Conference Paper

Variability of ambulacral structures in some diploporite cystoids

J. F. Bockelie

Paleontologisk Museum, Sarsgt. 1, Oslo 5, Norway

The ambulacral areas of more than 800 specimens of the Ordovician diploporite cystoid genera *Haplosphaeronis* Jaekel and *Eucytis* Angelin from Norway and Sweden have been studied. There is a positive correlation between size of the animal and the total number of brachiole facets. This indicates that ambulacral structures are added during growth of these genera. Several populations are studied and it is suggested that the variation in number of brachiole facets within a given population results from a combination of ontogeny, genuine variability within age-groups, ecological conditions and phyletic changes.

INTRODUCTION

The Upper Ordovician diploporite cystoids *Haplosphaeronis* and *Eucystis* (Sphaeronitidae) from Norway and Sweden occur in such quantities that variability studies could be carried out.

Samples of the same species exhibit obvious morphological variation the implications of which are not so clear. In the rhombiferan Callocystidae examples of ambulacral growth have been studied[1] (p. S. 117), where ambulacral side-branches are added on already existing ambulacra (Kesling, op. cit. Fig. 49). This variation is probably ontogentic. Theoretically four factors influence variation in fossil samples. These are: 1) ontogeny, 2) genetic variation within age groups, 3) ecological features effecting growth, and 4) phyletic changes. This paper attempts to distinguish variation due to these features which require study of large samples from several localities and horizons.

TERMINOLOGY AND MORPHOLOGY

The oral area of cystoids is usually surrounded by five ambulacra which start from corners of the mouth and end in brachiole facets (Fig. 1). In *Haplosphaeronis* and *Eucystis* both the number and length of the ambulacral furrows vary.

In *Haplosphaeronis* the ambulacral furrows branch fan-wise directly from each of the five oral corners (Fig. 1). Branching in the four ambulacra of *Eucystis quadrangularis* is more variable. In some cases furrows branch directly from the oral corners, in other cases the branching is ramified (Fig. 1). The radii are numbered in accordance with the system of Bather[2]; *i. e.* in a clockwise

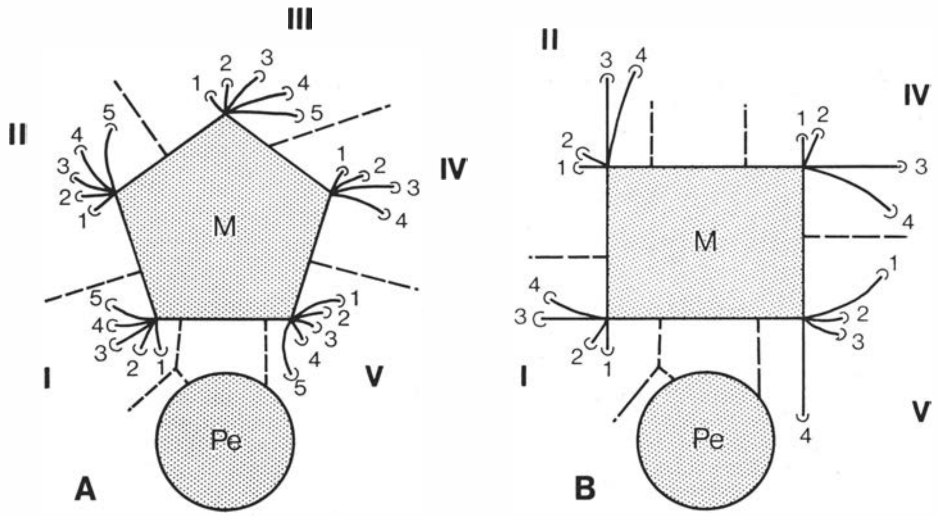

Fig. 1. The oral-anal area of *Haplosphaeronis* spp. *(A)* and *Eucystis quadrangularis (B)* with branching patterns of ambulacra (I, II, III, IV, V). Note absence of ambulacrum III in *E. quadrangularis*. Ambulacral facets are numbered clockwise (1—5). *M:* mouth, *Pe:* peristome. Dashed lines indicate plate sutures.

manner, starting with radius I at the left of the oral-anal line (Fig. 1). In *Eucystis quadrangularis* radius III is undeveloped, which apparently is common in the Sphaeronitidae[3]. Each brachiole facet in each radius is numbered in a clockwise manner and indicated by a superscript, *e. g.* II^1, III^2, V^4, *etc.* (Fig. 1). The number sequence does not necessarily indicate the order of formation of individual facets, but in several cases it does.

MATERIAL AND METHODS

The Swedish populations of *Haplosphaeronis* derive from Middle Ordovician Kullsberg Limestone[4], from the Kullsberg and Amtjärn quarries, and from the Upper Ordovician Boda Limestone[4] of Osmundsberget and Skålberget quarries, all in Dalarna, Central Sweden. The *Eucystis* samples come from the Upper Ordovician Boda Limestone of Skålberget and Osmundsberget. Most of the material occurs in flank facies of the Kullsberg and Boda carbonate mounds (»reefs«). Material from these facies may seem to have good preservation, but closer inspection reveals severe effects of pressure solution. Therefore vital structures are often completely dissolved. This feature together with the presence of fractures which resemble plate sutures has previously led to misinterpretations of the morphology. At times the use of *aniseoil* has revealed structures which otherwise are difficult to detect. The use of dyes, particularly ink of various colours, has also given very good results. In most populations approximately 50% of the specimens show structures which are needed for this study, although these proportions are sometimes much lower.

The Norwegian *Haplosphaeronis* come from the uppermost part of the Middle Ordovician of Tönnerud, Hadeland, Oslo Region. They occur in marlstones and nodular limestones with large amounts of terrigenous clay and are best prepared by dissolving in dilute hydrochloric acid. Silicone rubber casts made from the resulting moulds[5] reveal morphological details far better than the Swedish material, but the number of specimens available for study is smaller.

Variation in the length of ambulacral furrows and the size and number of facets has been studied in relation to the size of the animal. Means and ranges of the total number of ambulacral facets plotted against 1 mm thecal size classes (Fig. 4) show that considerable variation in total number of facets is due to growth.

In populations of *Haplosphaeronis* the mean numbers of ambulacral facets in each radius have been plotted as histograms as a percentage of the mean number in radius V. This enables recognition of a distinct distribution pattern of ambulacral facets in different populations of *Haplosphaeronis* (Fig. 5). In Fig. 3 letters denote the number of ambulacral facets in each radius in relation to the other radii. If the number of facets is the same in all radii the letter *a* is used. Where the numbers of facets are not equal in all radii the letters *b*, *c*, *d*, and *e* denote radii with progressively smaller numbers of facets. For example in a specimen with 4 facets in radii I and V, 3 in radii II and III and 2 in radius IV the lettering would be *a*, *b*, *b*, *c*, *a*. These latter methods are independent of variation in numbers of facets which is due to growth.

AMBULACRAL STRUCTURES OF *EUCYSTIS QUADRANGULARIS*, REGNÉLL

84 specimens from the Boda Limestone (Upper Ordovician), at Skalberget, Dalarna, Sweden, were studied. *E. quadrangularis* (Figs. 1, 2) is characterized by a quadrangular mouth[6] and only four ambulacra.

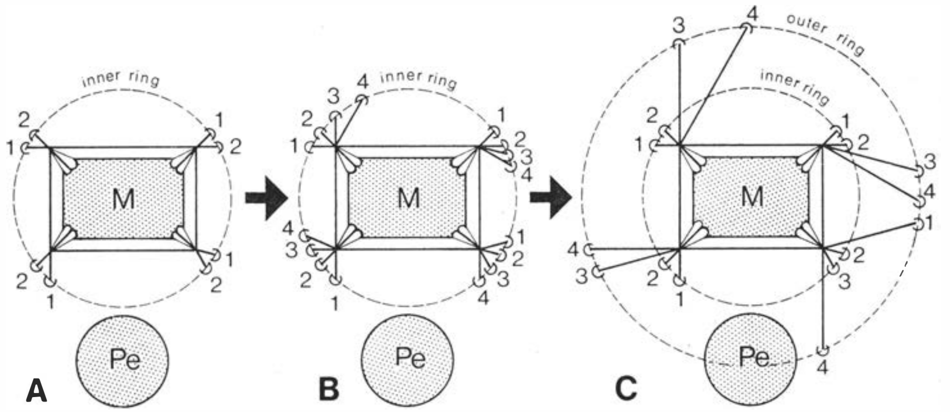

Fig. 2. Ontogenetic stages of *Eucystis quadrangularis*. Upper Ordovician, Skalberget, Dalarna, Sweden. A: species up to 7 mm thecal diameter, B: 7—10 mm diam., C: greater then 10 mm diam., the latter presumed adult stage. First ambulacral grooves formed in an inner »ring« close to mouth; in adult stages even an outer »ring« exists. Terminology as in Fig. 1.

Specimens range in size from 5 mm diameter with a total of 7 ambulacral facets to 15 mm diameter with 16 facets. In small specimens all the ambulacral grooves are short with their facets close to the margins of the peristome. The majority of larger specimens with thecal diameters from 12—15 mm have the ambulacral facets in two circlets; one close to the mouth, normally containing two facets per radius, and the other some distance down the theca also with two facets in each radius (this has also been observed in other *Eucystis* species by Prokop[7]). Intermediate conditions are common, whereby the »longer« ambulacral furrows may not extend as far down the theca as in typical examples. The fact that specimens with the greater number of larger grooves are bigger, may probably reflect ontogeny. Fig. 2. indicates presumed stages of such ontogeny. So far no specimens have been found with only one facet in each radius, but such a pattern is known in other species. In this population of *E. quadrangularis* the earliest growth stage must have been completed before the specimens reached 5 mm in thecal diameter.

With regard to the ambulacral patterns, 16 of the 24 possible patterns were encounterd in the sample (Fig. 3A). However, of these only one pattern is really

A E. quadrangularis

combination code in radius				no. of obser-vations
I	II	IV	V	
a	a	a	a	28
a	a	a	b	5
a	a	b	a	7
a	a	b	b	3
a	b	b	b	10
a	b	b	a	8
a	b	a	a	9
b	b	a	b	1
b	b	b	a	3
b	b	a	a	1
b	a	a	a	1
b	a	b	a	2
b	a	b	b	1
a	b	c	b	1
a	c	b	b	1
a	c	c	b	1

B Haplosphaeronis spp.

combination code in radius					no. of observations at loc. no.				
I	II	III	IV	V	1	2	3	4	5
a	a	a	a	a	18	3	2	5	9
a	a	a	b	a	5	2	3	5	22
a	a	b	b	a	1	2	1	3	3
a	a	b	b	b	1	-	-	-	-
a	b	b	b	b	4	-	-	3	-
a	b	a	b	a	-	-	-	1	2
a	b	b	b	a	14	1	1	8	14
a	b	b	a	b	1	-	-	-	-
a	b	b	a	a	1	-	-	-	-
b	a	c	b	a	-	-	-	-	1
a	b	a	c	a	-	-	-	-	2
a	b	b	c	a	-	7	-	10	27
a	b	b	c	b	1	-	-	-	1
a	b	c	a	a	-	-	-	-	1
a	b	c	c	a	-	-	-	-	2
a	c	b	b	a	-	1	-	-	-
a	c	b	c	a	-	-	-	1	1
a	c	c	c	b	-	-	-	-	1
a	b	b	c	a	-	1	1	-	-
b	c	c	c	a	-	-	1	2	-
a	b	c	d	a	-	-	-	-	2

Fig. 3. Letters denote number of ambulacral facets in a radius in relation to other radii. If equal number in all radii, the letter *a* is used. Where numbers of facets are not equal in all radii, the letters *b, c, d,* denote radii with progressively smaller numbers of facets. *A:* Frequency of observed combinations in *Eucystis quadrangularis*, Skalberget, Dalarna, Sweden. Note that radius III is undeveloped. *B:* similar combinations in *Haplosphaeronis* spp. from different localities. 1) Skalberget beds, Upper Caradoc, Amtjärn, Dalarna, Sweden; 2) Sphaeronitid Limestone, 5,5—6,0 m level, Upper Caradoc Tönnerud, Oslo Region, Norway; 3) Sphaeronitid Limestone, 21—22 m level, Upper Caradoc, Tönnerud, Oslo Region, Norway; 4) Kullsberg Limestone, Caradoc, Kullsberg quarry, Dalarna, Sweden; 5) Boda Limestone, 16 m level, Ashgillian, Osmundsberget, Dalarna, Sweden.

common: all four ambulacra have the same number of facets in 34% of the sample (28 specimens). Another interesting feature is that 63% of the specimens have ambulacra I and V with the same number of facets. In 26% of the specimens ambulacral grooves IV^4 and V^1 converge and are found closely set together on a small mound. The large number, 16, of ambulacral patterns in the population studied presumably represents in part addition of facets during growth. However, the repetition of similar patterns at different growth stages and the absence of 8 theoretically possible patterns indicates that addition of facets was not random and some of the variation was genetically controlled. The maximum number of grooves is five, present in ambulacrum I of two specimens.

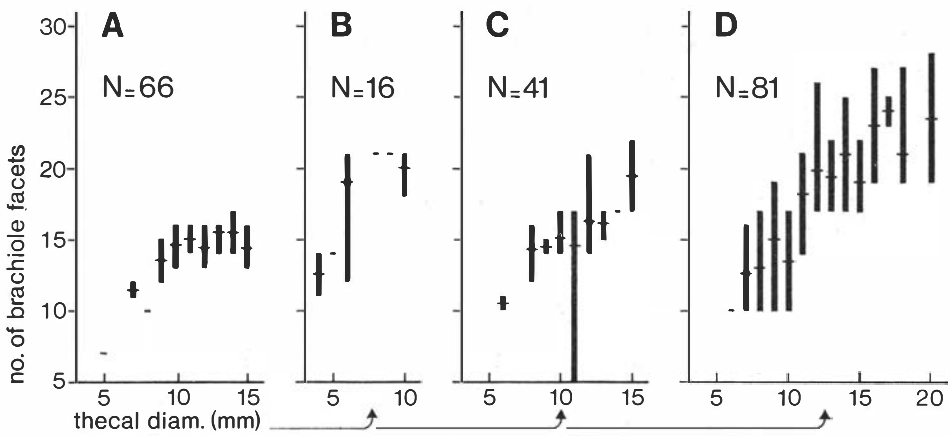

Fig. 4. Means and ranges of total number of ambulacral facets plotted against 1 mm thecal diameter classes in *Eucystis quadrangularis (A)* and three samples of *Haplosphaeronis* spp. *(B—D)*. A positive correlation between total number of facets and thecal diameter is most clearly seen in Fig. 4A. This may indicate transition from immature to mature animals. *A: Eucystis quadrangularis*, Skalberget, Dalarna, Sweden; *B—D: Haplosphaeronis* spp.; *B:* Sphaeronitid Limestone, 5.5—6.0 m level, Tönnerud, Oslo Region, Norway; *C:* Skalberget Beds, Amtjärn, Dalarna, Sweden; *D:* Boda Limestone- 16 m above base. Osmundsberget, Dalarna, Sweden. N: number of sample.

Fig. 4 shows that most specimens of this population had a full compliment of facets at a thecal diameter of 10—12 mm and thereafter did not develop any more. This suggests the onset of maturity and that a characteristic maximum number of facets occurred in *E. quadrangularis*.

Pattern of addition of ambulacral furrows in a radius

As mentioned above the number of facets in any radius increases with increasing size of the animal. The available material indicates that the grooves were normally added in a clockwise manner in each radius (Fig. 1). In radii I, II, and IV this pattern of addition occurs without exception. In radius V, however, it appears that ambulacral grooves 2 and 3 were the first formed, then 1 and 4 added later. This departure from the normal pattern in radius V may be caused by the presence of the anus which prevents as many facets being added in a clock-wise direction in just this one radius (Fig. 1). To compensate, at least one later facet was added in a counterclockwise direction in ambulacrum V. All ambulacral grooves were apparently formed close to plate sutures (Fig. 1).

AMBULACRAL STRUCTURES OF *HAPLOSPHAERONIS* SPP.

Of 800 Norwegian and Swedish specimens less than 35% show the ambulacral area well enough to be included in this study. The material belongs to at least three species, but at present characters for discriminating species are not sufficiently understood[5]. All Swedish specimens are referred to *H. oblonga* (Angelin, 1878), regardless of a stratigraphic distribution from late Llandeilian to upper Ashgillian[5, 6]. In Norway *H. kiaeri,* with two subspecies, occurs in the Caradoc, and a new species is present in the upper Llandeilian (Bockelie[5] and in preparation). *Haplosphaeronis* spp. have all five ambulacra normally developed.

Ambulacral pattern for all populations show some similarities (Figs. 3B, 5). Ambulacra I and V normally have the same number of facets, ambulacra II and III about 15% fewer, and ambulacrum IV has the smallest number. The repetition of this pattern suggests genetic control (Fig. 5).

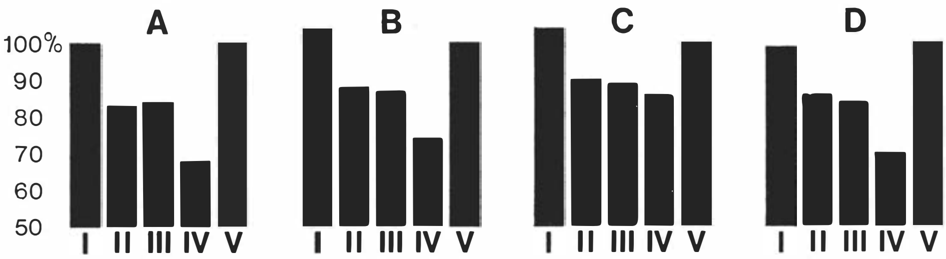

Fig. 5. Mean number of ambulacral facets in percentage of the mean number in radius V in four samples of *Haplosphaeronis* spp. Note that ambulacra I and V normally have the same number of facets, ambulacra II and III about 15% less than this and ambulacrum IV has the smallest number. The repetition of this pattern suggests genetic control. A. 16 m level, Boda Limestone, Osmundsberget; *B.* Kullsberg Limestone, Kullsberg quarry; *C.* Skalberget Beds, Amtjärn, all Dalarna, Sweden; *D.* Sphaeronitid Limestone, 5.5—6.0 m level, Tönnerud, Oslo Region, Norway. Sample sizes: A. 81, B. 37, C. 46, D. 18.

The Osmundberget population

81 specimens of *H. oblonga* s. l. from the same bedding plane approximately 16 m above the base of the Boda limestone, show a bimodal distribution when the numbers of the facets are compared with thecal diameter. A rapid increase in numbers of facets occurs between 10 and 12 mm diameter (Fig. 4); thereafter few facets are added. This abrupt increase in number of facets may indicate the onset of maturity or possibly that the animals lived for two years only. The length of the food grooves increases in a clockwise manner in each ambulacrum, as in *E. quadrangularis,* but again departures from this pattern occur commonly in ambulacrum V (Figs. 1, 6).

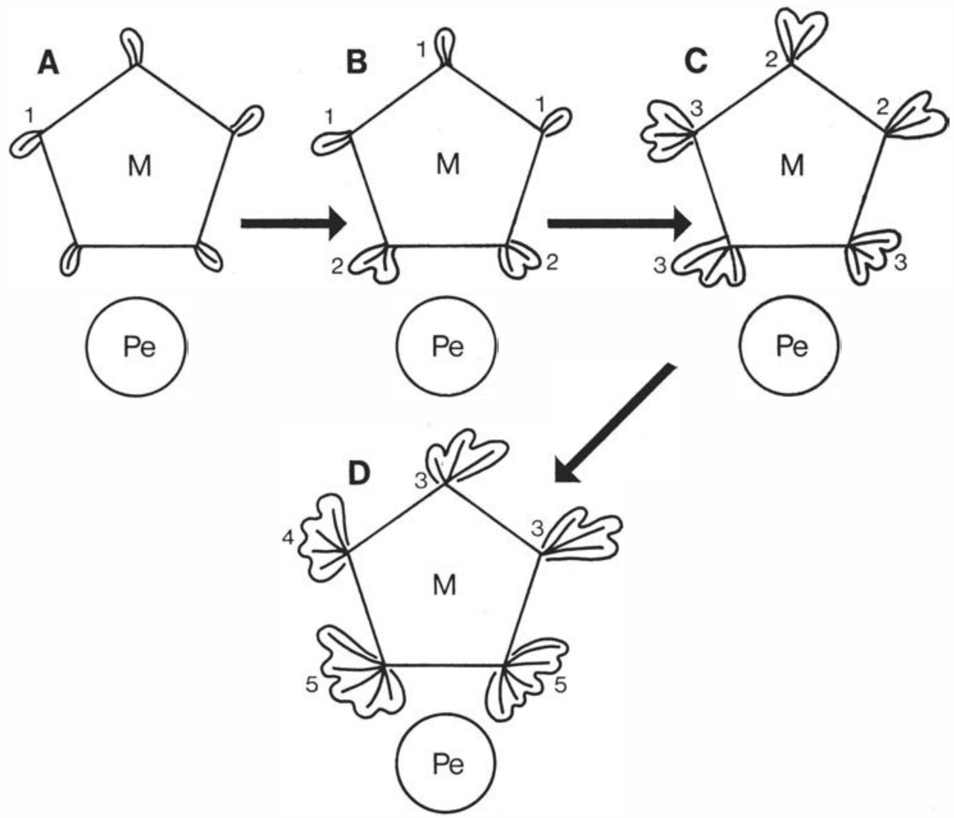

Fig. 6. Ontogenetic stages of *Haplosphaeronis* spp. based on specimens from 16 m level, Osmundsberget, Dalarna, Sweden. A. specimens with thecal diameter smaller than 8 mm; B. Specimen of 8—9 mm size; C. approximately 10 mm size, and D. 11—25 mm thecal diameter, the latter presumably adult stage. 1—5; numbers of ambulacral furrows in a radius; M. mouth; Pe. periproct.

Comparison with other populations

Stratigraphically older populations of *Haplosphaeronis* show similar increases in numbers of facets with size (Fig. 4), but never have as many facets as the Osmundberget population. However, because of the smaller numbers of well preserved specimens, results are less certain. The size of the onset of maturity appears to vary from population to population: approximately 12 mm at Osmundberget (Ashgill), 6—8 mm at Amtjärn, Dalarna (Upper Caradoc), and 4—6 mm at Tönnerud, Norway (Upper Caradoc).

Such differences may be due to different species becoming mature at characteristic sizes, *i. e.* that the variation is evolutionary in origin. Equally the differences in sizes of maturity may reflect different ecological conditions which effected growth rates. The population with the smallest thecal diameter at maturity is found in shales, presumably deposited below wave base. This may be a stunted population, but it is difficult to decide on available information.

SUMMARY AND CONCLUSION

Study of the ambulacra of several populations of *Haplosphaeronis* and one of *Eucystis quadrangularis* have patterns of variation which are of general interest. Ontogenetic variation is demonstrated by the positive correlation between the total number of ambulacral facets and the size of the animal. The transition from immature to mature animals seems to have been abrupt in the large populations of *H. oblonga* s. l. (Fig. 4). However, this is less clear in smaller populations of *Haplosphaeronis*.

The pattern in which the facets are added clockwise in each ambulacrum occurs in both genera. Quite possibly this pattern of addition was typical of the Sphaeronitidae. It certainly seems to be present in *Archaegocystis Jaekel*.

Some variation may be evolutionary. The stratigraphically youngest populations of *Haplosphaeronis* have a higher total number of brachiole facets than their forerunners and the size at the onset of maturity may also have changed with time. Differences in total number of brachiole facets may be due to ecological factors. It is known that the total number of arms in recent crinoid species is ecologically controlled.[8]

Haplosphaeronis and *Eucystis* lacked a stem and were usually attached directly to a firm substrate. They were thus unable to orientate the theca with respect to currents and may have lived in areas with constant current directions. Alternatively, the brachioles may have been sufficiently flexible to be orientated into currents. The large number of facets in ambulacrum I and V of *Haplosphaeronis* may have formed an effective collecting basket if currents passed over the oral area before reaching the anus. Alternatively these brachioles may have helped to prevent faecal matter from being deposited in the oral area. Various ornaments on the oral and anal plates as well as on the theca itself may have helped to create special current patterns over the theca (Bockelie, in preparation).

Acknowledgements. The author is indebted to Kgl. Svenske Vetenskapsakademiet, Gustav Lindström's minnefond, Nansen Fondet og de dermed forbundne Fond and to Paleontologisk Museum, Oslo, for financial support in collecting material and field data in a project of surveying Scandinavian echinoderms, of which this contribution is a part. The author is also indebted to Dr. C. R. C. Paul, University of Liverpool for valuable suggestions, critical reading of the manuscript and for correcting my English.

REFERENCES

1. R. V. Kesling, Cystoids. In *Treatise on Invertebrate Paleontology,* R. C. Moore (ed.). *Part S. Echinodermata 1 : 1.* Geol. Soc. Am. Lawrence, Ka. (1967)
2. F. A. Bather, The Pelmatozoa-Cystidea, in E. R. Lankester (ed.), *A Treatise on zoology,* London, **3** (1900) 38—77.
3. C. R. C. Paul, British Ordovician cystoids. Part 1. *Palaeontogr. Soc. monogr. London,* (1973) 1—64.
4. V. Jaanusson, On the series of the Ordovician system. *Rept. Intern. Geol. Congr., XXI Session, Norden, pt. IV.* Copenhagen (1960).
5. J. F. Bockelie, *Diploporitic cystoids (Echinodermata) from the Ordovician of Norway with remarks on Swedish form.* University thesis Univ. Oslo (1972) 1—72.
6. G. Ragnéll, *Non-crinoid Pelmatozoa from the Paleozoic of Sweden.* A taxonomic study. Acad. Diss. Lond. (1945) 255 pp.

7. R. Prokop, Sphaeronitidae Neumayr of the Lower Paleozoic of Bohemia. *Sbor. Geol. Palaeont. Praha (P)* **3** (1964) 7—38.

8. A. H. Clark, A monograph of the existing crinoids. Vol. I, part 2. *Bull. U.S. natn. Mus.* **82** (1921)

IZVOD

Varijabilnost ambulakralnih struktura u nekih diploporitnih cistoida

J. F. Bockelie

Pregledana su ambulakralna polja na više od 800 primjeraka ordovicijskih diploritnih cistoida rodova *Haplosphaeronis* Jaekel i *Eucystis* Angelin iz Norveške i Švedske. Između veličine životinje i ukupnog broja brahiolnih faceta utvrđena je pozitivna korelacija. To znači da se kod tih rodova ambulakralne strukture umnožavaju za vrijeme rasta. Proučavanjem više populacija može se zaključiti da je variranje broja brahiolnih faceta unutar jedne populacije rezultat kombinacije ontogenije, varijabilnosti unutar pojedinih starosnih skupina, ekoloških prilika i filogenetskih promjena.