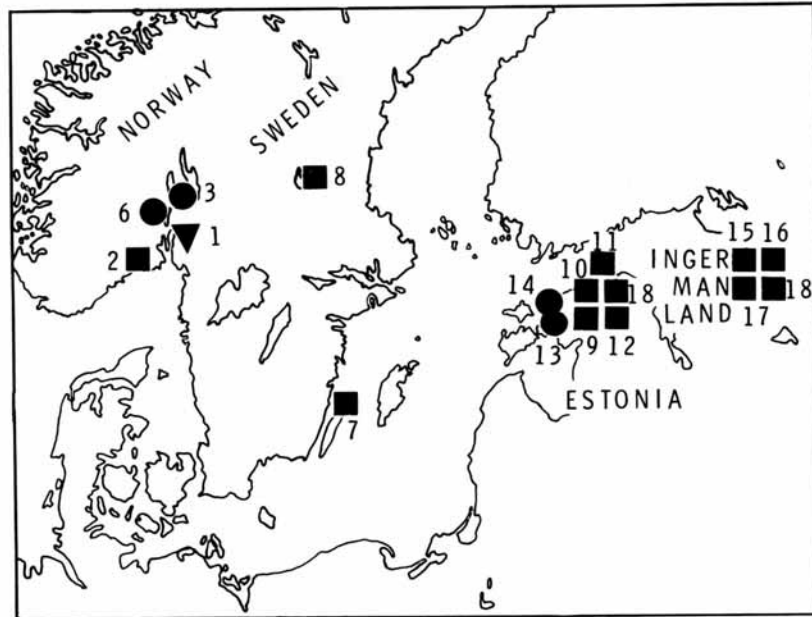


TAXONOMY, FUNCTIONAL MORPHOLOGY AND PALAEOECOLOGY OF THE ORDOVICIAN CYSTOID FAMILY HEMICOSMITIDAE

by J. FREDRIK BOCKELIE

ABSTRACT. Morphological aspects of the Middle-Upper Ordovician genus *Hemicosmites* are discussed. Most of the important features are related to respiratory functions, and the distribution and functions of the rhombs are evaluated. Five different patterns of rhomb distribution are outlined. Phyletic changes occur throughout the Ordovician in: (1) respiratory structures, (2) expansion of oral area, including addition of new plates, and (3) increased size of the arms. It is suggested that gonads were located in specialized appendages connected to the ambulacral furrows as previously suggested by Jaekel (1899), and that the genus, normally found associated with reefs and carbonate mud mounds, gave rise to *Caryocrinites* (Caryocrinitidae). Four new species are described, three from Norway and one from Sweden: *Hemicosmites papaveris*, *H. sculptus*, *H. sphaericus*, and *H. variabilis*. The type species of the genus, *H. pyriformis*, which is known from one specimen only, differs in many respects from all other known *Hemicosmites* species. It is either an aberrant specimen or the species is generically distinct from all others. This taxonomic question is left open due to lack of additional material.

HEMICOSMITES (Hemicosmitidae) is a rhombiferan cystoid consisting of a globular to poppy-head shaped theca with three armlike appendages, a stem, and probably a root structure (text-fig. 3). *Hemicosmites* belongs to a distinct group of cystoids, the Hemicosmitida, with an endothecal respiratory pore system (see Paul 1968). The inhalant pores consist of numerous holes forming a sieve (sieve-pores); the exhalant pores are simple (pore holes; text-figs. 3, 5). Representatives of the family Hemicosmitidae were confined to shallow-water environments in the Ordovician tropical seas of the Baltic Basin. Few people have studied *Hemicosmites* in detail, mostly because of the lack of well-preserved material and the fact that at first inspection the pore system does not seem to exhibit any distinct pattern of distribution. *Hemicosmites pyriformis* from Russia was first described by von Buch in 1840. In 1865 Kjerulf identified a loose plate from Norway as ?*Hemicosmites pyriformis*. During the latter half of that century several new species were described from different localities and strata (text-fig. 1). Jaekel (1899) gave a thorough description of *Hemicosmites* and other cystoids, and detected important morphological features of *Hemicosmites*. The first *Hemicosmites* recognized from Sweden (Thorslund 1936) was identified as *H. extraneus* Eichwald by Regnéll (1945) and described together with a new species, *H. oelandicus*. New material, particularly from Norway, but also involving a closer examination of Swedish and Estonian material, has made it possible to arrive at a more detailed concept of the genus. Modifications of the pore systems of *Hemicosmites* seem as important as those of diploporite cystoids. The respiratory system apparently developed more rapidly in tropical areas than in other climatic zones during the Ordovician. It is possible to discuss relationships between the two families Hemicosmitidae and Caryocrinitidae on the basis of the configurations in



TEXT-FIG. 1. Distribution of *Hemicosmites* species in the Baltic Basin during Lower (triangles), Middle (squares), and Upper (circles) Ordovician times. 1, *Hemicosmites?* sp. A.; 2, *H. papaveris* sp. nov.; 3, *H. variabilis* sp. nov.; 6, *H. sculptus* sp. nov.; 7, *H. oelandicus*; 8, *H. sphaericus* sp. nov.; 9, *H. rudis*; 10, *H. extraneus*; 11, *H. pocillum*; 12, *H. pulcherrimus*; 13, *H. verrucosus*; 14, *H. grandis*; 15, *H. malum*; 16, *H. levior*; 17, *H. oblongus*; 18, *H. pyriformis*.

the material studied. Not all the known *Hemicosmites* species have been investigated because the majority of the Estonian and Russian species are being revised by Professor R. F. Hecker (pers. comm.).

GEOGRAPHICAL AND STRATIGRAPHICAL DISTRIBUTION

From Norway most of the species are new, including *Hemicosmites papaveris* from 'Stage' 4bδ (upper Caradoc), *H. variabilis* from 'Stage' 5a (upper Ashgill), and *H. sculptus* from 'Stage' 5b (uppermost Ashgillian). In addition several loose thecal plates and parts of thecae probably belonging to *Hemicosmites* have been found in 'Stage' 3cβ-γ (Kjerulf 1865) and 'Stage' 5a. The Norwegian faunas thus contain species throughout the whole time range of the genus.

From Sweden, *Hemicosmites* is known in the Lower and Middle Ordovician only. In Lower Ordovician strata (upper Arenig) loose thecal plates are found on Öland, contemporary with the Estonian species *H. malum* (Pander), but they do not seem to be conspecific; indeed, they may belong to the Caryocrinidae. Two species of *Hemicosmites* can be identified in Sweden, *H. oelandicus* Regnéll from the Dalby Limestone (Jaanusson 1960), equivalent to the Jöhvi-Keila Stage boundary of Estonia, and *H. sphaericus* sp. nov. from the Kullberg Limestone of Kullberg, Dalarna, equivalent to the Idavere-Jöhvi Stage of Estonia (text-fig. 2). Norwegian and Swedish faunas contain fewer species than those of Estonia.

There are several uncertainties as to the precise stratigraphical positions of the different species. *H. malum* (Stage C₁), *H. pyriformis* (Stage unknown), *H. pulcherrimus* (Stage D₁), *H. grandis* (Stage F₂), and *H. verrucosus* (Stage F₁) occur in Estonia, the former three being Middle, the latter two Upper Ordovician in

age. All known species from Ingermanland (Leningrad district) are of Middle Ordovician age (Stage C_1); here are included *H. malum*, *H. oblongus*, and *H. pyriformis* (Stage unknown).

It is interesting to note that individual species within the Baltic Basin have a restricted geographical as well as stratigraphical distribution. In fact Ingermanland and Estonia have only one species in common. It seems somewhat strange that the *Hemicosmites* associated with the Kullberg carbonate mud mounds should be replaced by other cystoids in the late Ordovician of Sweden, whereas they were still flourishing in similar environments in the Oslo Region. The reason may be the high degree of specialization that can be seen in the respiratory structures and possibly also in other structures.

The distributional pattern of *Hemicosmites* has been somewhat uncertain since many loose thecal plates were formerly all identified within the genus. The same even applied to complete specimens of other genera, and *Hemicosmites* has been used by many authors as a collective name for different cystoids, playing a role similar to the name *Echinospaerites*. '*Hemicosmites*' was described from the U.S.A. by Hall (1864), and from Britain by Forbes (1848) and Salter (1866). By the end of the last century many of the problems were clarified. *Hemicosmites subglobosus* Hall is now known as *Coelocystis*, and *H. rugatus* (Salter) and a specimen identified by Forbes as *H. oblongus* belong to the family Caryocrinidae. Thorvald (1935, p. 159) mentioned *Hemicosmites* from the Upper Ordovician of the south of France, but no species name was given. Regnéll (1945, p. 98; 1948, p. 17) also referred to this record. However, as far as can be seen from available sources, all southern European genera appear to be caryocrinids. *Hemicosmites jaekeli* Sun (1936) from Yunnan may be a *Hemicosmites*, judging from the plate pattern. If it is, it is the first representative known from outside the Baltic Basin. *Hemicosmites* species are known from Norway (Kjerulf 1865; Brøgger 1882; new data here), Sweden (Thorslund 1936; Regnéll 1945, 1948b; new here), Estonia and Russia (Pander 1830; von Buch 1840, 1845; Verneuil and Keyserling 1845; Jaekel 1899). Most of the described specimens were collected during the last century, and details concerning localities and stratigraphical position are often unknown. The oldest known species was *H. malum* (Pander 1830) according to Jaekel (1899, p. 308; see also Regnéll 1948b, p. 16, footnote), from the '*Echinospaerites* Limestone', C_1 , which is probably of Aseri age, C_{1a} (text-fig. 2), and thus a correlative of the *Didymograptus murchisoni* Zone, but a loose thecal plate of an even older possible *Hemicosmites* has been found at the Arenig-Llanvirn boundary of Norway. The youngest species of the genus are found in Norway (*H. sculptus* sp. nov.) and Estonia (*H. verrucosus* Jaekel), both from the uppermost Ordovician (Hirnantian).

At present sixteen species are considered to belong to *Hemicosmites*, four of which are new. A list of the species and present locations of types is given below. For those types that I have seen the species is marked with an asterisk.

*1. *Hemicosmites pyriformis* von Buch, 1840 (p. 20, pl. 1, figs. 11, 12); type species of genus. Paläontologisches Museum, Museum der Naturkunde der Humboldt Univ., D.D.R. Unnumbered specimen. Type locality, Pulkowa, Ingermanland, U.S.S.R. Type stratum not given. Figured here Pl. 43, figs. 3-5.

2. *H. extraneus* Eichwald, 1840 (figured specimen from pl. 11, fig. 5 of Eichwald 1860). A specimen considered to be the type is located at Leningrad University, Dépt. Hist. Geol., Catalogue no. 1/3207. Type locality, Spitham, Estonia (see Regnéll 1945, p. 101). Type stratum, D_3 (Vasalemma). Figured here Pl. 44, figs. 1-3.

3. *H. grandis* Jaekel, 1899 (p. 310, text-fig. 73). According to Jaekel (1899) preserved in Leningrad, but now at Paleontological Institute in Moscow. Type locality, Haapsalu, Estonia. Type stratum, F_2 (uppermost Ashgill).

4. *H. jaekeli* Sun 1936 (p. 481, pl. 2, fig. 3). Catalogue no. S. 1281 in Geol. Surv. China, Nanking. Type locality, Kweichow, China. Type stratum, Llandeilo age beds. The true nature of this species is difficult to settle, but it may belong to *Corylocrinus* (Caryocrinidae).

5. *H. levior* Jaekel, 1899 (p. 309). No figure given and description inadequate. Type not located. According to Bassler and Moody (1943) the type locality is Zarskoje Selo, near Leningrad, U.S.S.R. Type stratum, C_1 . This species is coeval with *H. malum* Pander and it may be a junior synonym.

6. *H. malum* (Pander, 1830), pl. 29, fig. 1. Leningrad University, Dept. Hist. Geol., Catalogue no. 1/324. Type locality, Zarskoje Selo, near Leningrad, U.S.S.R. Type stratum, C_1 .

7. *H. oblongus* (Pander, 1830) (p. 146, pl. 2, figs. 22, 23). No information given as to where the type is located. According to Bassler and Moody (1943) the type locality is near Leningrad, U.S.S.R., and the type stratum is C_1 . Jaekel (1899) did not mention *H. oblongus* and may have rejected it as a separate species, because of its deformed theca.

*8. *H. oelandicus* Regnéll, 1945 (p. 99, pl. 3, fig. 12). Naturhistoriska Riksmuseet, Stockholm, Sweden. Catalogue no. Ec4362. Type locality, Böda, Öland, Sweden. Type stratum, Lower Chasmops Limestone (= Dalby Limestone), upper Llandeilo.

*9. *H. papaveris* sp. nov. Paleontologisk Museum, Oslo, Norway. Catalogue no. 94644. Type locality, Steinvika, Langesund, Oslo Region, Norway. Type stratum, Encrinite Limestone (upper Caradoc).

10. *H. pocillum* Jaekel 1899 (p. 310). No figure given. According to Jaekel (1899) the material is preserved at the University of Tartu (formerly Jurjew) and in Leningrad. No type was chosen. According to Hecker (written comm.) this material or parts of it is at the Paleontological Institute in Moscow. Type locality, unknown. Type stratum, D₁.

11. *H. pulcherrimus* Jaekel, 1899 (p. 310, pl. 18, fig. 6). According to Jaekel (1899) the type was in Leningrad, but it is now at the Paleontological Institute in Moscow (Hecker, pers. comm.). Catalogue no. 15355 (257/657). Type locality, Sack, near Tallinn (formerly Reval), Estonia. Type stratum, D₁. Figured here Pl. 44, fig. 9.

12. *H. rudis* Jaekel, 1899 (p. 310, fig. 74). According to Jaekel (1899) one specimen is located at the University of Tartu and one in Leningrad. No type was chosen. One or both of these specimens are now at the Paleontological Institute, Moscow, according to Hecker (pers. comm.). Type locality, Vassalemma, Estonia. Type stratum, D₁.

*13. *H. sphaericus* sp. nov. = *H. extraneus* Regnéll, non Eichwald. Paleontologisk Institute, Uppsala, Sweden. Catalogue no. D 325 (= UM ec95 as used by Regnéll 1945, p. 101, pl. 3, fig. 13). Type locality, Kullsberg, Dalarna, Sweden. Type stratum, Kullsberg Limestone, lowermost part (lower Caradoc).

*14. *H. sculptus* sp. nov. Paleontologisk Museum, Oslo, Norway. Catalogue no. 97066. Type locality, Svartøy, Ringerike, Oslo Region, Norway. Type stratum, 'Stage' 5b (uppermost Ashgill—Hirnantian).

*15. *H. variabilis* sp. nov. Paleontologisk Museum, Oslo, Norway. Catalogue no. 97079. Type locality, Kalvsjø Quarry, Hadeland, Oslo Region, Norway. Type stratum, 'Stage' 5a (uppermost Ashgill).

16. *H. verrucosus* Eichwald 1856 (p. 124). Leningrad University Dept. Hist. Geol. (figured specimen from pl. 11, fig. 3a, b, of Eichwald 1861). Cat. no. 1/327. Type locality, Soutlep, Nouck Peninsula, Estonia. Type stratum, F₁ (upper Ashgill).

The following additional species names were included in the list given by Bassler and Moodey (1943): *Hemicosmites altus* Jaekel (1918, p. 97, fig. 88), based upon a single plate only; this is hardly a recognizable feature. *H. elongatus* Pander (1867, p. 124) is a manuscript name 'that got into literature by accident' (Regnéll 1948b, p. 17, footnote). *H. porosus* Eichwald 1860 is, according to Jaekel (1899, p. 310), probably a synonym of *H. verrucosus*. Eichwald (1860, p. 636) figured only two infra-laterals of *H. porosus*.

PALAEOECOLOGY OF HEMICOSMITES

Within the Baltic Basin *Hemicosmites* species have been found only in beds indicative of regressive conditions, whether locally or regionally, and are mostly associated with bioherms or carbonate mud mounds. Representatives of the genus may have been present within the Basin throughout the Ordovician, but shallow-water areas are now seldom preserved in the area. The fact that individual species have a limited stratigraphical as well as geographical distribution may indicate a high degree of specialization. Within some populations, however, there is considerable structural variation even within the same age groups of individuals. Such variation has also been found amongst other cystoids (Bockelie 1978), and may either be due to natural variation within age groups, or indicative of dimorphism.

A study of *Hemicosmites papaveris* sp. nov. from the Oslo Region gives some possible indication of adaptation to narrow ecological niches. Three bioherms in the Encrinite Limestone (upper Caradoc) are found along a line perpendicular to the palaeoshore. Each of these bioherms has a different echinoderm fauna. *H. papaveris* lived on the bioherm furthest away from the palaeoshore at Steinvika, Langesund, and on death

Series	Graptolite zones	East Baltic stages	Oslo Region stages	NORWAY	SWEDEN	ESTONIA	INGER-MANLAND
Ashgill	Dicellograptus anceps	Porkuni <i>F_{II}</i>	5b	6		14	
	Dcomplanatus	Pirgu <i>F_{IC}</i>	5a 4d	3 4 5		13	13?
	Pleurograptus linearis	Vormsi <i>F_{Ib}</i>	4c				
		Nabala <i>F_{IA}</i>					
Caradoc	[?] Dicranograptus clingani	Rakvere <i>E</i>	4bδ	2			
	[?] Oandu <i>D_{III}</i>		4bδ			9 11 12	
	[?] Keila <i>D_{II}</i>		4bβ		8		
	Diplograptus multidentis	Johvi <i>D_I</i>	4bα		7	11? 18?	18?
		Idavere <i>C_{III}</i>				9? 10	
	Nemagraptus gracilis	Kukruse <i>C_{II}</i>	4aβ				
Llandeilo	Glyptograptus teretiusculus	Uhaku <i>C_{IC}</i>	4aα ₃₋₄				
Llanvirn	Didymograptus murchisoni	Lasnamägi <i>C_{Ib}</i>	4aα ₁₋₂	1			
	Aseri <i>C_{IA}</i>					15 16 17	
Arenig	Didymograptus bifidus	Kunda <i>B_{III}</i>	3c				
	Didymograptus hirundo	Volkhov <i>B_{II}</i>					
	Didymograptus extensus	Latorp <i>B_I</i>	3b				

TEXT-FIG. 2. Stratigraphical distribution of *Hemicosmites* species. The numbers refer to the same species as in text-fig. 1. In addition: 4, *H.?* sp. B; 5, *H.?* sp. C; Stratigraphical correlation based mainly on data from Männil (1966). Upper and lower boundaries of *D. clingani* Zone, however, are somewhat uncertain.

fell into hollows in the bioherm. Other specimens were washed off the bioherm and broken, and disarticulated plates were distributed in the 'back reef' zone. A second bioherm about 250 m further towards the palaeoshore was also inhabited by *Hemicosmites*, but in much smaller numbers. On this bioherm, crinoids dominated together with some *Heliocrinites*. Roots of crinoids are very common on the flanks of this bioherm. A third bioherm, at Ässtranda, Porsgrunn, of approximately the same size as the other two, and located about 10 km further towards the shore, contains no *Hemicosmites*. Instead, numerous *Heliocrinites* seem to have replaced *Hemicosmites*. Even in other areas with presumed shallow water deposits, *Heliocrinites* seem to have replaced *Hemicosmites*, both in the Oslo Region and in Dalarna, Sweden.

'Stages' 5a and 5b (uppermost Ashgill) of the Oslo Region contain *Hemicosmites* species associated with carbonate mud mounds (5a) and with 'reefs' (5b), respectively. The two environments, each with a different species, may have differed in current velocities, substrate, suspended nutrition, and sedimentation rates.

In Dalarna several carbonate mud mounds of Middle and Upper Ordovician ages

occur. Only in the Middle Ordovician of the Kullsberg carbonate mound is a *Hemicosmites* species found (*H. sphaericus* sp. nov.). Its relation to the mound is not quite clear because of faults within the mound itself, but it may have lived on the flanks or have been an element in a pioneer community found immediately below the mound. A few loose thecal plates possibly belonging to the same species have been found immediately below the Kullsberg Limestone at Amtjärn. No remains of *Hemicosmites* are known from the Upper Ordovician of Sweden. However, a species of the closely related *Caryocrinites* (Caryocrinitidae) has been described from Upper Ordovician beds at Skålberget in Dalarna (Regnéll 1945). Several loose thecal plates from other localities in Dalarna may belong to this genus.

In Estonia *Hemicosmites* is also known to be associated with bioherms, both in the Middle and Upper Ordovician (Männil 1966). Some are known from outside bioherms and carbonate mud mounds, but such occurrences are rare. The oldest *Hemicosmites*? sp. A, from the upper Arenig-lower Llanvirn of the Oslo Region, Norway, is from detrital shallow-water limestones. Only a loose thecal plate has been found (Kjerulf 1865). *H. oelandicus* Regnéll, represented by a single specimen only, also occurs in shallow-water limestones of clastic type, in the Dalby Limestone (lower Caradoc) of Öland, Sweden.

Hemicosmites lived attached to the sea bottom and may have had a root structure of the same type as the closely related *Caryocrinites*. *Hemicosmites* may have been a passive rheophile type filter feeder in the same way as known in several stalked crinoids (Breimer 1969). This type of feeding position has also been suggested as one of the possibilities for *Caryocrinites* (Sprinkle 1975). *Hemicosmites*, living in a shallow water environment could, as inferred from the arm construction, also direct its arms into the currents (text-fig. 3).

RELATIONSHIP TO OTHER FAUNAS

During the Ordovician Period most cystoids occurred within particular provinces. The superfamily Hemicosmitida was dispersed throughout the northern Hemisphere. Of the Hemicosmitidae, *Hemicosmites* was restricted to the Baltic Basin, possibly with the exception of one Chinese species (Sun 1936). The oldest unquestionable species is found in Estonia, probably indicating that the genus arose in the Baltic Basin. The other genus, *Tricosmites*, is known exclusively from the lower Silurian of Estonia. The family Caryocrinitidae may have had a wider distribution, both stratigraphically and geographically. The oldest representatives of the Hemicosmitida are loose thecal plates recently collected from Öland, Sweden, but their generic position is uncertain at present. From the Middle Ordovician of Burma, Bather (1906) described *Caryocrinites aurorus*, *C. avellanus*, and *C. turbo*, the oldest known more or less complete specimens. *Caryocrinites* (under the name *Stribalocystites*, now considered to be a synonym by Frest 1975) is common in the Silurian of North America, and has also been reported from the Silurian of Estonia (Schmidt 1858).

Various authors have commented on the distribution of the Hemicosmitida in southern Europe, but the various genera are difficult to determine, because of the lack of oral areas. The family Heterocystitidae is based on the Silurian *Heterocystis* from North America, and may be a crinoid (type lost or mislaid; Paul 1969). Representa-

tives of the family Thomacystidae (*Thomacystis*) are found only in the Upper Ordovician of Britain.

Within the Hemicosmitida, the genera *Hemicosmites*, *Tricosmites*, and *Caryocrinites* occur together in the Baltic Basin. Similarities in construction of *Hemicosmites* and *Caryocrinites*, and the fact that *Caryocrinites* later replaces *Hemicosmites* in its environment strengthen the possibility that these two genera are closely related.

MATERIAL AND METHODS

For this study museum collections have been used only to a limited extent. In museum collections in Oslo only a few thecal plates were present. Some specimens of *H. extraneus* and *H. sphaericus* sp. nov. were borrowed from Naturhistoriska Riksmuseet, Stockholm (RM) and from the Paleontologiska Institutionen (UM), Uppsala, both Sweden. From the Humboldt Museum (HM), Berlin, D.D.R., the type specimen of *H. pyriformis* was borrowed, and some working material was also borrowed from Estonia. Photographs of types and figured specimens in Leningrad and Moscow have been placed at my disposal by Professor Hecker and Dr. Tanja Koren.

The greater part of the material has been collected personally in Norway and Sweden from 1971 onwards. Field work was intended to assemble as much new information as possible on morphology, stratigraphy, and palaeoecology of cystoids. The precise stratigraphical and geographical positions of several other cystoid species and genera were ascertained and several cystoids new to Norway were obtained. It has proved valuable to collect large blocks containing cystoids, often completely surrounded by matrix, to ensure that fragile and delicate structures are not lost, and also to collect associated fossils for stratigraphical purposes. Orientated samples were taken, as well as samples for thin section analyses to facilitate palaeoecological interpretations.

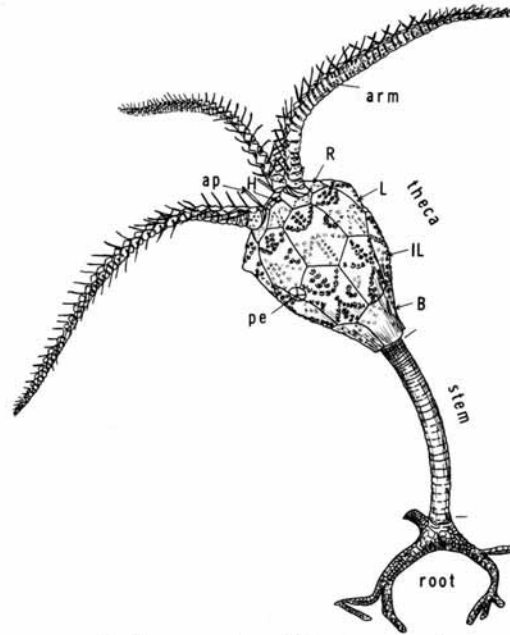
Hemicosmitids are generally found in marlstones and limestones, and the thecae are often more or less complete, whereas arms, stems, and roots are mostly lost. Disarticulation of cystoids may be due to differences in the construction of the sutural area of the thecal plates. Infilling or replacement of the fossils are common, secondary calcite or fine-grained sediment being most usual. Cystoids other than hemicosmitids often have pyrite infilling skeletal cavities or lining the thecae, occasionally totally replacing the skeleton. Pyrite commonly fills the pore canals in all cystoids.

The majority of the samples have been prepared chemically because of the toughness of the sediments. Cystoids have been completely dissolved to reveal both a mould of the external side of the thecae and the internal steinkern. When decalcified the material was cast in silicone rubber. This preparation has allowed study of structures which could not have been detected by mechanical preparation.

FUNCTIONAL MORPHOLOGY

A cystoid can be divided conveniently into three separate parts, the theca, the subjective system, and the stem (text-fig. 3), and separate elements of each can be described individually.

Thecal plates. Representatives of the Hemicosmitida have a restricted number of thecal plates arranged in definite circlets. The exact number of plates in each of these circlets may vary, but three or four circlets are always present (text-fig. 4A). Members of the superfamily Glyptocystitida on the other hand, have a theca with five circlets of plates termed basals (B, plural BB), infra laterals (IL, ILL), laterals (L, LL), radials (R, RR), and orals (O, OO). Jaekel (1899) distinguished the Glyptocystitida (referred to by him as Regularia) from the other rhombiferan cystoids (referred to as Irregularia) by the number and the arrangement of thecal plates. He considered the regularity in the Glyptocystitida to indicate a primitive stock, and believed a homology to exist between plates of members of this group and the others. Jaekel (1899, p. 308,

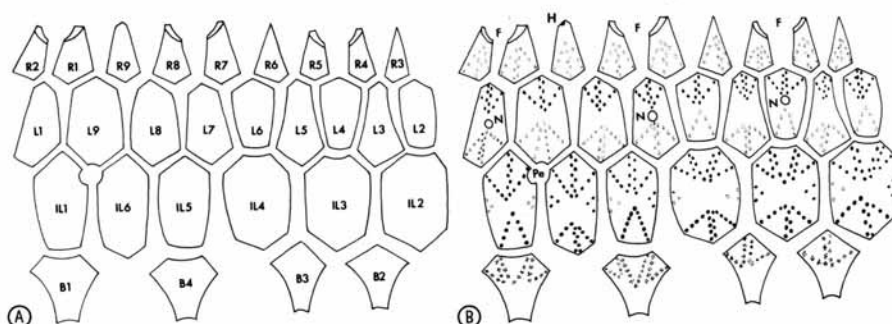


TEXT-FIG. 3. Reconstruction of *Hemicosmites* based on material of *H. papaveris* sp. nov. (theca) and similarities in construction of arms of *Caryocrinites* (Sprinkle 1975). Stem reconstruction based on *H. porosus* (Hecker, 1964), and roots based on structures associated with *H. papaveris* sp. nov.; ap—additional appendages (gonads?); B—basal plate; H—hydropore; IL—infra-lateral plate; L—lateral plate; Pe—periproct (anal opening); R—radial plate.

text-fig. 72) showed an interpretation of the plate arrangement in *Hemicosmites extraneus* Eichwald, with four basals (B1–B4), six infra laterals (IL1–IL5 + ILa), nine laterals (L1–L5 + three unnumbered LL), and nine radial plates, unnumbered. He considered the plates given numbers (e.g. B1, IL2 etc.) to be homologous with corresponding plates of the Glyptocystitida. It is doubtful if this is true. Not only are the plates of Hemicosmitida less constant than Jaekel thought, but even in Glyptocystitida some variation occurs.

A general formula for the Hemicosmitida may be given as 3–4 BB, 6 ?ILL, 8LL, 9 RR, and ?OO. This formula may not always be constant even within a species, though it usually is. Several modifications occur and are most clearly expressed in the family Caryocrinitidae, where tegminal plates replace the radials and orals. Even in the Hemicosmitidae new plates may be intercalated between the radials (see p. 375), and the number of lateral plates can vary within populations. Jaekel (1899, p. 294) noted that one specimen of *H. malum* had seven ILL plates instead of the usual six. For descriptive purposes it may thus be useful to regard the numbering of plates not

as indicative of homology, but only as a descriptive convenience. I prefer to number the plates consecutively in each of the plate circlets clockwise in oral aspect (as suggested by Paul 1969, p. 194), commencing just left of the hydropore, which later seems to be a fixed point in the Hemicosmitida (text-fig. 4B).

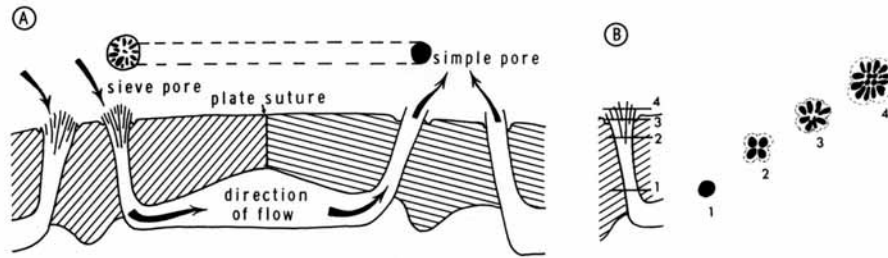


TEXT-FIG. 4. Plate diagram (A) and pore distribution (B) on *Hemicosmites*. B1-B4—basal plates; IL1-IL6—infra-laterals; L1-L9—lateral plates; R1-R9—radial plates. All plates are numbered in clockwise manner; using R9 as a starting point. This plate contains the hydropore. H—hydropore; F—arm facet; N—nodes on lateral plates; Pe—periproct. Cluster of pores in fig. B: sieve-pores are inhalant; larger simple pores are exhalant.

Thecal pores. Pore rhombs in all rhombiferan cystoids are composed of sets of thecal canals which open at the external surface of the thecal plates. Jaekel (1899) used the term dichopore for such canals. However, the canals can open either in slits (in *Glyptocystitida*) or in a pair of pores (*Hemicosmitida*). Paul (1972) suggested the term cryptorhomb to denote rhombs in which the dichopores open in pores, as in *Hemicosmites*. Each such dichopore opens in a pair of pores, one large *simple pore* at one end and a *sieve-pore* at the other (text-fig. 5). In a few cases, as noted in *Caryocrinites ornatus* by Jaekel (1899), sieve-pores can be present at both ends of the dichopore and still be functional. This situation, however, is unusual in the genus, but typical of *C. roemerii* Jaekel.

The simple pores generally have an internal diameter of 0.20–0.22 mm and the canals leading from them seem to have the same diameter throughout. The sieve-pores, as seen on the outer surface, occur as a variable number of holes, often radially arranged. If the plate surface is slightly abraded the appearance of the sieve-pores may alter (text-figs. 5B, 6E). With increased abrasion it becomes evident that all the sieve-pores are connected to a single canal leading from the plate interior towards the external surface. As the canal approaches the external surface it shows a fourfold petaloid cross section. Further outwards the four lobes separate and are themselves divided into four; thus the sieve-pores have a basic fourfold pattern.

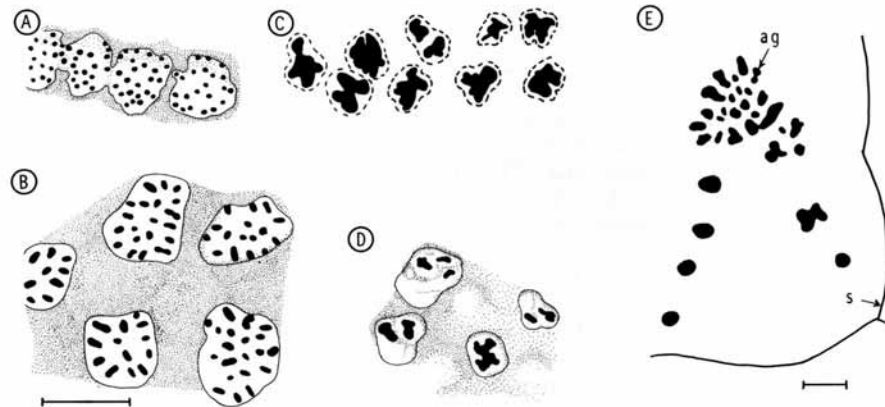
In thecal plates in which numerous sieve-pores occur, notably in the lower half of most LL-plates, it may not be easy to decide which of the pore-holes belong to individual sieve-pores. This is most difficult in some of the later species (*H. papaveris* sp. nov. and *H. sculptus* sp. nov.). For convenience I have chosen to call such pores



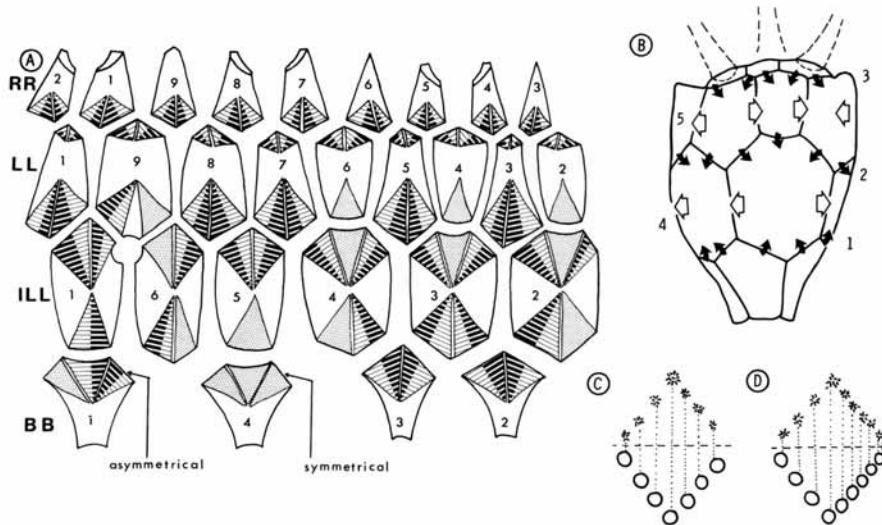
TEXT-FIG. 5. Section through a theca of *Hemicosmites*. A, longitudinal section through a dichopore showing water inlet through a sieve-pore and the outlet through the simple pore; immediately above the longitudinal section is the appearance of sieve-pores and simple pores on the outer surface, with the dichopore canal dashed. B, vertical section through a sieve-pore and corresponding horizontal sections at different levels (and growth stages) to show increased complexity of sieve-pores through the plate (1-4); highly schematic.

aggregated pores (text-fig. 6E). Aggregates of pore-holes are related to current system 2 (text-fig. 7D and text below) and show a radiating pattern as if the pores belong to one sieve-pore (text-fig. 6E). The tendency to aggregation of pores takes place in stratigraphically older species such as *H. extraneus*, but is not as marked as in later species. Aggregated pores form by the amalgamation of adjacent sieve-pore clusters during growth and are most obvious near the centre of the LL-plates.

Distribution of pore-rhombs. The rhombs on the theca of *Hemicosmites* are grouped to form five distinct flow systems (text-fig. 7B). Three of these inhalant-exhalant systems are *vertical systems* and exhibit a flow direction more or less parallel to the



TEXT-FIG. 6. Stratigraphical reduction of sieve-pores of *Hemicosmites* species (A-D). A, *H. extraneus* (RM Ec5280, lower Caradoc, C_{III}); B, *H. sphaericus* sp. nov. (PMO A35441, Kullberg Limestone, lower Caradoc); C, *H. papaveris* sp. nov. (PMO 94650, Encrinite Limestone, upper Caradoc—abraded specimen); D, *H. sculptus* sp. nov. (PMO 97066, 'Stage' 5b, upper Ashgill); E, aggregated sieve-pores (ag) of the earliest-formed pores (close to the plate centre) as seen in *H. papaveris* (PMO 94627). Scale bar is 1 mm (A-D at same scale).



TEXT-FIG. 7. Rhomb distribution and current patterns on a theca of *Hemicosmites*. A, Distribution of symmetrical and asymmetrical rhombs over the theca, mainly based on data from *H. extraneus* (RM Ec27604), but found in all species. B, Current patterns over the theca inferred from the distribution of inhalant and exhalant pores. Arrows indicate ex-current flow directions. Black arrows—exhalant vertical systems (1-3); white arrows—exhalant horizontal systems (4-5). C, symmetrical rhomb; D, asymmetrical rhomb. Plate terminology as in text-fig. 4A.

long axis of the theca (text-fig. 7B). Of these the lower system (1) involves rhombs across the basal circlet and the lower part of the infra-lateral circlet, the exhalant current being directed from the base upwards. The second system (2) involves pores of the upper half of the ILL plates and the lower part of the LL plates, with the exhalant currents directed from LL towards ILL plates (text-fig. 7B). The third and upper system (3) is formed by rhombs of the lower half of the RR plates and the upper half of the LL plates. The exhalant current was directed from the RR plates to the LL plates (text-fig. 7B). Sea water would pass around the theca with different speed at different levels. Knobs in the upper half of the LL plates probably caused strong water currents around the theca at this level and reduced the possibility of recirculation in the pore-system. Exhalant water from flow system (3) would enter the sea-water which was passing quickly around the theca, and the possibility of recirculation would be reduced. A strong water current may also have been present at about mid-height of the theca just below the anus. Exhalant water of systems (1) and (2) would emerge at this zone. A resultant respiratory flow pattern would be directed from the base upwards and from the adoral area downwards. This type of flow pattern around the theca agrees well with the ideas expressed by Paul (1972, text-fig. 12) for the diploporite cystoid *Haplosphaeronis*, and may be typical for cystoids in general.

Two other systems of pore-rhomb distribution are also present, with flow directions perpendicular to the long axis of the theca; these systems (4 and 5) may be termed

horizontal systems (text-fig. 7B). They are located at the two zones of maximum water current flow; system 4 is on the ILL plates, and system 5 on the LL plates. The horizontal systems may be partly or completely missing (see below).

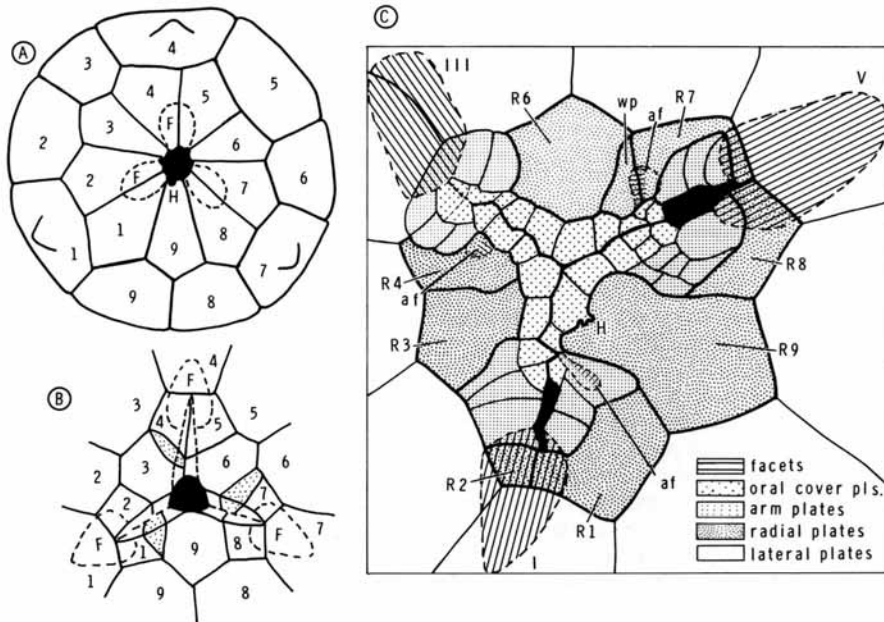
Symmetrical and asymmetrical pore-rhombs. Some of the rhombs show symmetrical arrangements of the pore-pairs, whereas others do not. In symmetrical rhombs the number of pore-pairs in each of the half rhombs is equal (text-fig. 7C), whereas in asymmetrical rhombs it is not (text-fig. 7D). In extreme cases there may be twice as many canals in one half rhomb as in the other. Analysing twenty-five specimens of *H. extraneus*, asymmetrical rhombs are found to be arranged as in text-fig. 7A. This pattern occurs without exceptions. In all cases where rhombs can be seen in other species they conform to this pattern. Asymmetrical rhombs of the lateral series are most typical in the lower part of L1, L3, L5, L7, and L8. L9 has both a symmetrical rhomb and an asymmetrical one. This may have something to do with the position of the anal opening. Plates L2, L4, and L6 all have asymmetrical rhombs. The pore distribution of the lateral series would of course be reflected in the upper half of the infra-lateral plates. In the basal series the two pentagonal plates have asymmetrical rhombs, whereas in B1 two asymmetrical and one symmetrical rhomb are present. In B4 all three rhombs are symmetrical. The distribution of the type of rhombs in the lower part of the ILL plates is naturally dependent upon the pattern of the basal plates (text-fig. 7A). The pores of the radial series are more complex because of the small space available for their development, but even here the limited available information suggests that a pattern following the preceding one exists in most species. The distribution of the symmetrical and asymmetrical rhombs seems to be constant within all species of *Hemicosmites*, probably including the type species *H. pyriformis*. In the holotype of this last species, however, there is some doubt because no pores have been traced in the radial plates. Whether the absence of such pores is typical of *H. pyriformis* cannot be ascertained at present, because no more material of the species has been found.

The pattern of rhomb distribution may be important for respiration, and seems to indicate that the highest respiratory potential of the animal was on the side opposite the anus, and involving the infra-lateral and lateral plates (respiratory systems 1 and 2). In general, asymmetrical rhombs have the higher number of pores along the longer sides of the inhalant half-rhombs. In the laterals this side is always along the vertical line of the plates (text-fig. 7A). The presence of asymmetrical rhombs would have led to different amounts of oxygen/carbon dioxide exchange in the two sides of the rhombs, causing respiratory gradients within the theca.

Most of the specimens studied have a fixed pattern of rhombs, with sieve-pores and simple pores arranged as in text-fig. 4B. In two cases, however, anomalies have been found, where the pores have different positions. In *H. extraneus* (RM Ec27604) the rhomb connecting IL5:IL6 (consisting of one canal only) has a sieve-pore where the simple pore should be present, and vice versa. In *H. sphaericus* sp. nov. (PMO A35441) the abnormal condition is found in rhomb L9:R9, where one canal has the pores reversed. This situation took place at some early ontogenetic stage, because pores formed later in that same rhomb continued to grow in a normal manner. These pathological conditions do not seem to have affected the

animal in any way, and these canals may have functioned like all other pores of that rhomb.

Plates of the oral area. The triangular mouth is situated at the summit of the theca and is bordered by nine radials (R1–R9). Between these, *wedge plates* are often intercalated, but their number varies (text-figs. 8, 9). The relationship between wedge plates of *Hemicosmites*, adoral accessory plates of *Thomacystis* (Paul 1969, p. 192), and the various accessory plates present in the Caryocrintidae (Frest 1975) is difficult to evaluate at present. However, the wedge plates are formed mostly by initial growth under the radial plates as wedges and they appear on the surface in (?)adult specimens. Wedge plates are found between radials 3 and 4 and between radials 6 and 7 in *H. papaveris* sp. nov.



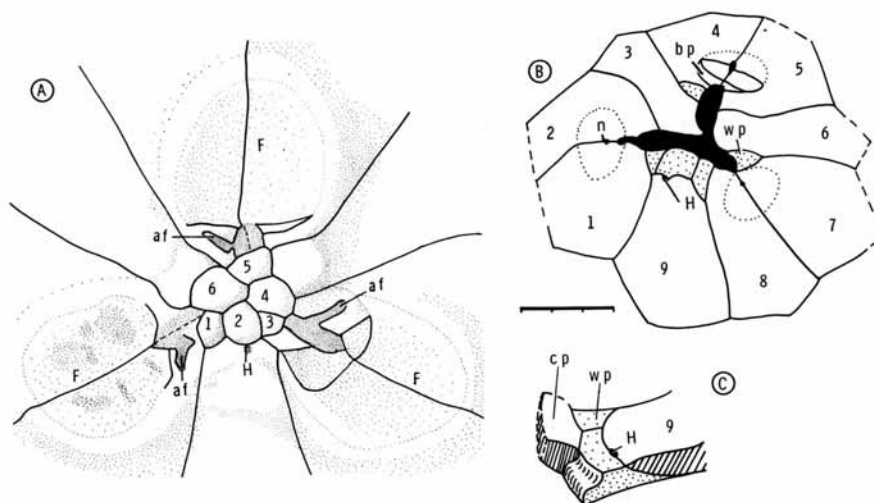
TEXT-FIG. 8. Oral area of *Hemicosmites*. A, positions of arm facets (F) in relation to lateral cirlet (lower cirlet) and radial cirlet (containing arm facets) of *H. extraneus*; oral plates omitted (black, centre). H—hydropore; N—nodes on lateral plates; B—oral area of *H. pyriformis*. Mouth (black centre) roughly triangular. Ambulacral furrows leading out to arm facets (F) ending on lateral cirlet. Three wedge plates (dotted) in radial cirlet. Specimen figured by Jaekel (1899, fig. 69). C, *H. pyriformis* (Holotype). Relationship between different plates of the oral area. Arm facets reaching down to lateral cirlet (white). Radial plates overgrown or incorporated in arm plates (R5 and R2 not exposed). R1, R8, R7, R6, R4 partly overgrown or incorporated in arm plates. Oral cover plates are biserially arranged, and this arrangement presumably continues on to the arms. Three accessory facets present adjacent to the arm facets, and arranged in an anti-clockwise manner. They may represent reproductive structures. I, III, V—radial; ap—arm plates; af—additional facet; H—hydropore; F1–9—radial plates; wp—wedge plate.

In some specimens of *H. papaveris* sp. nov. a wedge plate may be present between R9 and R1. Some or all the plates bordering the upper portion of R9 may also be wedge plates. In *H. papaveris* (PMO 94635) three plates occur along the upper border of R9, and they are all formed in the same way as the wedge plates, and may thus be comparable to these (text-fig. 9C). In this species important modifications of many of the plates of the oral area have taken place. Species stratigraphically older than *H. papaveris*, such as *H. extraneus* from the lower Caradoc, have only occasional wedge plates, which, when present, are very small. The slightly younger *H. sphaericus* sp. nov. (Caradoc) from Sweden has wedge plates clearly developed along the same sutures as *H. papaveris*. Thus wedge plates were present by Caradoc times. *Hemicosmites* with large wedge plates normally have larger oral areas than species with smaller such plates. In consequence, wedge plates may be important for increasing the size of the oral area relative to the theca. Many species show this, including the type species, *H. pyriformis* (text-fig. 8B, C). Jaekel (1899, fig. 69) figured these wedge plates (text-fig. 8B), but did not comment on them. The mouth of *Hemicosmites* was covered by a number of small, irregular plates, for which the name oral cover plates is appropriate. Extensive material of *H. papaveris* has shown that these cover plates are formed by growth at the upper surface of the radial plates or the wedge plates (text-fig. 9C). Cover plates are most probably homologous with the ambulacral covering plates. If homologous with the oral plates of other rhombiferan cystoids as suggested by Jaekel (1899), they were not homologous with the orals of glyptocystitids. The number of cover plates varies from one to ten, possibly more, and the sequence in which they are formed does not appear to be systematic. The correlation of such plates even in different individuals of the same population is difficult, let alone between species. In young specimens of *H. papaveris* only one plate may be present, covering the mouth; this may be equivalent to the central plate of *Caryocrinites*. In adult specimens of *H. papaveris* and *H. extraneus* alternating plates continue from the central plate towards the arm facets. They may well continue on to the arms as cover plates, possibly biserial, but in most specimens of different species the configuration is not simple. In the holotype of *H. pyriformis* (text-fig. 8C), the oral cover plates are developed in the same manner as ambulacral cover plates in rhombiferan cystoids such as the glyptocystitids, with a biserial arrangement continuing on to the arms. Even here, a few regularities occur (text-fig. 8C, Pl. 43, fig. 3). The variability of such plates among the species of *Hemicosmites* may indicate that from this genus may have developed the tegminal plates of *Caryocrinites*. To trace these evolutionary trends in detail would require well-preserved material, which is not currently available.

Hydropore. At the upper border of R9 a pore or a slit is always present. This pore is here interpreted as a hydropore, which is thus located on a straight line between the mouth and the anus, as in most other cystoids. The gonopore in various cystoids is generally found slightly offset to the left of this line.

Gonopore. No pore is present that could be identified as a gonopore, and for this reason the pore here identified as a hydropore is taken as a gonopore by some authors.

Just before the ambulacral furrows reach on to the large arm facets, anti-clockwise directed side branches occur; one branch to each of the three ambulacral furrows is present. The best examples are seen in the holotype of *H. pyriformis* (text-fig. 8C,



TEXT-FIG. 9. Oral areas of *Hemicosmites*. A, *H. extraneus* (Alliku, Estonia, Rõõmusoks Collection, 1975, no number (TE)). Note that no wedge plates are present and number and distribution of oral cover plates (1-6) is simple. Accessory facets (af) are also present; F—arm facets; h—hydropore. B, *H. papaveris* sp. nov. (PMO 94635) containing wedge plates (dotted) along sutural area of radial plates (1-9); ap—arm plate; H—hydropore; n—nerve canal. C, Growth of wedge plates from underneath the radials in contrast to oral cover plates with lateral growth (PMO 94635); H—hydropore at upper part of R9.

Pl. 43, fig. 3) and in one specimen of *H. extraneus* from Alliku, in Estonia (text-fig. 9, Pl. 43, fig. 12). The side branches are about 1 mm long and are slightly irregular. The branches end in a deep pit surrounded by an elevated facet-like structure, but no facets of the types generally associated with appendages occur. If appendages were directed from these facets, they would probably not consist of calcareous plate elements, but rather appear as soft papillate structures (text-fig. 3). Such accessory facets occur in specimens of all species that I have studied and they are all built in the same manner. It is difficult to decide, because of different states of preservation, whether such structures did occur on every single specimen. The fact that no gonopore has been found might indicate the nature of the accessory facets. Jaekel (1899, p. 301) suggested that these facets had 'Abhangsorgane' which might have served a different function from that of the arms, and he suggested that these 'arm rudiments' served some function in reproduction. I am inclined to agree with Jaekel in this. Accessory facets have been found in many specimens of different species. They may have been present early in ontogeny, because at least one specimen of *H. papaveris* sp. nov., with a thecal diameter of 6 mm, had these facets. Whether or not accessory facets are found in both sexes cannot be ascertained at present.

In recent crinoids it is well known that the gonads are located in the arms. In *Caryocrinites* (*Caryocrinitidae*) Frest (1975) described holes associated with arm facets and he pointed out that these might have borne small brachioles or pinnules

having a sensory function. It may be possible that the 'brachiole rudiments' served two functions, both sexual and sensory. In other cystoids, like *Eucystis* (Diploporita), respiratory pores are found arranged in a particular way around the mouth and basal portion of the ambulacra (Bockelie 1972) and in these animals the papillae covering the pores could perform a sensory function in addition to the primarily respiratory function. In a blastoid (*Pentremites rusticus*) Katz and Sprinkle (1976) described some of the respiratory structures as specialized to serve as brood pouches, besides functioning in normal respiration.

In most of the specimens studied the 'arm rudiments' are associated with the additional wedge plates of the oral area. In the holotype of *H. pyriformis* one of the accessory facets is located on one of the arm plates (text-fig. 8C).

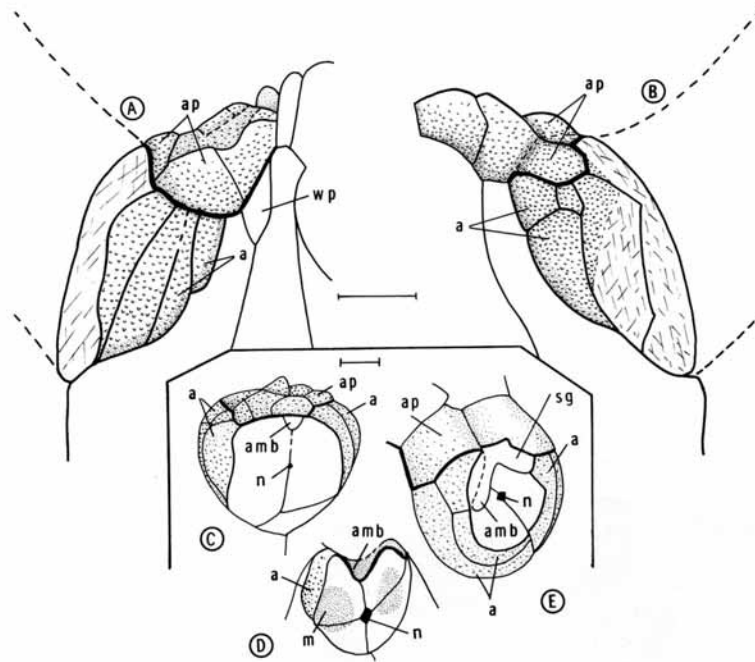
All recent echinoids and crinoids have separate sexes as far as is known, but it is often difficult to distinguish them morphologically, at least externally (Hyman 1955, p. 6). Sexual dimorphism may have been present in cystoids. In populations of *Hemicosmites* it is not unusual to find different types of thecal shape: flat-topped forms and forms with a dome-shaped oral area. This has been observed both in *H. papaveris* and in *H. variabilis*, and may be a sexual character.

Periproct. The periproctal opening is located on the side of the theca, about mid-height, and is surrounded by three plates, IL1, IL6, and L9 (text-fig. 4B). Jaekel (1899, p. 295), however, noted some anomalies in the position of the anal opening. In *H. malum* this opening was located along the IL1:IL6 suture, and thus slightly below the normal position. Jaekel did not mention whether this was found in one specimen only, or if it really is typical for primitive species as he suggested. One additional specimen of *H. malum* (B.M. (N.H.) 29094) has also been found with have the anal opening in this position. In one specimen of *H. pyriformis* (see Jaekel 1899, pl. 19, fig. 4) the anal opening occurs in the 'Caryocrinites' position, i.e. at the upper border of L9 (Jaekel 1899, p. 296). To my knowledge, in all other specimens of known species the anal opening occurs where IL1, IL6, and L9 meet. This anomaly may well indicate the close relationship between Hemicosmitidae and Caryocrinitidae, and the trends of evolution.

The anal opening was covered by a pyramid of five, or occasionally four, triangular plates (text-fig. 21C, D). These plates were moveable, and could open to let out faecal matter, probably in the form of pellets.

Subvective system. Most cystoids lose their subvective appendages very soon after death. However, in a few specimens of *Hemicosmites extraneus* and *H. papaveris*, as well as in the holotype of *H. pyriformis*, remains of the basal portions of such appendages are preserved. *Hemicosmites* possessed biserial appendages (arms) with alternating sizes of brachiolar plates (text-figs. 3, 8C). In cross section a U-shaped food groove is present, similar to that seen in *Caryocrinites* (Sprinkle 1975, fig. 1d). Immediately below the food groove an additional canal, probably representing one of the aboral radial nerve canals(?) is present (text-fig. 10C, D). Because only the basal portions of the arms are preserved, it is difficult to compare these plates of *Hemicosmites* with the arms of *Caryocrinites* as described by Sprinkle (1975). One specimen of *Caryocrinites* (text-fig. 10E; Pl. 43, fig. 2) has a basal portion of the arms that

resembles *Hemicosmites* (text-fig. 10c; Pl. 43, fig. 1), but both genera seem to be variable (text-fig. 8c). The arms were attached to the facets formed at the sutures of two adjacent radial plates; occasionally an adjacent lateral plate may be incorporated, in which case three plates meet in the facetal area. In the holotype of *H. pyriformis* the major portion of the facet is on the lateral plates and either one or two laterals are incorporated in the facetal area in addition to the distal portion of the adjacent radial plates (text-fig. 8c). This type of facet is considered to be a highly evolved stage for *Hemicosmites*.

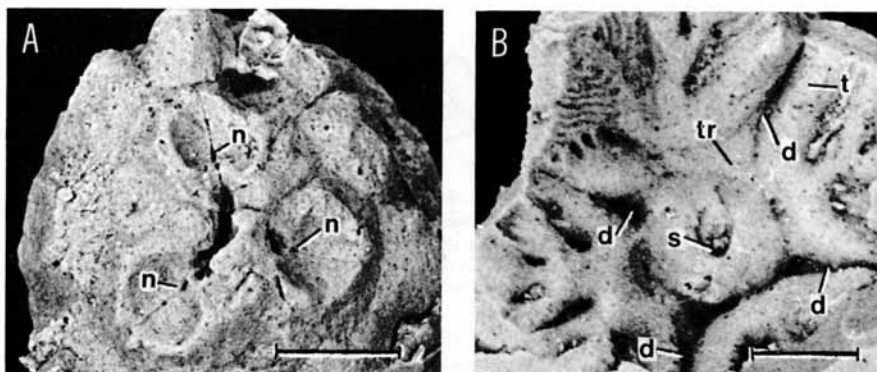


TEXT-FIG. 10. Arm facets and arm plates of *Hemicosmites* (A-D) and *Caryocrinites* (E). A, B, view of both sides of an arm of *H. extraneus* (RM Ec5283); C, frontal view of arm of *H. extraneus* (RM Ec5283); D, frontal view of arm of *H. papaveris* sp. nov. (PMO 94635); E, arm of *Caryocrinites ornatus* (PMO A21227). a—brachial element; amb—ambulacral furrow; ap—arm cover plate; n—nerve canal; wp—wedge plate. Scale bars indicate 1 mm.

The outer limits of the arm facets are somewhat irregular and several arm plates form the proximal portions. In the oldest species, like *H. extraneus*, a fairly clear distinction can be made between arm plates and oral cover plates (text-fig. 10A, B). Five arm plates are preserved on either side of the arm in RM Ec5283 (text-fig. 10A, B; Pl. 43, fig. 1). The plates on either side may vary considerably in shape and size. The oral cover plates continue on to the arms where they are gradually reduced in size as they change into arm cover plates. However, no clear distinction can be made as

to where the oral cover plates are transformed into arm cover plates. Arm cover plates may be biserial, but certain irregularities have been found both in *H. extraneus* and *H. papaveris*. Problems in detecting sutures between such cover plates because of their small size and abrasion may account for these irregularities. In *H. pyriformis* the distinction between arm plates, radial plates, and wedge plates may be difficult to establish. In the holotype some arm plates are incorporated in the oral portion and cover some of the radial plates (i.e. R5 and the greater part of R2). The shapes of the arm plates may vary considerably from one arm to the other in the basal portions (text-fig. 8c). The arm cover plates, however, are arranged biserially outwards on to the arms (text-fig. 8c). In this respect the arms of this species resemble those of other cystoids, e.g. *Echinospaerites* (work in preparation). Whereas the oral cover plates were more irregularly distributed in the other *Hemicosmites* species, they show a distinctive orderly distribution in *H. pyriformis*. When present as oral cover plates, they have an irregular ornament, but become smoother when entering the arms. Arm types found in *Caryocrinites* (Sprinkle 1975) may be similar to those of *Hemicosmites*, since these two genera have many other features in common. One specimen of *H. extraneus* (RM Ec5283) with the basal portion of the arm preserved may have a facet for a pinnule preserved just where the arm plates become free from the facet (text-fig. 10c; Pl. 43, fig. 1). The structure is not well preserved, but if this really is a facet for a pinnule it may further strengthen the hypothesis of a close relationship between *Hemicosmites* and *Caryocrinites*, even with regard to the arm structures.

Nerve system. In contrast to crinoids, cystoids show no traces of nerve canals on the inner side of the thecal plates. For this reason very little is known about the nerve system of cystoids. In *Hemicosmites* and a few other cystoids nerve canals have been found leading out into the arms. Only three radial nerves off a presumed oral nerve ring were present in *Hemicosmites* leading to the arms (text-fig. 11A). A basal nerve



TEXT-FIG. 11. Nerve system of *Hemicosmites*. A, nerve canals (n) leading off the oral nerve ring into the arms in *H. papaveris* sp. nov. (PMO 94644). B, interior of the basal portion of the theca of *H. variabilis* sp. nov. (PMO 97096). d—depressions in sutural area, three of which continue somewhat upwards, one being closed; s—hollows for presumed nerve canal leading into stem interior; t—thickened portion of basal plate, also in the other plates; tr—triangular space where basal nerve ring may have been situated.

ring giving off branches to the stem was probably also present in *Hemicosmites*. One specimen of *H. variabilis* (text-fig. 11B; Pl. 42, fig. 3) shows the interior of the basal portion. The basal plates are thickened internally; and these areas (t) approach each other at the plate sutures, leaving three open and one closed depression along the plate sutures (d). In the base the depressions form triangular spaces (tr). In addition other minor depressions occur in the basal portion of the basal plates. Consequently several depressions exist along the inner side of the basal portion of the theca, where an aboral nerve ring could have been present. A hollow centre of the basal portion could have contained nerve canals leading down into the stem(s). According to Sprinkle (1975) no traces of the aboral nerve system seem to continue into the arms of *Caryocrinites*. On the basis of current information it cannot be decided if this holds for *Hemicosmites*. An aboral nerve ring also seems to be present in the sessile diploporitic cystoid *Haplophaeronis* (Sphaeronitidae) from Norway (work in preparation).

Stem and attachment. In some specimens of *H. papaveris* parts of the proximal portion of the stem are found. It is set in a socket, reaching about 1 mm into the base of the theca. The lumen of the columnals (Moore *et al.* 1968) is circular, its radius about one-third that of the columnal. The circular individual columnal has numerous, simple crenulae and a faint crenulate suture.

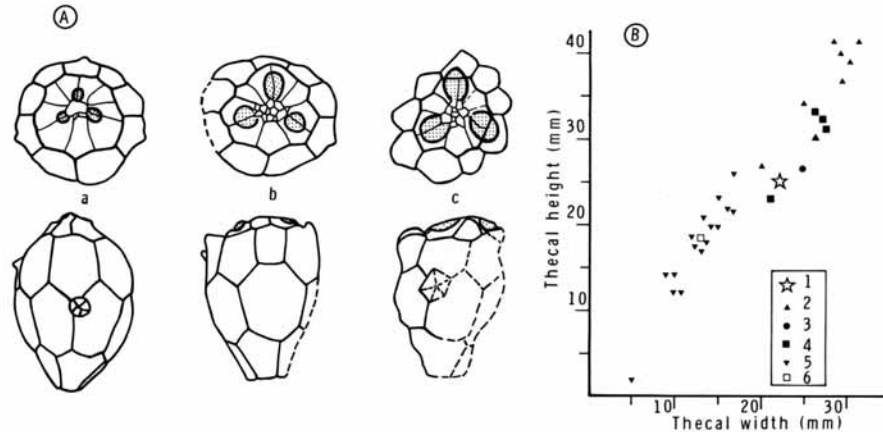
In *H. papaveris* no differentiation of the nodals has been seen, whereas in *H. extraneus* (RM Ec5280) the noditaxis (series of one nodal and all the corresponding internodals; see Moore *et al.* 1968) may contain three internodals. In a specimen of *Caryocrinites* sp. (PMO A21227) the noditaxis may be similar to that of *H. extraneus*. *H. porosus* (Hecker 1964, pl. 2, fig. 9) may have a xenomorphic stem (e.g. the proximal and distal columnals are quite different). So far no other species with such a long stem has been found, for which reason it can only be assumed that there is a possible xenomorphic structure of the stem in other *Hemicosmites* species (text-fig. 3).

As yet neither the root structures nor attachment plates are known, and there are no indications of what the distal portion of the stem looked like. Since *Hemicosmites* always seems to be present within or around carbonate mud mounds and bioherms, where other echinoderms have been found attached, it can be assumed that *Hemicosmites* species were provided with root structures similar to that of *Caryocrinites*. At the locality at which *H. papaveris* is most common, root structures are very common, but it is not known if these roots are related to *Hemicosmites* or to crinoids. No attachment discs are known from localities in the Oslo Region or Sweden where *Hemicosmites* occur, whereas root structures are present. It is thus assumed that root structures may be present in *Hemicosmites* (text-fig. 3).

Growth. The life-span of *Hemicosmites* is unknown, but it has been suggested that other cystoids could live for 3–4 years (Paul 1967). During growth certain changes and modifications of the theca and the thecal structures take place. Some of these changes are of minor importance, whereas others may be important or even critical for the animal. The most important features are related to the respiratory pores and the oral area. The distinction of which observed features are due to ontogenetic changes and which merely fall into the natural variation of the population at different stages of development, can only be made on the basis of large collections illustrating different growth stages in the same population (Bockelie 1978). As the animal grew

some new features were added (e.g. pores) and some could become modified by resorption. Several growth stages, however, are perceivable on *individual specimens*, because growth stages can be incorporated in the structures of the adult. Such features may pertain to growth lines of thecal plates (Breimer and Macurda 1972) and to the pore system.

The ratio of thecal height to width of *H. papaveris* changes very little; thus the shape is almost constant, irrespective of the animal's age (text-fig 12B). In *H. variabilis* on the other hand, the large spines of the lateral plates are most obvious in young individuals (Pl. 41, fig. 11), but less so in adults.

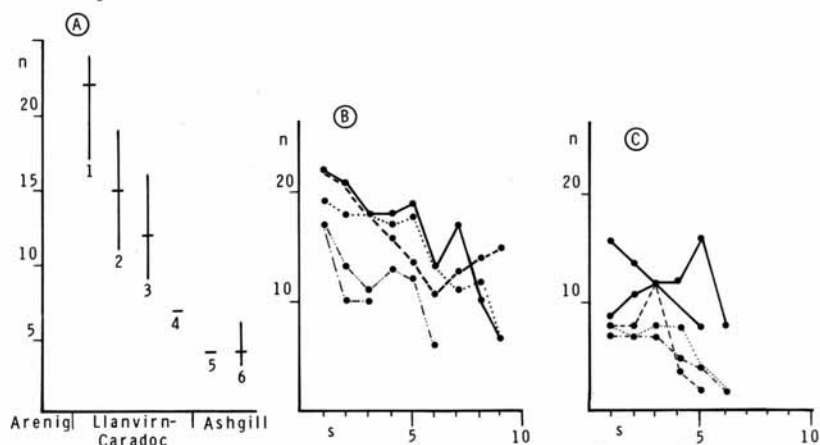


TEXT-FIG. 12. A, phylogenetic trends in the oral area of *Hemicosmites*. Changes of shape and size of arm facets with time; (a) *H. extraneus* (RM Ec2760); (b) *H. papaveris* sp. nov.; and (c) *H. variabilis* sp. nov. Upper row in oral view, lower row in lateral view. Note the change from spindle shape to irregular poppy-head shape (a-c). *H. papaveris* (holotype, PMO 94644) is shown in different lateral position than the other two, because the periproctal area of this species is not preserved. B, thecal height/width ratios in different *Hemicosmites* species shows almost no change with time (species 2-6). 1—*H. pyriformis* (type of genus); 2—*H. extraneus*; 3—*H. oelandicus*; 4—*H. sphaericus* sp. nov.; 5—*H. papaveris* sp. nov.; 6—*H. sculptus* sp. nov.

Growth of rhombs. The rhombs expand in size during life by addition of new dichopores. As a result the record of ontogenetic development may be retained in the skeleton, even though parts of individual dichopores may change somewhat by resorption to fulfil functional requirements as the animal grew. The simple pores of a pore-rhomb seem to have the same diameter and general appearance whether formed at an early or late stage. The number of holes in individual sieve-pores on the other hand may show significant differences. There is a tendency towards fewer numbers of such holes in sieve-pores close to the plate sutures (text-fig. 13B). The greatest differences relate to sieve-pores of the lateral plates. In a specimen of *Hemicosmites rudis* the sieve-pores contain symmetrically arranged, slightly elongated pores. In the first formed sieve-pores seven to eight holes are present, whereas in the last formed, closest to the plate suture, only two holes were observed (text-fig. 13C).

Similarly 9–16 pores occur in the first formed sieve-pores of *H. pyriformis* and only 4–8 in the last formed (text-fig. 13c). The number of holes in sieve-pores of the basal plates is not well known because of the poor preservation of many specimens, but in general fewer pores are present than elsewhere in the theca. In most cases, smaller examples of *H. extraneus* have fewer holes per sieve-pore than larger specimens. This implies that the number of holes in a sieve-pore increases with growth in this species. This would explain why the largest number of pores per sieve-pore occurs in the central, oldest parts of the LL plates, and also why aggregated pores are found in the oldest-formed dichopores of the LL plates.

Pore-rhombs of the thecal plates do not normally reach the plate centre, which means that in the earliest ontogenetic stages the cystoids may have had direct O_2/CO_2 exchange through the thin skeletal plates. Infra-lateral and lateral plates of *Hemicosmites* have rhombs, some of which reach closer to the plate centre than others of the same plate. This means that some rhombs were formed at an early ontogenetic stage, and some later during ontogeny. The *major rhomb system* comprises the vertical systems 1, 2, and 3. The *horizontal system* 4 and 5 came into operation later in ontogeny. It would be advantageous for a cystoid that relied on diffusion to distribute oxygen internally to have as many rhombs as possible equally distributed over the thecal surface. All points inside the theca would then be equidistant from the oxygen source. With growth of the theca larger areas without rhombs may have developed adjacent to the intercirclet sutures, and rhombs of systems 4 and 5 were then developed here.



TEXT-FIG. 13. Pores of *Hemicosmites* species. A, trend towards reduction in the number of holes in sieve-pores throughout the Ordovician. 1—*H. extraneus*; 2—*H. sphaericus* sp. nov.; 3—*H. pyriformis*; 4—*H. papaveris* sp. nov.; 5—*H. variabilis* sp. nov.; 6—*H. sculptus* sp. nov. Mean value (horizontal line) and total range of observations. n—number of holes in sieve-pores. B, number of holes in individual sieve-pores in L9 of five specimens of *H. extraneus*. n—number of pore holes; s—order of sieve-pore formation. C, same in laterals of *H. pyriformis* (solid lines), and *H. rudis* (various types of broken lines). Note that all the last formed sieve-pores (end of connected lines) always have fewer pores than earlier formed sieve-pores.

Plates of the oral area. As mentioned above there is an increase in the number of oral cover plates with increasing size of the animal, but the sequence in which these plates were formed is not known in detail. Wedge plates may occur early in ontogeny, and seem to be associated with the facets of the sexual structures, and this may indicate that additional facets were formed after the major parts of the theca were in operation.

PHYLOGENY OF *HEMICOSMITES* AND RELATION TO OTHER GENERA

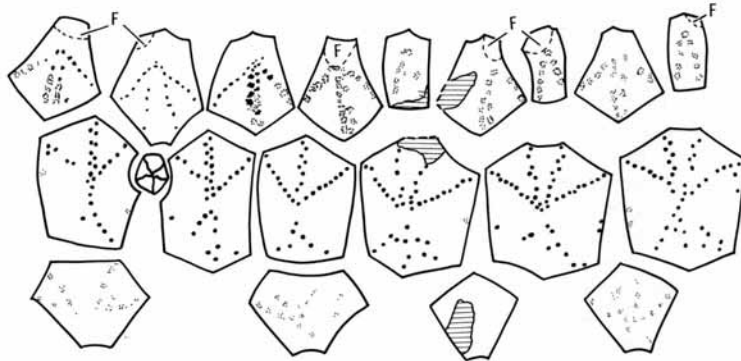
Several features of *Hemicosmites* show systematic changes with time, such as reduction in the number of pore holes in sieve-pores (text-fig. 13A). The size of the individual holes increased during the Ordovician, and seems to correspond with an increase of mean size of sediment particles in the *Hemicosmites*-dominated environments. Better material is needed for detailed measurements to calculate the dependencies. A reduction of the pore systems during the Ordovician can also be observed. Not only does the number of dichopore canals become reduced in number, but some of the rhomb systems (text-fig. 7) show marked reductions. However, more material is needed to distinguish ontogenetic changes from the phyletic ones, particularly because most of the Upper Ordovician species are smaller than those in the Middle Ordovician. In *Hemicosmites* it is possible to distinguish between 'early' and 'late' forms. *H. extraneus* appearing in the lower Caradoc has arm facets concentrated in a small area at the thecal summit (text-fig. 12A). During the Middle and Upper Ordovician the facets migrated outwards from the summit and the species changed their shapes from spindle to poppy-head types (text-fig. 12A). The changes can best be studied in the radial plates which alter from being long and narrow to short and broad. In addition, wedge plates expand in the same manner. The expansion of the wedge plates is probably a consequence of the enlargement of the size of the oral surface.

With changes of thecal shape the arm facets gradually increased in size relative to the thecal diameter. In later species like *H. papaveris* and *H. sculptus* the facets may be in contact with, and even incorporate, the upper part of the laterals. The most extreme situation is reached in *H. pyriformis* (age unknown) where the arm facets occupy the greater part of the lateral plates (text-fig. 8C). The radial plates are here reduced even more than in other *Hemicosmites* species.

These changes as outlined above are stages in a phyletic trend that, if continued, would lead to a *Caryocrinites* organization. A further reduction of the radial plates involves the facets migrating further outwards from the mouth. Also, an increase occurs in the number of oral cover plates organized in the manner found in *H. papaveris*, among others, with a central plate (text-fig. 20A). The addition of wedge plates is also an indication of the same phyletic trend. The only other difference between representatives of the two families involves the position of the periproct, which in *Caryocrinites* is located at the upper border of a lateral plate. Phylogenetically this could be achieved by an orally directed migration of the periproct, as suggested by Jaekel (1899). One specimen of *H. pyriformis*, characterized as 'kümmerliches Exemplar', was recognized by Jaekel to have the periproct in a '*Caryocrinites* position' (Jaekel 1899, pl. 18, fig. 4). This highly abnormal situation shows that these two representatives of two different families may be closely related. Most known species

of *Caryocrinites* have numerous arm facets, but several species of this genus are known with only three facets, as in *Hemicosmites*, e.g. *Caryocrinites sphaeroidalis* (Miller and Gurley), *C. stellatus*, and *C. tribrachiatus* Frest (see Frest 1975). The only constant difference between representatives of the two families is the number of thecal plates. Both families are characterized by an equal number of basals and infralaterals of the same type. In *Hemicosmites* species nine laterals are normal, but up to eleven such plates are present in anomalous specimens. Jaekel (1899, p. 295) noted that the IL plates around the periproct, i.e. IL1, IL6, and IL5, are smaller than IL2, IL3, and IL4. Jaekel stated that the width of the IL plates increased in *Hemicosmites* during Ordovician time. He further suggested that this would lead to a gradual reduction in size of L6, and this can be seen on available material. He then predicted that a total reduction of L6 might have taken place. Such a reduction would lead to a *Caryocrinites* organization.

I regard the phyletic changes in *Hemicosmites* as indicative of the gradual transformation of morphological structures from those found in Hemicosmitidae to those of the Caryocrinitidae. This and the fact that Upper Ordovician species of *Caryocrinites* occur in Sweden (*C. septentrionalis* Regnéll 1945), and in Estonia during the lower Silurian (*C. ornatus*; F. Schmidt 1858, p. 221; Regnéll 1948b, p. 35), I take as reasonable grounds to suggest that *Caryocrinites* is a descendent of *Hemicosmites*. Other representatives of the two families are not known in sufficient detail to indicate phyletic trends, but the variability in morphology of some *Hemicosmites* species indicates that this genus could have given rise to other genera of Caryocrinitidae. The latter family had a greater number of successful representatives than the Hemicosmitidae, and this may be related to the construction and number of arms that occur in some of the Caryocrinitid genera.



TEXT-FIG. 14. *H. pyriformis* von Buch. Plate arrangement and thecal pores as observed on the holotype. Note that the arm facets reach well down on to the LL-plates. No pores are found on the radials (cf. text-fig. 8c). F—arm facets; ruled lines indicate parts not exposed. Distribution of pores gives minimum information. More pores may be present but have not been observed. Thick dots in some laterals indicate strong abrasion of that part of the thecal surface. All pores in lateral series are sieve-pores.

SUMMARY AND CONCLUSIONS

This study covers only a limited portion of the existing material of *Hemicosmites* species. Altogether about 100 specimens have been studied, belonging to seven or eight species, of which by far the most belong to *H. extraneus* and *H. papaveris*. Many of the observations may be relevant for all species of the genus, but when considering species variation and the diversity of recent faunas it is not possible to judge whether all the observations are typical for all species. The remaining species are being studied in Moscow by Professor Hecker, and this will add valuable information to complete the picture of this genus. It seems likely, however, that the genus as a whole was limited to the Baltic Basin, that it occurred exclusively in Middle and Upper Ordovician shallow-water environments, and that no more than about twenty species existed. In fact there is a possibility that some of the existing species may be regarded as synonyms when studied in detail.

The degree of variability within the described species has shown the importance of using as large collections as possible for taxonomic discrimination. This applies particularly to *H. variabilis* which, if single specimens had been found at different localities, would easily have ranked as at least two, possibly three species. Other species, such as *H. extraneus*, seem remarkably constant, though some variation does exist. The variation in number of thecal plates in each of the plate series has made it necessary to regard the plate numbering as only a convenient way of grouping them, and suggests that any attempt to compare individual plates of *Hemicosmites* with those of other genera of other families may, at present, be pure speculation.

The distribution and function of the thecal pores seem to be important for the animal, as in other cystoids. In fact, all cystoids studied in detail have specialized thecal pores that underwent modifications during their evolutionary history (text-fig. 13A). *Hemicosmites*, with its typical endothecal pore system, is only one lineage of experiments in respiratory specialization. From the available material the formation and distribution of the pore system over the theca of various species can be recognized. Five different patterns of pore-rhomb distributions exist, and it is possible to see these structures in terms of function and the utilization of current patterns around the theca to carry waste water away (text-fig. 7). Because of poor preservation, this study has not incorporated specimens with abnormal plate distribution. Such studies, however, may be important for understanding details of pore function.

Important ontogenetic and phyletic changes are found in the formation of intercalated plates, such as wedge plates, and the number and distribution of oral cover plates. The sequence of formation of these plates, and their correlation with tegmental plates of *Caryocrinites* or even other genera of other families in the same superfamily, are obscure. Nevertheless, during the Ordovician an increase in both size and number of such plates enlarged the oral area. This may have been effected by the increased size of the arm facets. Larger facets may indicate longer arms. The facets, and therefore the anus, also came to be situated further apart and together all these changes may have increased the efficiency of food collecting. Specialization of the thecal pores and the evolution of the arms (of which we have only indirect evidence) seem to be the most important evolutionary changes.

The locations of gonopore and hydropore have often been disputed, since in fact

no typical gonopore is present in *Hemicosmites*. There were accessory furrows adjacent to, and connected with, the ambulacral furrows. As Jaekel suggested, these may have borne papillate structures that could have contained gonads and themselves have been sexual structures. It may be argued that such structures could even serve more than one function.

The subvective system appears to be very similar to that of *Caryocrinites*, and this, together with other morphological features that are manifest both ontogenetically and phylogenetically, has led to the suggestion that *Caryocrinites* is a descendent of *Hemicosmites*, even though they are placed in two different families (Caryocrinitidae/Hemicosmitidae).

SYSTEMATIC PALAEOLOGY

Superfamily HEMICOSMITIDA Jaekel, 1918

Diagnosis. Theca composed of circlets of plates with three or four BB, six to ten ILL, eight or more LL and a variable number of RR plates. Rhombs with inner side of strongly folded delicate laminae perpendicular to suture, each pore usually terminating in a simple pore at one end and a sieve-pore at the other. Lower Ordovician–Lower Devonian.

Remarks. The diagnosis is emended to take account of *Thomacystis* Paul (1969) in the Thomacystidae. At present four families are assigned to the Hemicosmitida, i.e. Hemicosmitidae, Caryocrinitidae, Thomacystidae, and Heterocystitidae. However, the latter may be a crinoid (Paul 1969, p. 191). Similarities between *Caryocrinites* and *Hemicosmites* may be due to a closer relationship than recognized by some authors, but differences are sufficiently clear to separate them into two families.

Family HEMICOSMITIDAE Jaekel, 1918

Diagnosis. Family of the Hemicosmitida with four BB, six ILL, eight or nine LL, and a circlet of nine RR plates. Variable number of oral cover plates and inserted plates in the oral area. Facets few, one in each of the three radii, or occasionally two in each radius. Periproct lateral, never above LL.

Remarks. At present three genera can be included within the family: *Hemicosmites* von Buch, 1840, *Tricosmites* Jaekel, 1918, and *Oocystis* Dreyfuss, 1939. *Oocystis* has a plate arrangement similar to that of *Hemicosmites*, containing 4BB, 6ILL, 8LL, and 'a set of small plates present above LL' (Kesling 1967, p. S225; = radials). The oral surface of *Oocystis* is not known in detail. Its systematic position should thus be left open at present. *Tricosmites* has a periproct in the same position as in *Hemicosmites*; other features also suggest closeness to *Hemicosmites*.

Corylocrinus von Koenen, 1886, formerly assigned to the Hemicosmitidae, cannot now be placed there because it lacks radial plates. The variable number of plates in the oral area puts this genus closer to *Caryocrinites* than to *Hemicosmites*, though it is very much in an intermediate position. Unfortunately, no material of *Oocystis*, *Tricosmites*, and *Corylocrinus* has been available for this study. For *Corylocrinus*, however, important diagrams have been presented by Renard (1968).

Genus HEMICOSMITES von Buch, 1840

Type species. Hemicosmites pyriformis von Buch, 1840.

Synonyms. Hexalacystis Haeckel, 1896 (Type: *Hemicosmites verrucosus* Eichwald, 1856). See also Jaekel 1899, p. 307.

Diagnosis. A genus of Hemicosmitidae with four BB, six ILL, nine LL, and nine RR. Oral area with variable number of cover plates and inserted plates. Periproct situated at the border of IL1:IL6 and L9, except in one species, where it is along the suture IL1:IL6. Hydropore present at upper part of R9. Three short ambulacral grooves, ending in large facets at approximately 120° intervals, each facet generally shared by two RR and two RR and one L plate. One R without facets between each pair of facet-bearing RR. With or without wedge plates.

Remarks. A gonopore has not been found on the theca. Jaekel (1899, p. 308) noted the presence of 'additional brachiole facets'. Such structures have been found in some specimens of different species, anticlockwise to the larger facets, and with ambulacral furrows branching and leading to them. The minor facets are small and have no real facet area. They may have been supports for structures containing gonads (see p. 377). The hydropore is located in the upper part of R9 and may be an irregular hole or slit, surrounded by complex knobs, folds, etc. These give a rugose pattern to that part of the plate, and often obscure the pore hole. The basal portion of the holotype of *H. extraneus* has an additional plate between the BB and ILL series (bordering B1:B4:IL6:IL5). This must be regarded as abnormal and is not apparent in any other material available to me. One specimen of *H. papaveris* has ten LL plates, and this is also abnormal.

Jaekel (1899) distinguished three groups of *Hemicosmites* species. Group A, which includes the type species, has a globular theca with nodes and facets reaching down on to three laterals. Group B, including *H. extraneus* and *H. sphaericus*, contains species with oval to pyriform thecae with facets adjacent to the mouth, not reaching to the laterals, and nodes on three or all laterals. The third group has cup-shaped thecae, flattened above the strong, but not always equally developed nodes on the laterals (Jaekel 1899, p. 310). *H. papaveris* can be assigned to the latter group, although some specimens also seem to belong to group A in that the facets extend far down on to the laterals. Whether Jaekel's grouping reflects differences sufficiently great to erect new taxa cannot be established at present.

Details of the type specimens of the species described below are given on p. 365.

Hemicosmites pyriformis von Buch, 1840

Plate 43, figs. 3-5; text-figs. 8c, 14, 15

- 1840 *Hemicosmites pyriformis* von Buch, p. 59, pl. 1, figs. 1-3, 6-8, 11, 13.
 1844 *Hemicosmites pyriformis* von Buch; von Buch, p. 108, pl. 1, figs. 11, 12.
 1899 *Hemicosmites pyriformis* von Buch; Jaekel, p. 97, pl. 17, fig. 6.
 1943 *Hemicosmites pyriformis* von Buch; Bassler and Moody, p. 166.
 1945 *Hemicosmites pyriformis* von Buch; Regnéll, pp. 98, 100.
 1967 *Hemicosmites pyriformis* von Buch; Kesling, p. S219, fig. 120, 1a-b.

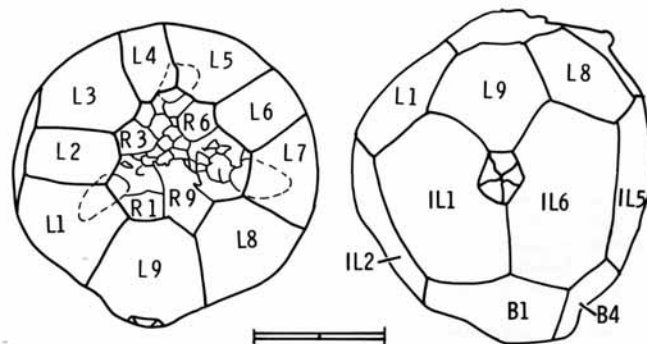
Diagnosis. *Hemicosmites* with smooth globular theca, at least one wedge plate, facets below thecal summit, system 4 somewhat reduced, systems 3 and 5 not present. Holes in sieve-pores radially arranged, numerous; all thecal plates short, no knobs present.

Material. One specimen, the holotype, has been seen for this study. Jaekel (1899, fig. 69) also figured another specimen and there is one specimen in the B.M.(N.H.) London labelled *H. pyriformis*, but it is probably misidentified.

Description. Thecal outline globular. Mouth situated on the summit of the theca and present above three facets of unequal construction. The hydropore is present at the upper left margin of R9 (text-figs. 8c, 15). The circular anal opening, lacking a surrounding rim, has five movable triangular plates covering the anus. A stem was present in life. Thecal height/width ratio is 1.09 (text-fig. 12b). One wedge plate is present between R6 and R7. Plate thickness about 1 mm. Basals of moderate size (height/width ratio 0.9), infra-laterals of moderate length (h/w ratio 1.2) and laterals long (h/w ratio 1.5). Three laterals have a rectangular shape. The plate surface is almost smooth. Simple pores have a tube, less prominent than in *H. extraneus*. No umbones are present on the laterals. Rhombs of system 4 are almost completely reduced, and of systems 3 and 5 completely reduced (text-fig. 14). Complete rhombs occur across all the intercirclet sutures. In the basals sieve-pores have mostly four, but occasionally up to eight, pore holes. Due to abrasion of the surface these pores are not well preserved (text-fig. 13c). Sieve-pores are present in small depressions which rarely coalesce, and individual pores lack rims. The pores are mostly elongated, often radially arranged. Simple pores are not connected by rims, but occur as single cylinders. Pore diameter is about 0.20–0.21 mm. No LL:RR rhombs are present.

The mouth, situated at the thecal summit, was completely covered in life with plates associated with the ambulacra. These strongly ornamented cover plates continue on to the arms (text-fig. 8c; Pl. 43, fig. 3) in a similar fashion to that of *Lovencystis* Regn ell, 1945 and *Echinosphaerites* (Bockelie, work in preparation). A series of smooth biserially arranged arm plates (text-fig. 8c) grew from the contact between the radials and the oral cover plates. Their shapes and sizes are variable. On the holotype the plates forming the arm in radius I have covered R2 almost completely on their left side, thus being in contact with L2 (text-fig. 8c). Arm plates of radius III cover R5 completely. Arm plates of radius V have an arrangement more typical of other *Hemicosmites* species.

Arm facets are tongue-shaped and reach well down on the laterals. In radius I four plates are incorporated in the facet: R1, R2, L1, and L2; in radius III R4 (part of this plate is reduced or not exposed), parts of R6 (remaining covered by arm plates), L4 and L5 (R5 is not exposed and may be reduced). In radius V parts of R7, R8, and L7 are incorporated in the facet (text-figs. 8c, 15).



TEXT-FIG. 15. *H. pyriformis* von Buch. Holotype in oral and lateral view. Terminology as in text-fig. 3. Note that arm facets reach on to laterals. Radials reduced or assimilated. Oral cover plates numerous. Scale bar = 1 mm.

Remarks. *H. pyriformis* differs from all other known *Hemicosmites* species in the construction of the oral area. No other species has such strongly developed arm plates, nor shows such a degree of reduction of radial plates. There are no LL:RR rhombs in the type. Whether this is constant in the species is not known at present. Although known only from one specimen, *H. pyriformis* may differ sufficiently from all other species generally referred to *Hemicosmites* to necessitate the eventual erection of a new genus for these species. However, I consider that more material of *H. pyriformis* is needed to verify whether the differences as outlined above are constant before making such a split at the generic level. At present this cannot be safely established; in fact, the type specimen of *H. pyriformis* may be simply an aberrant specimen. A specimen referred to as *H. pyriformis* in the collections at the British Museum (Natural History; E7592) does not have the same features as the type specimen, but instead the facets lie closer to the mouth and do not appear below the radials, which also have pores. Of other specimens also referred to *H. pyriformis* in the same collection, E29094 may belong to *H. malum*. A further specimen, (E29093), strongly abraded, bears holes or depressions caused by an organism that at some stage sat on the thecal surface in the basal portion. These depressions are similar to those found in *H. malum* in other collections.

Hemicosmites sphaericus sp. nov.

Plate 41, figs. 2, 4, 6; text-figs. 6B, 15, 16

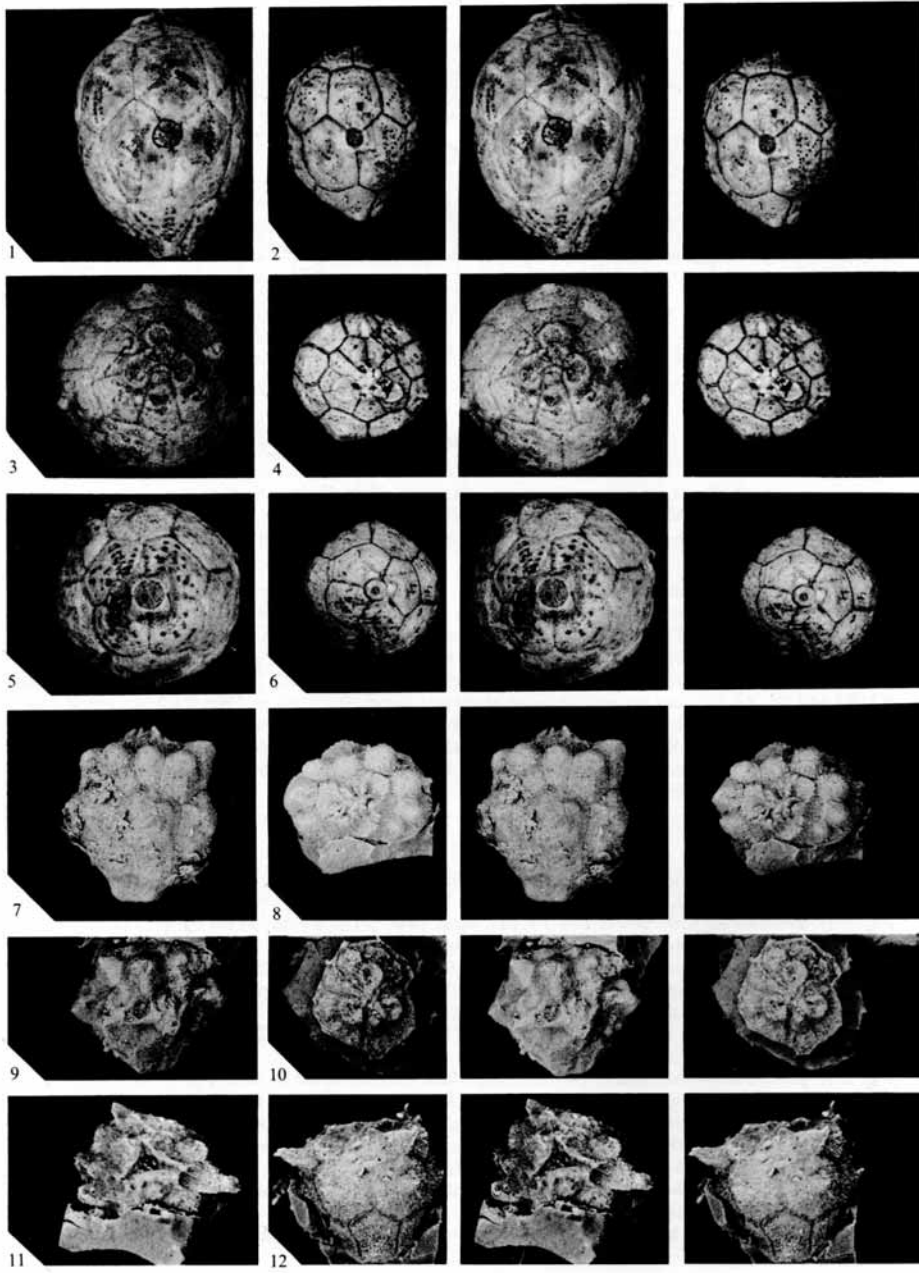
- 1936 *Hemicosmites* sp.; Thorslund, p. 26.
 1945 *Hemicosmites extraneus*; Regnéll (*non* Eichwald 1860), p. 100, pl. 3, figs. 13-14.
 1948 *Hemicosmites extraneus*; Regnéll (*non* Eichwald 1860), pp. 30-31.
 1968 *Hemicosmites* sp. nov.; Paul, p. 729, pl. 138, fig. 1.

Diagnosis. *Hemicosmites* with variable thecal shape; mostly spherical; smooth surface; wedge plates developed; facets just below thecal summit; slight reduction of horizontal system 4; holes in sieve-pores radially arranged; all plates relatively short; knobs not normally present.

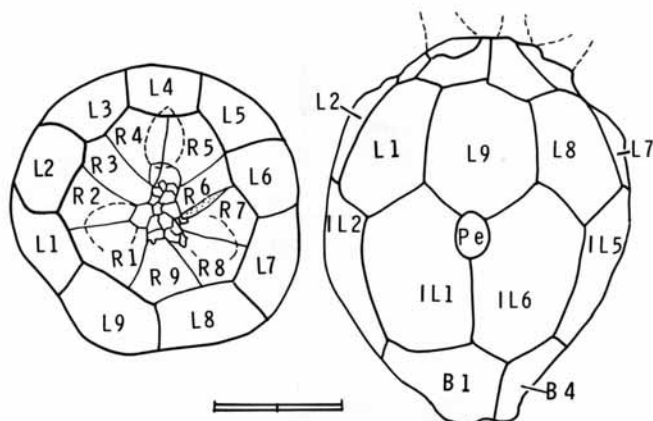
Material. Fourteen more or less complete specimens and several isolated plates in RM, UM, and PMO collections, from Kullberg Limestone, flank facies (upper Llandeilo-lower Caradoc), Kullberg Quarry, Kullberg, Dalarna, Sweden.

EXPLANATION OF PLATE 41

- Figs. 1, 3, 5. Stereophotograph of *Hemicosmites extraneus* Eichwald, RM Ec27604, lateral, oral, and basal views, $\times 1$; Odinsholm, Estonia.
 Figs. 2, 4, 6. *Hemicosmites sphaericus* sp. nov., Holotype (UM D325 = Ec95 of Regnéll 1945), lateral, oral, and basal views, $\times 1$; Kullberg Quarry, Sweden.
 Figs. 7, 8. *H. variabilis* sp. nov., cast of PMO 79081, lateral and oral views, $\times 1-5$. Kalvsjø, Hadeland, Oslo Region, Norway.
 Fig. 9. *H. variabilis* sp. nov., cast of PMO 97079, lateral view; locality as for fig. 7; $\times 1-5$.
 Fig. 10. *H. sculptus* sp. nov., cast of Holotype (PMO 97066), oral area, note strongly granulated surface, $\times 1$; Ø. Svartøy, Ringerike, Oslo Region, Norway.
 Figs. 11, 12. *H. variabilis* sp. nov., cast of PMO 97075, oral area and lateral view, $\times 4$; Note three spiny laterals. Locality as for fig. 7.



BOCKELIE, *Hemicosmites*

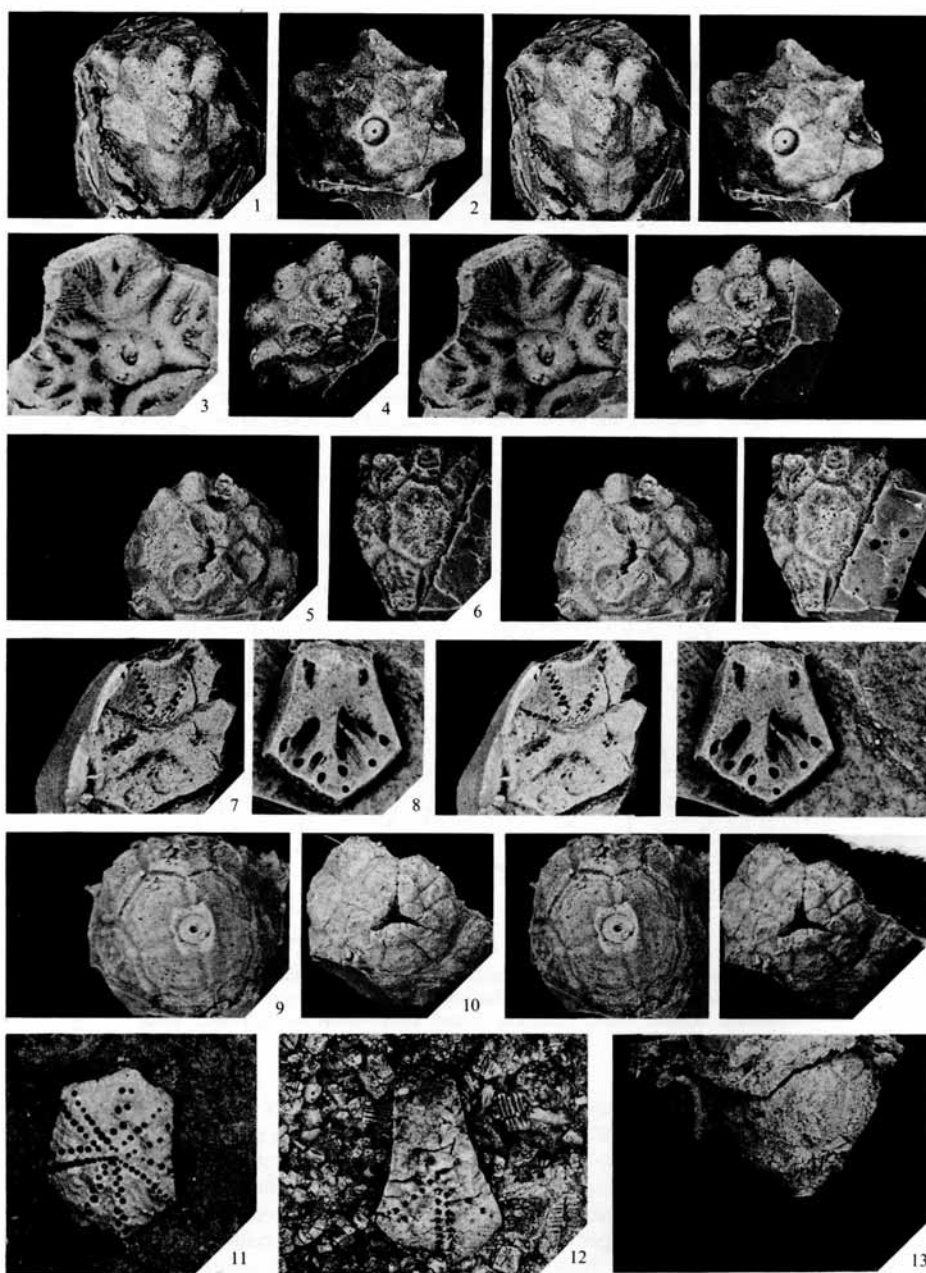


TEXT-FIG. 16. *H. sphaericus* sp. nov. Holotype (UM D325 = Ec95 as used by Regnéll 1945). Terminology as in text-fig. 3. Note that arm facets do not reach on to the laterals. One wedge plate is present (dotted). Scale bar = 1 cm.

Description. Thecal outline generally oval to globular, tapering slightly towards the base. Mouth situated on the thecal summit and usually above or level with the three facets (text-fig. 16). The hydropore is present on the raised portion of R9. The circular anal opening may have a rim, and may also project slightly outwards (text-fig. 15). Five movable triangular plates cover the anus. A stem was present in life. Thecal height/width ratio varies between 1.1 and 1.4, but 1.2 is the average (text-fig. 12). Wedge plates present between R3:R4 and R6:R7, but may occasionally also be present along other sutures. Plate thickness about 1 mm. Basals short (height/width ratio 0.9), infra-laterals (h/w ratio 1.2) and the laterals and radials are shorter than in *H. extraneus* (text-fig. 17). Plate surface smooth, but uneven in well-preserved specimens. The simple pores have a thin tube, less prominent than that of *H. extraneus*. The umbones of the laterals below the facets may have weakly developed nodes.

EXPLANATION OF PLATE 42

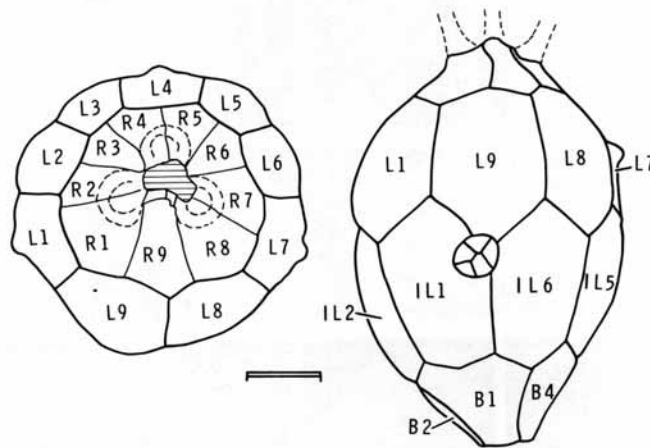
- Fig. 1. *Hemicosmites variabilis* sp. nov., cast of Holotype (PMO 97079), lateral view, $\times 1.5$; Kalvsjø, Hadeland, Oslo Region, Norway.
 Fig. 2. *H. variabilis* sp. nov., cast of PMO 97077, basal view, $\times 1.5$; locality as for fig. 1.
 Fig. 3. *H. variabilis* sp. nov., cast of PMO 97096, internal view of base, $\times 1.5$; locality as for fig. 1.
 Fig. 4. *H. variabilis* sp. nov., cast of holotype (PMO 97079), oral view, $\times 1.5$; locality as for fig. 1.
 Figs. 5, 6. *H. papaveris* sp. nov., cast of holotype (PMO 94644), oral view, $\times 1.5$; Encrinite limestone (Caradoc), Steinvika, Langesund, Oslo Region, Norway.
 Figs. 7, 8. *H. variabilis* sp. nov.; 7, cast of IL-plate (PMO 97097); 8, cast of L-plate (PMO 97098); locality as for fig. 1. $\times 4$.
 Fig. 9. *H. papaveris* sp. nov., cast of base of PMO 94628; locality as for fig. 5. $\times 1.5$.
 Fig. 10. *H. papaveris* sp. nov., cast of oral area of PMO 94635, showing wedge plates at the boundary between the lower radials (R9) and the triangular mouth; locality as for fig. 5. $\times 2$.
 Fig. 11. *H.?* sp. A, PMO 20147, presumably an IL-plate; note the strongly developed half-rhombs of vertical system, $\times 2$; 'Stage' 3c β - γ (Arenig-Llanvirn), Vækkera, Oslo.
 Fig. 12. *H.?* sp. C, PMO 64616, lateral plate, larger than others found in the Oslo Region, $\times 1$; 'Stage' 5a (Ashgill), Gran, Hadeland, Oslo Region, Norway.
 Fig. 13. *H. papaveris* sp. nov., cast of PMO 94606 to show presence of stem adjoint to the base, $\times 1.5$; locality as for fig. 5.



BOCKELIE, *Hemicosmites*

Complete rhombs are developed across all intercirclet sutures. Only between the laterals and the radials do some irregularities occur, with half rhombs in a few places. Occasionally some rhombs are also reduced. Between sutures of infra-laterals weakly developed rhombs are present, but are not seen in IL4:IL5. In the basals a reduction occurs in some specimens between B1:IL2. Incomplete rhombs are reduced between most lateral plates of system 5, but present between L8:L9. In the basals each sieve-pore has four holes; sieve-pores of the laterals may have varying numbers of such holes (maximum 20) depending on the age of the animal, and whether or not it is the last-formed pore (text-fig. 22). PMO A35440 (12 mm thecal diameter) has few holes in sieve-pores of laterals, and always four holes in the last-formed sieve-pore (closest to the plate suture). Sieve-pores of radial plates generally have four holes only. The sieve-pores are always set in shallow depressions which rarely coalesce, and individual pores lack rims. The pores may be circular (0.07–0.10 mm diameter) or elongated, and are often arranged radially. Simple pores are also set in slight depressions and have weak rims. The internal diameter of simple pores is generally about 0.20–0.22 m. PMO A35424 was cut and polished and shows calcified dichopores, similar to those of *H. extraneus* (Pl. 44, figs. 5, 7, 8).

The mouth, situated on the thecal summit, was completely covered in life with plates associated with the ambulacra. The facets are located immediately below the thecal summit. Plates have been found leading down on to the facets, including one or two biserially arranged arm plates, probably similar to those of *Caryocrinites* (Sprinkle 1975).



TEXT-FIG. 17. *H. extraneus* Eichwald. RM Ec27604. Terminology as in text-fig. 3. Note the short ambulacral furrows, and arm facets not reaching on to laterals. Spindle shape common. Ruled lines = orals not exposed. Scale bar = 1 cm.

Remarks. Of known *Hemicosmites* species, *H. sphaericus* is close to *H. extraneus*, but differs in having a smooth external surface, whereas the surface of *H. extraneus* is rugose. Further, the thecal outline of *H. sphaericus* is more globular, and may occasionally also be pear-shaped. All thecal plates tend to be shorter than those of *H. extraneus* (text-fig. 17) and the thecal plates of *H. sphaericus* do not have strongly impressed sutures. In adult specimens *H. extraneus* has more holes in individual sieve-pores and strongly calcified dichopores within the theca. *H. sphaericus* differs from

H. oelandicus in that the latter is more spherical and has shorter IL plates (text-fig. 18). Wedge plates occur in *H. sphaericus*, but have not been seen in the unique type of *H. oelandicus*, which is not sufficiently well preserved to allow comparisons of plates of the oral area or the pore systems.

Hemicosmites papaveris sp. nov.

Plate 42, figs. 2-5; text-figs. 19, 20A, 21A-D

Diagnosis. Poppy-head shaped species with slightly granulated surface; wedge plates developed; facets level with thecal summit; reductions of most horizontal pore systems; holes in sieve-pores usually radially arranged; basals and infra-laterals long; laterals and radials short; knobs developed on three or all laterals.

Material. Several artificially produced moulds, of which fifty more or less complete specimens and numerous plates were cast. All specimens in PMO collection, from inside bioherm of Encrinite Limestone (upper Caradoc), Steinvika, Langesund, Oslo Region, Norway.

Description. Theca poppy-head shaped with slightly convex or flattened oral area, almost straight sides, and concave basal plates. Height/width ratio of theca varies between 1.3 and 1.6 (average 1.4). Mouth situated on thecal summit and usually level with the three facets. A possible hydropore is present at the upper raised portion of R9. The circular anal opening is covered with five triangular plates; in PMO 94629 the anal opening is quadrangular, with four cover plates only (text-fig. 21C, D). Wedge plates are present in most specimens, but best seen in adults. Thin lath-like additional plates are present in PMO 94619 (text-fig. 21B) along the upper portion of sutures R3:R4 and R6:R7. Plate thickness is about 1 mm. Height/width ratio of basals 1.05 (text-fig. 23), of infra-laterals 1.3, of laterals 1.4, and of radials 1.5. Most specimens have nine laterals, but PMO 94619 and 94633 each have ten lateral plates.

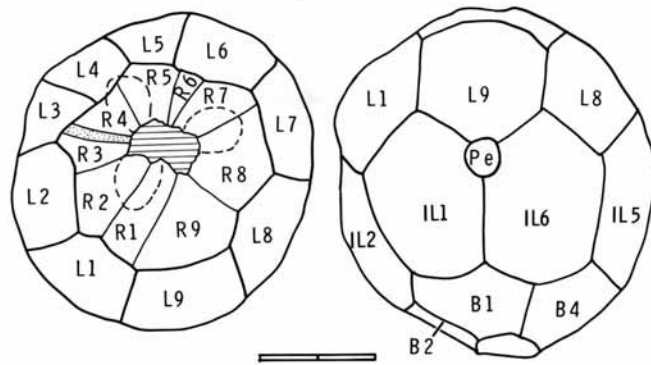
Due to severe pressure solution the exact configuration of pore rhombs in individual specimens is difficult to establish. A composite diagram shows only slight reduction of most pore systems; system 5 is almost completely reduced. Traces of calcified dichopores were found, but severe recrystallization obliterates most of the thecal canals. The peristome is covered by a number of oral cover plates, one central plate in young specimens (text-fig. 21A) and several plates in adults (text-fig. 19). Arm facets are often 2.5 mm in diameter. The size and width of corresponding ambulacral furrows are dependent on the size of the individual. In PMO 94635 parts of the arm plates are present. When the oral cover plates are lost, a triangular mouth can be seen. A hydropore is located in the upper portion of R9 and in contact with the oral cover plates or wedge plates; the slit opens within a tumid, rugose area. In one specimen a stem fragment, 2 mm diameter and 3 mm long, is present (Pl. 43, fig. 13). Numerous root structures occur in the bioherm with this species, and the lack of discs and other attachment structures may indicate that a root structure was present in *H. papaveris*.

Remarks. *H. papaveris* belongs to group C (Jaekel 1899, p. 310) comprising poppy-head shaped *Hemicosmites* species, often with strongly developed nodes on the upper half of the laterals. It differs from the somewhat older *H. rudis* in having more faintly developed ridges with simple pores. It also differs from *H. pocillum* in the lack of knobs on the umbones of the infra-laterals.

Hemicosmites variabilis sp. nov.

Plate 41, figs. 11, 12; Plate 42, figs. 1-4; text-fig. 22

Diagnosis. *Hemicosmites* with variable thecal shape; smooth or rugose surface ornament; wedge plates present, facets just below or level with thecal summit; reduction of horizontal systems 4 and 5; sieve-pores with few holes; ILL plates and LL plates with strongly developed, often projecting, umbones; basals, laterals and radials short; infra-laterals long.



TEXT-FIG. 18. *H. oelandicus* Regnéll. Holotype (RM Ec4362). Terminology as in text-fig. 3. Note that arm facets do not reach on to laterals. No proper wedge plates are present, but one additional radial plate (dotted) is present. Scale bar = 1 cm.

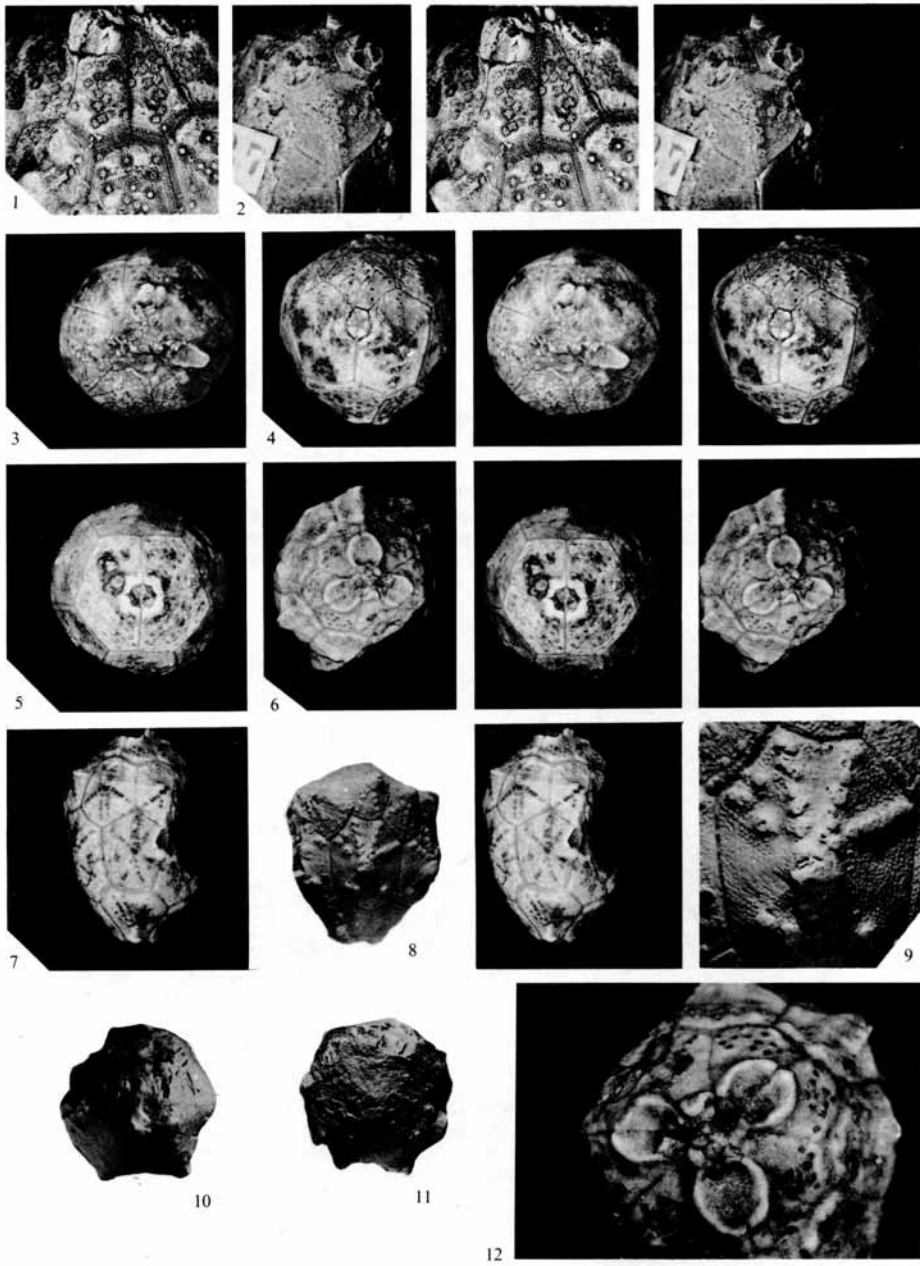
Material. Eight more or less complete specimens and several isolated thecal plates, all in PMO collections, from flank facies of 'Stage' 5a lime mudbank (upper Ashgill), Kalvsjø Quarry, eastern side, Lunner, Hadeland, Oslo Region, Norway.

Description. Thecal outline variable, with two different kinds occurring within the same collections: one has very strongly developed projections on the umbones of the laterals, and weak projections on the infra-laterals (Pl. 41, figs. 7, 12), while the other has equally strong development of projections on the umbones of both plate series (Pl. 41, fig. 9). All specimens come from the same locality and strata. The mouth is situated on the thecal summit and is usually level with the three facets (text-fig. 22). A hydropore is present in the upper raised portion of R9. The anal opening is circular and may have a rim; it never projects outwards. No cover plates have been found on the anal opening. One specimen (PMO 97081) has a quadrangular anal opening. A stem was present in life. Wedge plates are present in most specimens, but are not always easy to detect because the sutures are indistinct. Plate thickness is about 1.5 mm, in a few cases as much as 1.9 mm. Basals are short (height/width ratio 0.9), infra-laterals long (ratio 1.3), laterals and radials short (ratios 1.3 and 1.3 respectively), as seen in text-fig. 23.

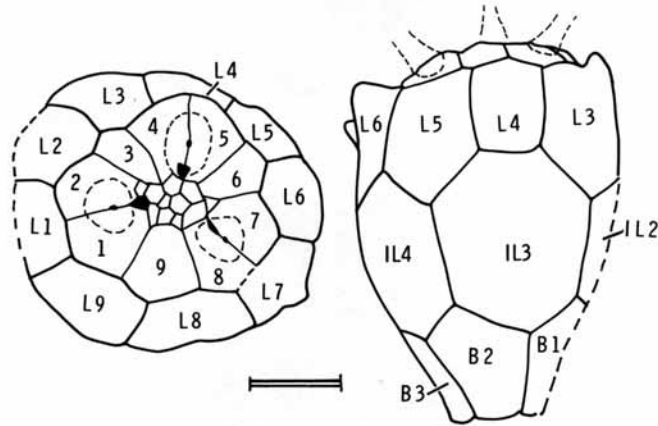
The plate surface is smooth in some specimens and strongly rugose in others, but never has spiny ornament. Simple pores are raised and relatively prominent, but very few in number. Rhomb systems 4 and 5

EXPLANATION OF PLATE 43

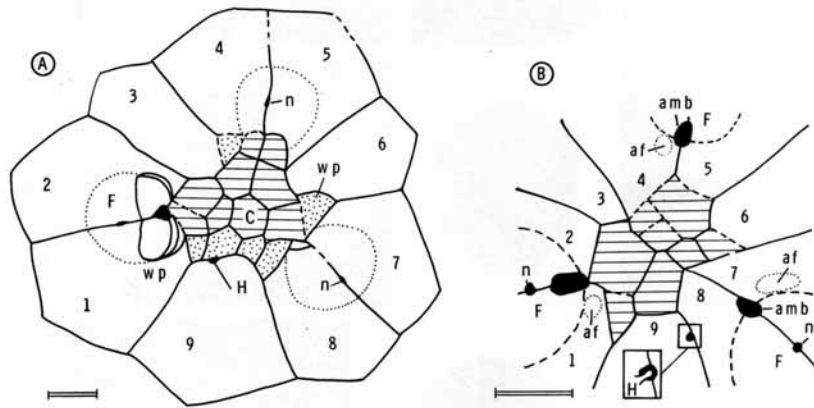
- Fig. 1. *Hemicosmites extraneus* Eichwald, RM Ec5283, showing base of arm; Odinsholm, Estonia (Llandeilo-Caradoc). $\times 1.7$.
- Fig. 2. *Caryocrinites ornatus* Say, PMO A21227, showing base of arm; Silurian. Lockport, New York, U.S.A. $\times 1.7$.
- Figs. 3, 4, 5. *H. pyriformis* von Buch, Holotype, Humboldt Museum, D.D.R., oral area, lateral view, and basal view, $\times 1.3$; Pulkowa, Leningrad district, strata unknown.
- Figs. 6, 7. *H. extraneus* Eichwald, oral area and lateral view, $\times 1.5$; Stage D₁ (Caradoc), Alliku, Estonia. (A. Rõõmusoks Collection, no number).
- Figs. 8-11. *H. verrucosus* Jaekel, Holotype, Leningrad Geol. Inst. 1/327. 8, lateral view; 9, IL-plate; 10, basal view; 11, oral view. $\times 3$.
- Fig. 12. *H. extraneus* Eichwald, details of oral area of fig. 6; scar in anticlockwise position for arm facets: additional facets. $\times 3$.



BOCKELIE, *Hemicosmites*, *Caryocrinites*



TEXT-FIG. 19. *H. papaveris* sp. nov. Holotype (PMO 94644). Terminology as in text-fig. 3. Note poppy-head shape and arm facets which do not reach on to the laterals in this specimen. The specimen is arranged differently in lateral view from previous figures, because periproctal area is not exposed. Scale bar = 0.5 cm.



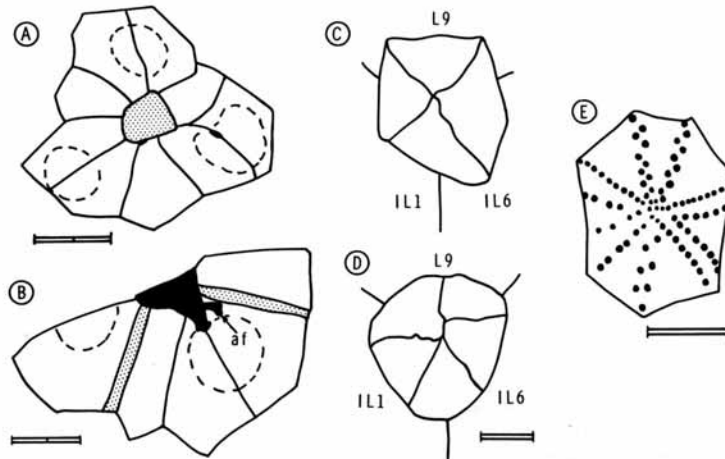
TEXT-FIG. 20. Oral area of *Hemicosmites* species. A, *H. papaveris* sp. nov. (PMO 94638). B, *H. sculptus* sp. nov. 1-9—radials; H—hydropore; af—accessory facet; ap—arm plate; F—arm facet; n—nerve canal; wp—wedge plate. In fig. B inserted square indicates details of shape of hydropore. Scale bar = 1 mm.

seem to be completely absent and the remaining systems are weakly developed. Only traces of vertical system 1 have been seen on the basals, and most sieve-pores of the other systems seem to have from two to four relatively large holes.

Calcified dichopores were found in some specimens, whereas the internal surfaces of isolated plates show only faint traces of dichopore walls. The pore system is set in deeply sunken areas of the plate interior, particularly in basal and radial plates, but also on the inside of laterals.

In life the mouth was completely covered with plates associated with the ambulacra; the facets are large and level with the thecal summit. Oral cover plates are spinose and form a strongly irregular area. Arm facets grew on to the lateral plates which were then incorporated in the facets (text-fig. 22). No arm plates have been found.

A young specimen, only 5 mm in thecal diameter, has three very large, flaring laterals, giving it a stellate appearance (Pl. 41, figs. 11, 12). In young stages the oral area thus apparently grew faster relative to other parts of the body.



TEXT-FIG. 21. A and B, oral area of *Hemicosmites papaveris* sp. nov. A, young specimen with a central plate only, ruled (PMO 94642); B, specimen with two oral laths in radial circlet, dotted (PMO 94619); C and D, anal pyramid of *H. papaveris* sp. nov. C, specimen with four plates (PMO 94629); D, pyramid with the normal five plates (PMO 94605); E, IL-plate of *H.?* sp. A (PMO 20147). Note the asymmetrical distribution of pore holes in a rhomb, typical of *Hemicosmites* species. Well-developed rhombs of series four present; somewhat unusual in *Hemicosmites*, but present in early species. Scale bar = 0.5 cm.

Remarks. *H. variabilis* shows resemblances to the possibly contemporaneous *H. verrucosus* Eichwald (cf. Jaekel 1899, pl. 18, fig. 5). Photographs of the latter species (Pl. 43, figs. 8–11) indicate that it has more numerous pore rhombs, and less strongly developed ornament which is often of a different type; in addition, the umbones of the infra-laterals of *H. variabilis* are more strongly developed, comprising almost the entire plate. In extreme cases the infra-laterals of *H. variabilis* may have a blunt spine-like shape. As mentioned above (p. 396), the variation in shape

of *H. variabilis* is so great that if the specimens had not been found at the same locality and from the same strata, they would have been regarded as belonging to at least two different species.

Hemicosmites sculptus sp. nov.

Plate 41, fig. 10; text-fig. 20B

- 1897 *Caryocrinus* sp.; Kiær, pp. 17, 75.
 1945 '*Caryocrinus*' sp.; Regnéll, p. 105.
 1948b *Caryocrinus* sp.; Regnéll, p. 37.
 1967 *Caryocrinites* sp.; Kesling, p. S141, fig. 64.

Diagnosis. *Hemicosmites* with strongly granulated surface; raised arm facets; limited number of oral cover plates; sieve-pores few, normally 2-4 irregular pores in each sieve-pore.

Material. The holotype is from 'Stage' 5b 'reef' limestone (uppermost Ashgill-Hirnantian), East Svartøy, Ringerike, Oslo Region, Norway. In addition two worn specimens (PMO 7288 and PMO 97047) and a thecal plate (PMO 97067) are thought to belong to this species. All the additional specimens are from 'Stage' 5b at Stavnestangen, Ringerike.

Description. Mouth covered by six spiny, densely packed cover plates and two wedge plates. Oral surface strongly irregular with rough sculpture and deep incisions between three arm facets. The facets are raised well above the oral cover plates. The hydropore-bearing R9 is pointed and reaches above the level of the arm facets. Sieve-pores were detected on R1 (3 pores, each with 3 pore holes), R3 (4 pores with 2, 3, 4, and 5 pore holes), R4 (4 pores with 3, 2, 1?, and 2 pore holes); the average number of pore holes per sieve-pore is 3 (text-fig. 13A). At least one wedge plate and six oral cover plates are present on the holotype (text-fig. 20B).

Remarks. The strongly spinose surface and raised arm facets in *H. sculptus* differ from those in other known *Hemicosmites* species. The proximal portion of the facets has a gentle slope in an anti-clockwise direction (text-fig. 20B, Pl. 41, fig. 10) in the holotype, in the position where the additional facets are present in other species. These slopes may be traces of similar structures.

Hemicosmites? sp. A

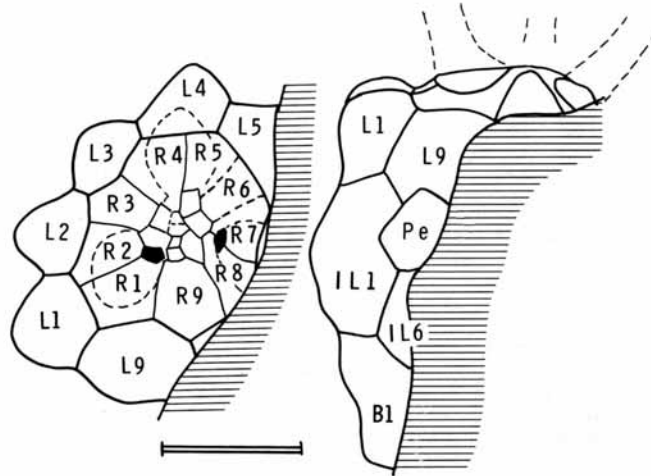
Plate 42, fig. 11; text-fig. 21E

- 1865 (?)*Hemicosmites pyriformis* von Buch; Kjerulf, p. 4.
 1882 *Hemicosmites* sp.; Brøgger, p. 42.
 1945 *Hemicosmites* sp.; Regnéll, p. 100.
 1948a *Hemicosmites?* sp.; Regnéll, p. 33, fig. 5.

Material. One single plate of the lateral series (PMO 20147). This is the specimen mentioned by Kjerulf, Brøgger, and Regnéll and subsequently described by Regnéll (1948a); it is from the Orthoceratid Limestone, 'Stage' 3c β - γ (upper Arenig-lower Llanvirn), Vækkerø, Oslo, Norway.

Description. The plate is an IL, possibly IL3 (text-fig. 21E). The height of the plate is 12 mm, the width 9 mm. The plate thickness (1.5 mm) is like that of most *Hemicosmites* species. The surface is corroded, and the pore holes of the simple pores are clearly visible; the number of the pore holes depends on the size of the seven half rhombs. The configuration of the pores indicates a strongly developed current system 4, more strongly developed than in other known *Hemicosmites* species.

Remarks. The plate is clearly similar to other *Hemicosmites* species in some respects, but the fact that only a single example is known makes it impossible at present to put a firm generic name to it. Recent finds of plates of a possible caryocrinitid in contemporaneous deposits on Öland, Sweden, may indicate that the *Hemicosmites?* sp. A plate could also be a caryocrinitid, but more and better-preserved material is needed to decide this. However, the plate described here is more than twice the size of those from Öland and is certainly not conspecific. Some uncertainties as to the precise stratigraphical position of the plate exist. The lithologies in which it was found may indicate the upper half of 'Stage' 3c β or all of 'Stage' 3c γ ; in either case it is very close to the Arenig-Llanvirn boundary.



TEXT-FIG. 22. Oral and lateral view of *H. variabilis* sp. nov. Holotype (PMO 97079). Terminology as in text-fig. 3. Note the strongly developed nodes on all laterals, and that at least two facets reach well down on to the laterals. Several specimens have all three facets reaching this far down. Note also the large periproct and irregular shape of theca. Scale bar = 0.5 cm.

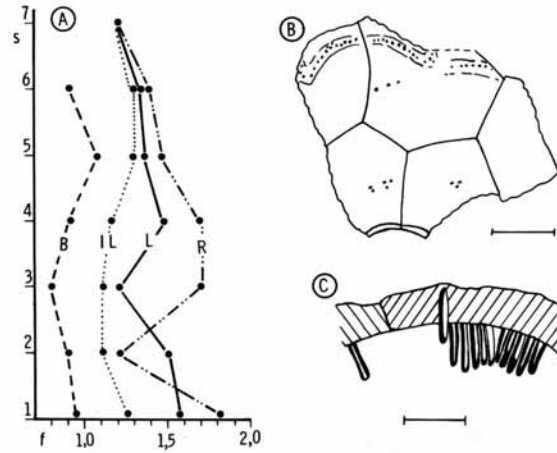
Hemicosmites? sp. B

Text-fig. 23

Material. One specimen only, a basal portion of a theca (PMO 97095), from 'Stage' 5a (upper Ashgill), Kalvsjø Quarry, Lunner, Hadeland, Oslo Region, Norway.

Description. Two basal plates, B2 and B3, and three infra-laterals are preserved. The theca might have been about 40–45 mm high. Apparently four basals were present. The surface ornament of the plate is strongly irregular and deep incisions exist between contiguous plates. Because of partial pressure solution, details of the plate surface are missing, and no sieve-pores can be seen. The open pores on the other hand are fairly well preserved and their distribution differs somewhat from that normally found in *Hemicosmites* species in that they all occur on the crests of strong ridges. Intra-circling rhombs are present on at least one suture, indicating that pore system 4 was present.

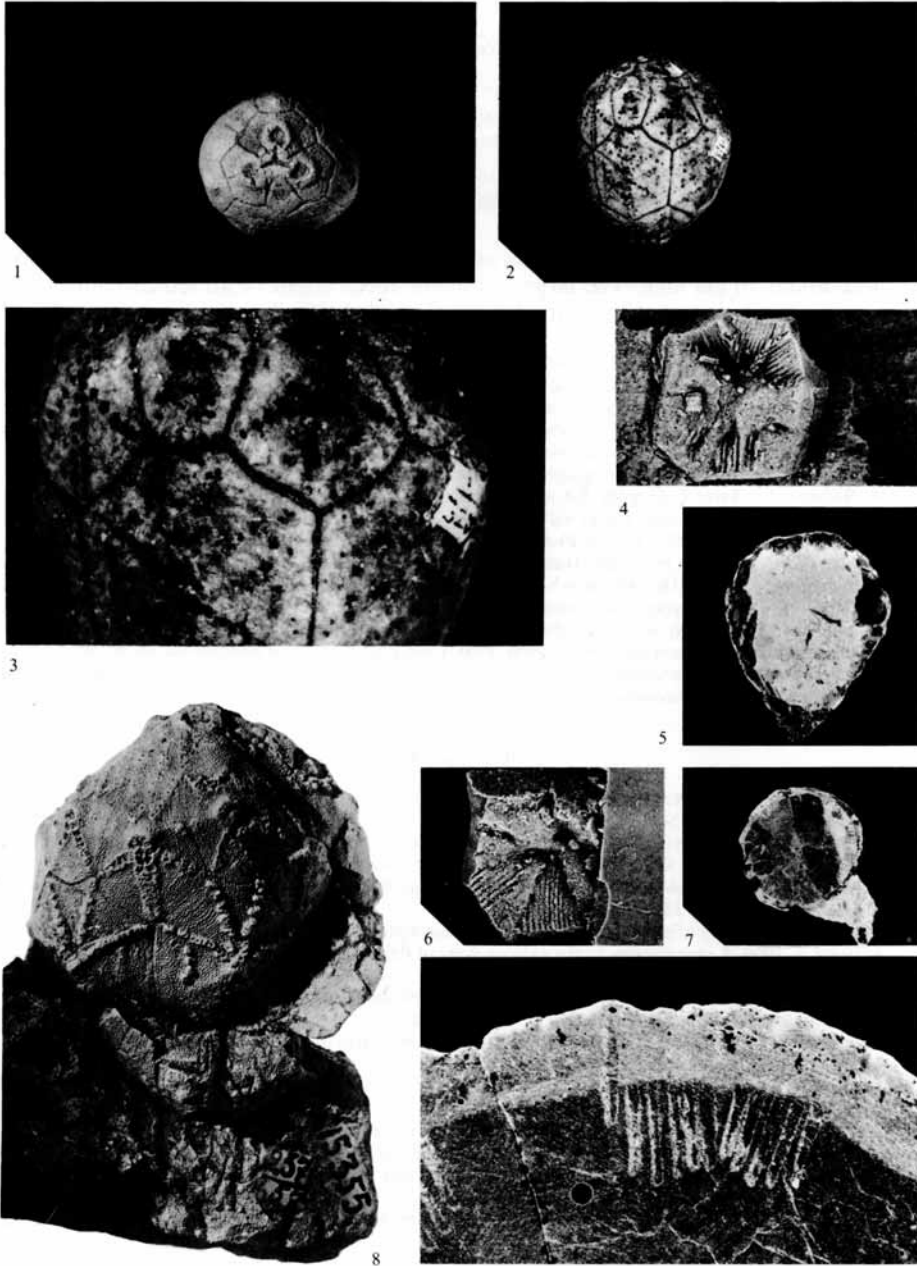
Remarks. Since the distribution of pores differs from other species referred to *Hemicosmites*, and also from patterns seen in *Tricosmites* and *Caryocrinites* (Caryocrinitidae), the generic affinity of this specimen is left open at present.



TEXT-FIG. 23. A, average plate height/plate width of basals (B), infra-laterals (IL), laterals (L), and radials (R) of various *Hemicosmites* species. Note that most plates tend to become shorter with time (1-7). 1—*H. extraneus*; 2—*H. pyriformis* (stratigraphical position unknown); 3—*H. oelandicus*; 4—*H. sphaericus* sp. nov.; 5—*H. papaveris* sp. nov.; 6—*H. variabilis* sp. nov.; 7—*H. sculptus* sp. nov. B, plate diagram of *Hemicosmites?* sp. B (PMO 97095). Pores few, size of specimen large (scale bar = 1 cm). C, section through a plate of *H. sphaericus* sp. nov. (PMO A 35424/2) showing size and distribution of dichopores inside the theca. Note that two groups of dichopores converge and that they do not reach equally deeply into the theca. Scale bar = 0.5 cm.

EXPLANATION OF PLATE 44

- Figs. 1-3. *Hemicosmites extraneus* Eichwald, Holotype, oral and lateral views, and details of lateral side; Leningrad University Geol. Dept. 1/3207; D₃ (Caradoc), Spitham, Estonia. 1.2 × 1; 3 × 3.
 Fig. 4. *H. variabilis* sp. nov., cast of inner side of IL-plate (PMO 79099), × 2; locality as for Pl. 42, fig. 1.
 Fig. 5. *H. extraneus* Eichwald, sagittal section of RM Ec5282, showing dichopore canals inside theca, × 1; Odensholm, Estonia.
 Fig. 6. *H. variabilis* sp. nov., cast of inner side of L-plate (PMO 97100), × 2; locality as for Pl. 42, fig. 2.
 Figs. 7, 8. *H. sphaericus* sp. nov., sagittal section of PMO A35424 to show dichopores inside theca; Kullberg Limestone. Kullberg, Sweden. 7, × 1; 8 × 8.
 Fig. 9. *H. pulcherrimus* Jaekel, Holotype. Palaeontol. Inst. Moscow 15355 (257/657), lateral view, × 2; D₃ (Caradoc), Sack, near Tallinn, Estonia.



BOCKELIE, *Hemicosmites*

Hemicosmites? sp. C

Plate 42, fig. 12

Material. Several loose blocks with plates (PMO 64616, 68422, 68423), from 'Stage' 5a (upper Ashgill), Gjøvik farm, Gran, Hadeland, Oslo Region, Norway.

Description. Large loose thecal plates of a *Hemicosmites?* species. Lateral plates measuring 20 by 12 mm in maximum dimensions. Plates are often strongly abraded, showing no trace of surface ornament. Traces of pores are present.

Remarks. The large size of the plates indicates that the complete specimen must have been about 10 cm high. The large size of the theca might be an indication of close relationship to the contemporary *H. grandis* Jaekel (1899).

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