp. A (Fig. 11K)	9	2			1							4	1												1											
Pentagonocyclicus (col.) undeterm.	22											5					4	1					1			11										
Pentagonocyclicus (col.) sp. B (Fig. 15G)	40	2		17								20											1													
Pentagonocyclicus (col.) sp. A (Fig. 15E)	3			3																																
Pentagonoellipticus? (col.) sp. A (Fig. 15B)	9											9																								
Pentagonocyclopa? (col.) sp. A (Fig. 11I)	123			107	1																	14														1
Cyclocyclicus? (col.) sp. E (Fig. 20F)	19	1										18																								
Cyclocyclicus (col.) sp. D (Fig. 20E)	29	1		2								24					2																			
Cyclocyclicus (col.) sp. C (Fig. 15H)	1											1																								
Cyclocyclicus (col.) sp. B (Fig. 20D)	290	14		76								178	5				6		4	1			4	1		1										
Cyclocyclicus? (col.) sp. A (Fig. 15D)	25	1		4	11							9																								
Circular col. undetermined	194	18										115				21						40														
Hol. cycl. col. type C (Fig. 13F)	3																						3													
Hol. cycl. col. type B (Fig. 13B)	38											1										8	5	8											7	9
Hol. cycl. col. type A (Fig. 11F)	4																					4														
Hol. col. five dev. type K (Fig. 20H)	18										4	5				3						2	4													
Hol. col. five dev. type J (Fig. 20G)	18			2							1											4	5													6
Hol. col. five dev. type I (Fig. 16F)	4																						3													1
Hol. col. five dev. type H (Fig. 16E)	10			1								1				1							7													
Hol. col. five dev. type G with spines (Fig. 16D)	3																						3													
Hol. col. five dev. type G (Fig. 16C)	6															1						5														
Hol. col. five. dev. type F (Fig. 14H)	4			1								1										1	1													
Hol. col. five. dev. type E (Fig. 14G)	4																					1	2													1
Hol. col. five. dev. type D (Fig. 14E)	13			3	6	2	1															1														
Hol. col. five. dev. type C (Fig. 13H)	4																		1			1										2				
Hol. col. five. dev. type B (Fig. 13G)	2	1																				1														
Hol. col. five. dev. type A (Fig. 11J)	3			1								1				1																				

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