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Mots-clés : Echinodermata. Ctenocystoidea. Cambrien moyen. Pologne.

Key words : Echinodermata. Ctenocystoidea. Middle Cambrian. Poland.

Summary. – Ctenoid apparatus, diagnostic of the Ctenocystoidea, and thecal plating of the kind occurring in the most primitive camptostromatid and eocrinoid echinoderms characterize *Jugoszovia archaeocyathoides* n. gen. and sp., common in coarse mudstones of the Usarzów Sandstone Formation of the Holy Cross Mountains, Poland. Being earliest Middle Cambrian in age (*Eccaparadoxides insularis* Zone of the *E. oelandicus* Stage), it precedes stratigraphically all other known ctenocystoids. The ctenoid apparatus in general organization and morphology of particular elements resembles the holothurian calcareous ring and probably served as an attachment to tentacular apparatus.

Résumé. – Un appareil de type ctenoïde et une thèque composée de plaquettes à disposition comparable à celle des Echinodermes primitifs Eocrinoïdes et Camptostromatides caractérisent *Jugoszovia archeocyathoides* n. gen et sp., très répandu dans les argilites grossières de la Formation des Grès d'Usarzów dans les Monts de Sainte-Croix en Pologne. Récolté à la base du Cambrien moyen (Zone à *Eccaparadoxides insularis* de l'étage à *E. oelandicus*), il précède tous les autres ctenocystoïdes connus. Le plan d'organisation de l'appareil ctenoïde et la morphologie d'éléments particuliers présentent des ressemblances avec l'anneau calcaire des Holothurides et servait probablement à l'insertion des tentacules.

Résumé, légendes des figures et des planches, traduction française : B. BADRÉ.

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INTRODUCTION

The Jugoszów section of the earliest Middle Cambrian rocks, located near Sandomierz at the eastern end of the Holy Cross Mountains, provides insight into a virtually unknown epoch in the evolution of the echinoderms, following the rich late Early Cambrian assemblages of articulated echinoderm skeletons and preceding those of the middle and late Middle Cambrian (see Paul and Smith, 1984). The Jugoszów echinoderm assemblage is of unusually low diversity, perhaps with only a single species present or at least strongly dominating, which may be connected with the Cambrian geographical high latitude position of the Holy Cross Mountains area. Fossils of what now appears to be the ctenoid organ of this organism had been misinterpreted as archaeocyathid cups when reported for the first time (Orłowski, 1959a). Only after well-preserved ctenocystoids from the Spence Shale of Utah (Robinson and Sprinkle, 1969) were described has the proper taxonomic identification of the Polish fossils been recognized (Sprinkle, 1973, 1992 ; Derstler, 1985 ; Dzik and Orłowski, 1993).

The Jugoszów ctenocystoid is even more unusual than earlier known members of the group in that it shares its pattern of thecal plating with the most primitive members of other echinoderm classes. This paper concerns description of fossil skeletons of *Jugoszovia archaeocyathoides* n. gen. and sp., reconstruction of its original appearance, and discussion on relationships.

The material is housed at the Department of Geology of Warsaw University (abbreviated UWWG).

GEOLOGIGAL OCCURRENCE

The material described in the present paper has been collected by the junior author while he was studying the Cambrian in the vicinity of Sandormierz (Orłowski, 1959a, b, 1964). The best preserved and complete specimens come from a few localities near Jugoszów which are briefly described below (for details see Orłowski, 1964).

Jugoszów 1a. — These are two artificial pits at the southern slope of the gorge between Jugoszów and Żdanów village, and the third one in its bottom (Orłowski, 1964). Light-grey quartz mudstones with thin clayish bands occur there. Beds are usually about 10 cm thick, some of them contain glauconite. Trace fossils are common on bedding planes. Most of the trilobite and echinoderm fossils are well within the mudstone beds and are randomly oriented. Trilobits abound in the locality, among them *Eccaparadoxides insularis* Westergård, 1936, indicative of its own zone (Orłowski, 1959b). Higher up in the section a ten meters thick fine-grained quartz sandstone (the Jugoszów sandstone of Orłowski, 1964)

occurs, with a similar assemblage of trilobites but devoid of echinoderms. They reappear higher associated with different index trilobites.

Jugoszów 3. — The strata are exposed in the valley slope undercut by the creek. Bedded fine grained grey quartz sandstones, clayish in places, with rare glauconite grains, are of varying thickness, usually about 10 cm thick, but may be as thin as 3 cm or reach up to 20 cm. Among trilobites occurs *E. pinus* Holm, 1887 indicative of its own zone ; thus, the strata are younger than in exposure 1a.

Usarzów 19. — A pit located about 250 m north of the boundary of the Osiny village, among *Robinia* trees, at the slope. The rock is a coarse-grained mudstone, clayish and thin bedded (6-8 cm), in places devoid of clay, with beds up to 15 cm. Trilobite assemblage with *E. pinus.*

Usarzów 20. — An exposure in the road from Osiny to Gołębiów village, within limits of Osiny, lithology and fossils like in Usarzów 19.

The strata cropping out at all these localities represent the Usarzów Sandstone Formation (Orłowski, 1975) developed as mudstones and standstones. It overlies the early Cambrian Kamieniec Shales that contain limestone concretions. The middle Cambrian relatively coarse clastics reach about 400 m in this part of the Holy Cross Mountains. Later, perhaps as a result of the global transgression in the *Triplagnostus gibbus* Zone at the beginning of the following *Paradoxides paradoxissimus* Stage, a fine-clastic sedimentation regime was restored.

MATERIALS AND METHODS

All together 116 specimens are in hand, most of them representing ctenoid apparatuses with small parts of thecae represented. Only two have both a ctenoid apparatus and a significant part of the theca in connection.

Preservation. — All originally calcareous fossils are preserved in the mudstones of the Usarzów Sandstone Formation as molds. The rock matrix is rather coarse which obliterates details of the morphology of minute echinoderm plates and makes them difficult to be cast in latex or silicone. Casting materials tend to infiltrate between the quartz grains making removal of ready casts difficult and destroying fossils when removed by force. Therefore, only casting substances which rather roughly reproduce the morphology of substrate can be used. A dentist's silicone molding plaster was applied which, although being not very precise in replicating details, enabled safe removal.

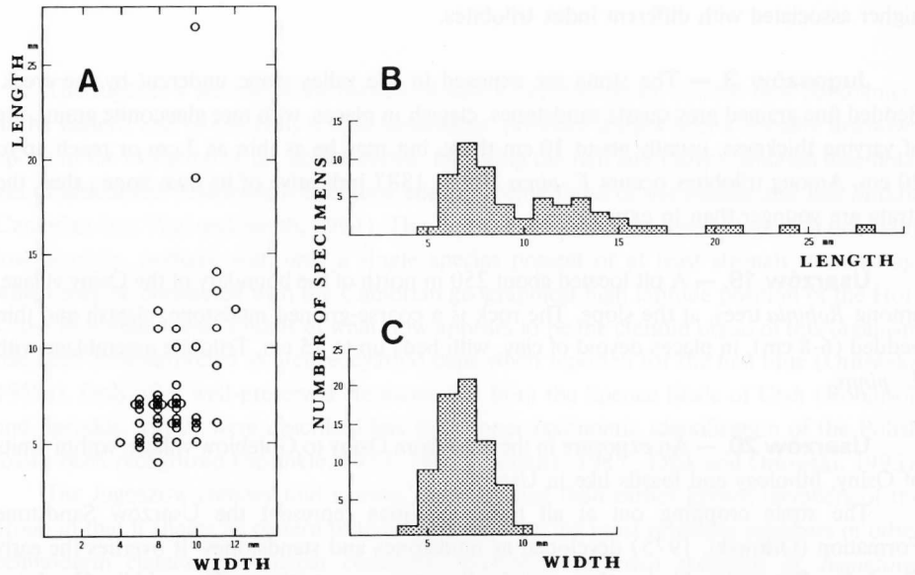

FIG. 1. — *Jugoszovia archaeocyathoides* n. gen. and sp. ; A, plot of widths of ctenoid apparatuses against lengths of preserved portions of thecae ; B, C, frequency distributions of the same measurements (with specimens showing only one of these dimensions measurable included). Note complete gradation between specimens with only small parts of the « neck » preserved and those associated with larger parts of the theca.

FIG. 1. — *Jugoszovia archaeocyathoides* n. gen. et sp. ; A, Variation de la largeur de l'appareil ctenoïde en fonction de la longueur conservée de thèque. B, C, Diagrammes de fréquence des mêmes mesures (incluant les exemplaires dont une seule dimension est mesurable). Noter la progression entre les spécimens conservant seulement de petites parties du « col » et ceux associés à de plus grandes parties de la thèque.

Predation as the main taphonomic factor. — All the studied echinoderm specimens from the Usarzów Sandstone Formation are damaged, in most cases only the ctenoid apparatus is preserved with a small part of theca immediately behind the end of ctenoidal plates (Fig. 1A, B ; pl. I, fig. 2-5). They were apparently cut off the main body. In some cases several specimens represented by ctenoidal apparatuses and small parts of thecae are found in elongated masses resembling a gut content or coprolite (pl. I, fig. 9, 10). If more complete specimens are rarely preserved, their body covers seem to be widely open and complexly folded. All this is suggestive of predation by unknown organisms. The pattern of « decapitation » of the ctenoid apparatuses is suggestive of action of some arthropods. Associated trilobites *Eccaparadoxides* are of size corresponding to that expected in possible predator, and there is good evidence that Cambrian trilobites were predatory on priapulids (Jensen, 1990). Some less commonly fossilized candidates for the role of predator, like those reviewed by Conway Morris and Jenkins (1985), can also be considered as likely.

SYSTEMATIC PALEONTOLOGY

Class *CTENOCYSTOIDEA* Robison & Sprinkle, 1969

Family **Jugoszoviidae** n. fam.

Diagnosis. — Ctenocystoids with their thecae covered with numerous, tightly arranged, polygonal plates.

Comparison. — The new family differs from the Ctenocystidae Sprinkle and Robinson, 1978, in the lack of any thecal frame and in elongated shape of the theca.

Genus JUGOSZOVIA n. gen.

Type species. — *Jugoszovia archaeocyathoides* sp. n.

Etymology. — From the name of Jugoszów village, the type locality.

Diagnosis. — Ctenoid apparatus composed of 41 plates in adult specimens. The theca tape-shaped at least in its part immediately behind the ctenoid apparatus.

Jugoszovia archaeocyathoides n. gen. and sp.

Ayacicyathus sp., Orłowski, 1959a, Pl. 1, fig. 1-6, Pl. 2, fig. 1-2.
Syringocyathus sp., Orłowski, 1959a, Pl. 2, fig. 3.
Syringosnema sp., Orłowski, 1959a, Pl. 2, fig. 4-5.
Orbicyathus sp., Orłowski, 1959a, Pl. 2, fig. 6-7.
Syringosnema sp., Orłowski, 1964, Pl. 11, fig. 7-8.
Ayacicyathus sp., Orłowski, 1964, Pl. 11, fig. 9-10.
« Archaeocyathids » from Poland, Sprinkle, 1973, p. 111.
Ctenocystoid, undescribed species, Derstler, 1985, fig. 3-11.

Holotype. — Specimen UWWG 2.2908 (Figs. 4-5).

Type horizon and locality. — Exposure 1a in Jugoszów near Sandomierz, Poland ; Usarzów Sandstone Formation, *Eccaparadoxides insularis* Zone of the *E. oelandicus* Stage, earliest Middle Cambrian.

Etymology. — The name refers to superficial similarity of the ctenoid apparatus to archeocyathid cups, which resulted in the original misinterpretation of the type material.

Diagnosis. — As for the family.

Distribution. — *E. insularis* and *E. pinus* Zones, vicinities of Jugoszów and Usarzów near Sandomierz, Poland.

Description. — Although there is no good evidence that more than one species is represented among the echinoderms from Jugoszów, rather inadequate preservation of morphological details in coarse mudstone and frequent cooccurrence of remnants of several within the same coprolithic associations leave some uncertaintly and the proposedly complete specimens may appear artifacts resulting from action of predators. However unlikely such possibility seems (in the holotype there is a continuation in plating between the « neck » and the main theca), it seems safer to discuss separately morphology of the ctenoid apparatuses and plating of thecae which are in most cases represented by different isolated specimens.

Ctenoid apparatus : The best representation of the ctenoid apparatus in its oral aspect is provided by the specimen UWWG 2.2844 (pl. I, fig. 1). It nicely shows its dorsoventral flattening and strictly symmetrical arrangement of the ctenoid plates. All together there are 41 such plates. Two sets of 18 small plates, probably loosely inserted in soft tissue, border the single ventral one, attached to a plug-like suroral, and four dorsal attached to peculiar shelves of the suborals (fig. 2A, B). As in other ctenocystoids the small plates that are nearest to those arming suborals are deflected laterally, as it is well shown by specimen UWWG 2.2909 (not figured).

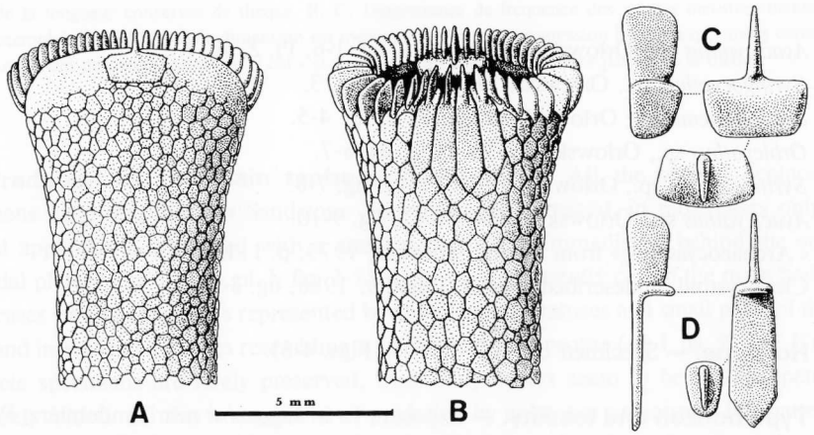

FIG. 2. — *Jugoszovia archaeocyathoides* n. gen. and sp. ; A, restoration of the ctenoid apparatus in ventral view ; B, same in dorsal view ; C, suroral plate in different views ; D, same for suboral plate.

FIG. 2. — *Jugoszovia archaeocyathoides* n. gen. et sp. ; A, Reconstitution de l'appareil ctenoïde en vue ventrale. B, Le même, en vue dorsale. C, Plaque surorale vue selon des faces différentes. D, Plaque suborale, de même.

Details of the morphology of suborals can be inferred from specimen UWWG 2.2914 (pl. I, fig. 10). The plates are rather thin, lanceolate in outline. They slightly widen aborally, and after reaching their greatest width they narrow angularly. At their adoral end all the four plates are bent under at a right angle to form transverse shelves (Fig. 2D). These shelves have rounded inner ends, as shown by specimens UWWG 2.2803 and 2804. The ctenoid plates that arm the shelves slightly widen distally and have their tips rounded.

The best preserved suroral is that in specimen UWWG 2.2914a. Its massive, trapezoidal body has a saddle-like anterior surface, gently convex at both lateral sides (Fig. 2C). In ventral view it is inversely trapezoidal in outline. It forms a kind of plug closing the ctenoid apparatus. The ctenoid plate attached to the plug-like body is larger than its neighbors. It is difficult to estimate its complete width in poorly preserved specimens but probably its base covers most of the thickness of the suroral and, immediately above a small basal indentation, it widens to almost the whole suroral thickness.

The anterior of the ventral surface of the theca, bordering the suroral from both sides, is covered with densely arranged sclerites. They are probably partially unified anteriorly whereas posteriorly they smoothly pass into a loose plating of small isometric sclerites as shown by specimen UWWG 2.2886 and only slightly worse UWWG 2.2917 (pl. I, fig. 4, 5). These are thus incipient large plates (Fig. 2A) homologous to « radial » plates in later ctenocystoids.

The dorsal margin of the theca behind the suborals and on both their sides is covered by relatively large elongated, probably polygonal plates of width similar to that of the suborals. They are easily recognizable in specimens UWWG 2.2912, UWWG 2.2918, UWWG 2.2418, and several others (pl. I, figs. 2, 3).

The length of the longest preserved specimen, UWWG 2.2780 (about 12.5 mm ; pl. I, fig. 6) is more than two times larger than the width of the ctenoid apparatus. Both its dorsal and ventral surfaces are smooth, with no plate boundaries visible. This shows that the thecal plates in *Jugoszovia* were originally densely arranged. Slight longitudinal depressions border the sides. The dorsal surface bends at an angle of 45° just in front of the ctenoid apparatus.

In all well preserved specimens their posterior ends are irregularly truncated, apparently significant parts of the thecae are missing there.

Theca : Only two specimens, UWWG 2.2913 and 2908, have their ctenoid apparatuses preserved in connection with larger thecal bodies. In UWWG 2.2913 the transition between the ctenoid apparatus and theca is obscure, only suboral plates are recognizable which are superimposed over the theca (pl. I, fig. 8). The pattern of plating, with large polygonal, rather tightly arranged plates and few smaller plates inserted (some elevated in a form of tubercles), suggests that this is the dorsal thecal wall. A transverse fold at the end of the body opposite to the ctenoid apparatus does not seem to represent any specific structure and is an effect of post-mortem deformation of the flexible theca.

Much more complete holotype specimen UWWG 2.2908 is crucial to interpretation of the general body appearance of *Jugoszovia*. The ctenoid apparatus is there three-dimensio-

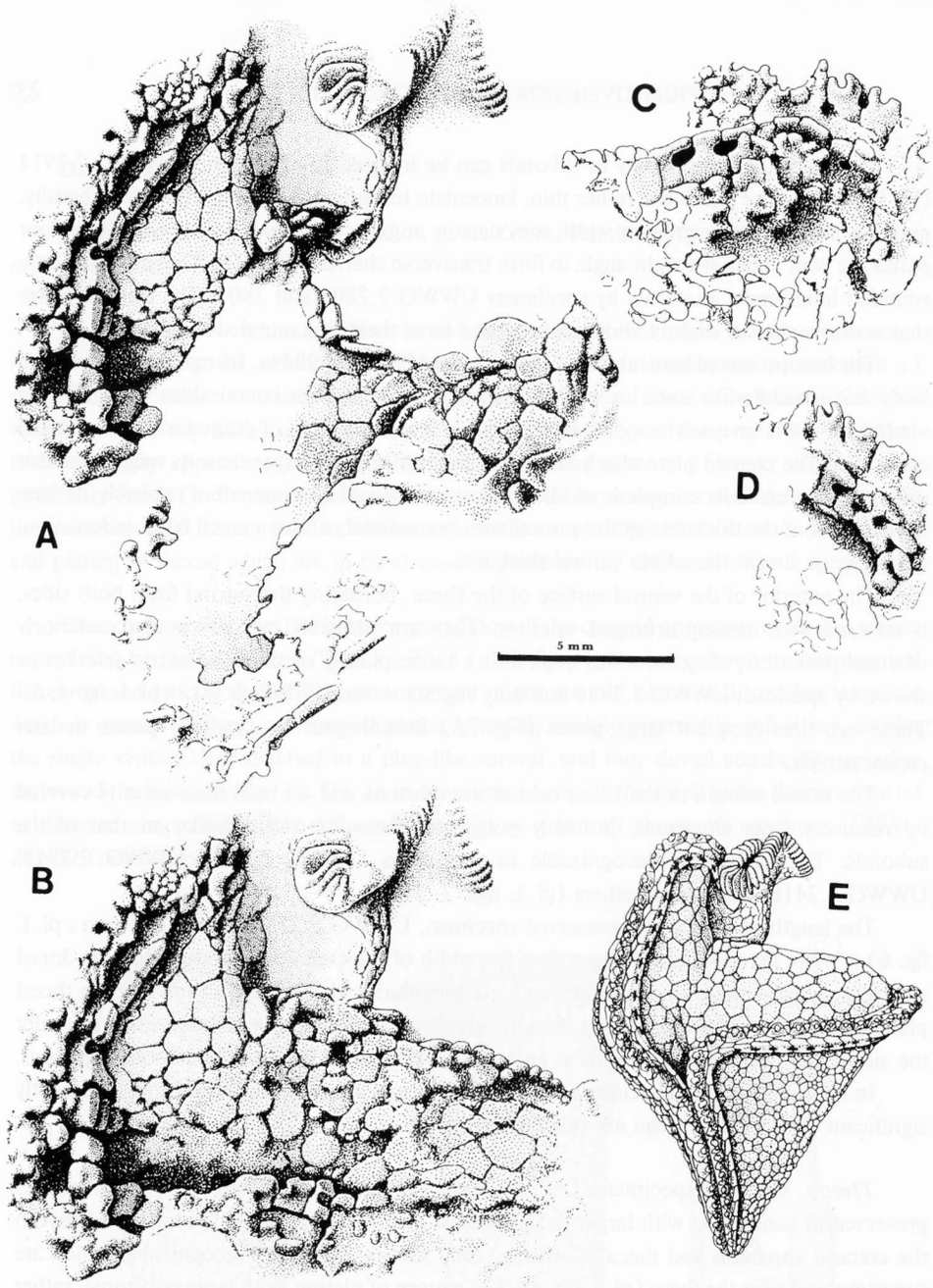

FIG. 3. — *Jugoszovia archaeocyathoides* n. gen. and sp., camera lucida drawings, Jugoszów 1a ; A,B, two successive stages in preparation of the holotype specimen UWWG 2.2908 (see pl. II, fig. 1, 2, note also the pattern of plasting at the boundary between the « neck » and theca) ; C, D, ambulacrum of specimen UWWG 2.2425 in two different views (see pl. I, fig. 7) ; E, proposed interpretation of the holotype specimen as it is preserved in the rock, not to scale.

FIG. 3. — *Jugoszovia archaeocyathoides* n. gen. et sp. ; A, B, Deux stades successifs au cours de la préparation de l'holotype UWWG 2.2908 (Voir pl. II, fig. 1, 2, et la disposition des plaques à la limite entre le « col » et la thèque). C, D, Ambulacre du spécimen UWWG 2.2425 selon deux vues différentes (Voir pl. I, fig. 7). E, Interprétation de l'holotype préservé dans le sédiment, pas à l'échelle. Dessins faits à la chambre claire. Jugoszów 1a.

nally preserved, being longitudinally folded along its ventral midline (Fig. 3A, B, E ; pl. II, fig. 1, 2). Despite a poor preservation the continuity of the layer of small plates building the base of the neck with that forming the frontal surface of the theca makes it rather unlikely that theses are pieces of different specimens accidentally fossilized together.

Thecal plating is relatively well preserved in the central part of the holotype. Irregularly polygonal plates, approximately 1.5 mm in diameter, cover most of its surface. In places some small platelets are intercalated. Details of the plate ornamentation are not recognizable but some of them show indistinct irregularly meandering riblets. Deep, point-like depressions in between plate margins are suggestive of the presence of a kind of epispires, but preservation in coarse sandstone do not provide fine details. Before preparation of the specimen, another, deeper layer of polygonal plates was visible (Fig. 3A, pl. II, fig. 2). Apparently, this is a continuation of the same thecal wall folded underneath in the aboral region of the theca. If the interpretation of the proposed way in which the « neck » was attached to the theca (Fig. 3E) is correct, this surface of the theca is dorsal.

This is supported by the morphology of plates covering dorsal surface of the « neck » in specimens UWWG 2.2419, 2843, 2896, 2918, 2919 and 2915 (pl. I, figs. 2, 3) where they are generally much larger than plates occurring ventrally. Some smaller ones are intercalated sparsely, as in the holotype. Also the second specimen with the ctenoid apparatus associated with theca UWWG 2.2913 shows the same arrangement of larger plates separated by smaller ones (pl. I, fig. 8).

Minute platelets covering the ventral surface of the « neck » immediately behind the suroral in specimens UWWG 2.2886 and UWWG 2.2917 (pl. I, figs. 4, 5) indicate that the ventral side of theca in *Jugoszovia* was covered with smaller plates than the dorsal side. One of the three specimens with ambulacral plates, UWWG 2.2424 from Jugoszów 3, may represent a large portion of the ventral body surface. The surface sculpture of the specimen (originally rather well recognizable but partially destroyed by repeated latex casting : see Orłowski 1964, Pl. 11, fig. 8) shows larger polygonal plates, approximately 1.0 mm in diameter, surrounded by rings of smaller ones, less than 0.3 mm in size. The body wall is folded, indicating once again its original flexibility. Specimens UWWG 2.2422 from the same locality, and UWWG 2.2920 from Jugoszów 15a are also built of minute sclerites and complexly folded.

Even if relatively complete, the holotype specimen, like all the Jugoszów thecae, is strongly deformed and hardly allows restoration of the original body shape. The body is sinusoidally bent in both sagittal and frontal planes (Fig. 3E). It was probably elongated and dorsoventrally flattened. Its complete length was probably less than 30 mm. Any restoration of the body shape based on available evidence can be only conjectural.

It remains unclear whether the largest echinoderm specimen from Jugoszów 3 (pl. II, figs. 3, 4) represents *Jugoszovia*. All its plates are large, some more than 3.0 mm in diameter. A few of them were thicker than others, with conically convex inner surface. The theca is at least 37 mm long, much larger than possibly corresponding part in any other specimen. We are not able to find features in the morphology of this specimen that could allow to match

it with any other Cambrian echinoderm group. Perhaps this is medially folded dorsal thecal wall of *Jugoszovia* but could also be a large eocrinoid theca.

Possible ambulacra : In the holotype specimen UWWG 2.2908 (Fig. 3A, B ; pl. II, fig. 1, 2), along the left margin of the large theca associated with the ctenoid apparatus there is a row of rather robust, vertically oriented plates which border a furrow. The other, external side of the furrow is also composed of relatively robust plates but their morphology is poorly preserved in coarse sediment. An accumulation of numerous small, poorly preserved but probably isometric sclerites follow them. Additional preparation exposed even more of them, apparently they covered the furrow from outside. This may represent roofing-over of the ambulacrum. Another possibility is that these are sclerites at the margin of the ventral surface of the theca.

The pore-bordering plates are sequential. It is well visible at least in the posterior part of the holotype specimen that large pores penetrate boundaries between massive vertical plates. In effect the plates are H-shaped. Despite poor preservation of the external side of the furrow some depressions corresponding in distribution to the pores are recognizable. This less then completely preserved left ambulacrum ends at the break of the rock piece and only a few robust plates, probably those bordering pores, can be identified behind and below the well preserved part (Fig. 3A).

Additional preparation of the holotype revealed another belt with H-shaped plates that runs transversely to the preserved dorsal surface of the theca (Fig. 3B). Numerous minute isometric sclerites are also associated with the belt. Closer to the left ambulacrum this belt is poorly preserved and it cannot be proven that both merge to form a continuous structure. Because of the presence of the robust plates behind the left ambulacrum, it seems more likely that the posterior part of the body was folded along the middle dorsal line and that the two lateral ambulacra were here close to each other (Fig. 3E).

Much better preservation of the ambulacral plates is provided by fragmentary theca UWWG 2.2425 (Fig. 3C, D ; pl. I, fig. 7) which lacks any remnants of the ctenoid apparatus but shows similar morphology of plates as in the theca attached to the ctenoid apparatus of the holotype. Here the vertical orientation of H-shaped pore plates is apparent. Their upper surfaces are widened and prolonged in one direction (posteriorly ?) to form a shelf and perhaps slightly overlap. This horizontal area contacts laterally with at least one row of polygonal plates. These are, in turn, followed by sclerites of complex morphology : wide basally, narrowing towards their free (?) ends which are convex laterally and deeply indented at the tips. The upper part of these plate has thus a roughly U-shaped appearance. Several small isometric sclerites are randomly distributed above and in between these larger plates. They may be either roofing (ambulacral cover) plates or may have been derived from adjacent parts of the theca. Thecal plates which are in contact with vertically oriented H-shaped plates are indistinctly polygonal and relatively large.

A few H-shaped sclerites, disarticulated and displaced, are preserved also in specimen UWWG 2.2424 which represents a large part of thecal wall (Orlowski 1964 : pl. 11, fig. 8).

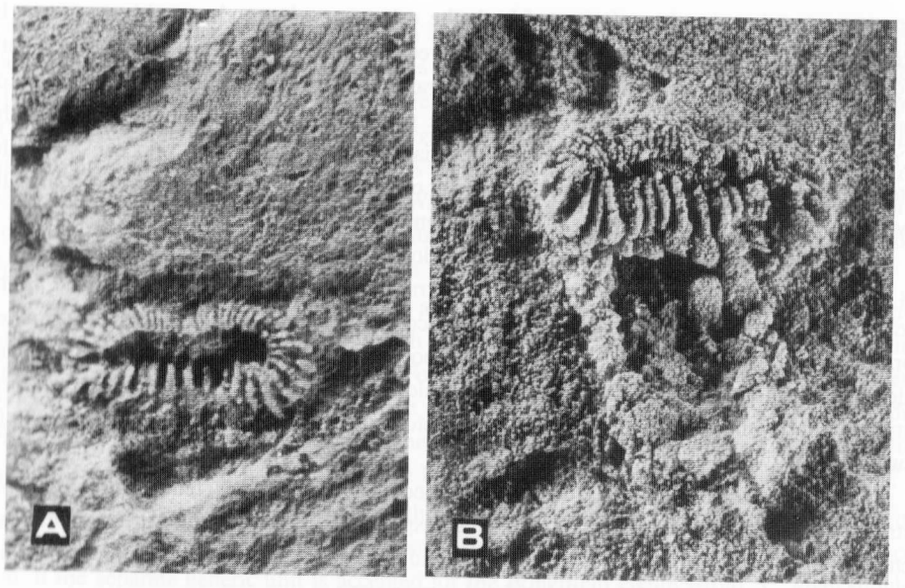

Fig. 4. — *Jugoszovia archaeocyathoides* n. gen and sp., Jugoszów 1a. Silicone casts of two relatively well preserved specimens. Both × 5 (see also pl. I, figs. 1-2) ; A, UWWG 2.2844, ctenoid apparatus in anterior view ; B, UWWG 2.2896, ctenoid apparatus and adjacent dorsal surface of the theca.

Fig. 4. — *Jugozsovia archaeocyathoides* n. gen. et sp., Jugoszów 1a. Moulages en silicone de deux spécimens assez bien conservés. × 5. A, UWWG 2.2844, vue antérieure de l'appareil cténoïde ; B, UWWG 2.2896, vue dorsale de l'appareil cténoïde et de la surface voisine de la thèque. (Voir aussi Pl. I, figs. 1, 2).

It shows a rather generalized morphology typical for early echinoderms. Although the possibility that some primitive edrioasteroid is associated with *Jugoszovia* cannot be completely excluded this is rather unlikely as no signs of radial or concentric arrangement of plates are recognizable.

FUNCTIONAL INTERPRETATIONS

The only part of the body of *Jugoszovia* which is known in detail, owing to numerous complete, even if partially preserved specimens, is its ctenoid apparatus. The medial suroral and four suborals on the opposite sides of the body are closely comparable to respective skeletal elements in other ctenocystoids and can be safely homologized with them.

Jugoszovia is probably the most primitive organization among the known, ctenocystoids. The plates of its ctenoid apparatus show much resemblance to the sclerites of the oral ring of the holothurians. Especially striking is the presence of prominent flat anterior

processes topping massive sclerites of both the calcereous ring and ctenoid apparatus. In Recent holothurians tentacles are located in between the anterior processes (Gage and Billett, 1986). Irrespective of whether the ctenoid apparatus and calcareous ring are homologous or only analogous, it seems reasonable to infer a presence of a tentacular apparatus in the Ctenocystoidea similar to that of the holothurians. Unlike the holothurian oral ring, the ctenoid apparatus does not show any pentameral organization. Instead, it is strictly bilaterally symmetrical, with differently built dorsal and ventral sides.

The mouth of *Jugoszovia* must have been located within the ring of ctenoid plates. It is thus somewhat surprising to find that the central part of the apparatus was plugged by the robust suroral plate, which was apparently in contact dorsally with transversely arranged prolongations (shelves) of the suboral plates. Food was thus either transported to the throat along both lateral sides of the suroral or, which seems rather unlikely because of firm arrangement of the thecal frame in later ctenocystoids, the apparatus changed its shape while swallowing.

The part of the theca of *Jugoszovia* immediately behind the ctenoid apparatus was strongly dorsoventrally compressed, which corresponds to similar shape of the body in other ctenocystoids. The main body was probably wider than the « neck », although this is not convincingly documented by available fossil specimens.

The thecal fragments associated with ctenoid apparatuses of Jugoszovia bear ambulacra similar to those of the helicoplacoids (Durham, 1993) and the edrioasteroid *Totiglobus* (Bell and Sprinkle, 1978). Possibly, the ambulacra from Jugoszów followed the helicoplacoid pattern as interpreted by Durham (1993), that is with pores exposed on sides, not to the interior of the ambulacral furrow.

As all specimens of *Jugoszovia* are strongly deformed it is also not possible to determine the degree of asymmetry in its body, although there is no reason to assume that in this respect it was much different from other ctenocystoids. Their anus is at the end of the body. According to Sprinkle (1992, p. 390), « ctenocystoids were apparently mobile, epifaunal ar barely infaunal detritus feeders that could probably swim short distances because of their streamlined shape and good bilateral symmetry. » This seems unlikely in case of *Jugoszovia*, which was probably epifaunal filter feeder, perhaps with some abilities to move on the sandy bottom.

EVOLUTIONARY RELATIONSHIPS

The best known ctenocystoid species is *Ctenocystis utahensis* Robison and Sprinkle, 1969, from the *Glossopleura* Zone of Utah and Idaho, which is represented by nearly 1.000 specimens (Robison and Sprinkle, 1969 ; Sprinkle and Robison, 1978). The *Glossopleura* Zone is of early Middle Cambrian age and corresponds to the late part of the *E. pinus* Zone ;

it is thus younger than the occurrences in the Jusgoszów section. Maximum length of the theca of *C. utahensis* is 9.0 mm, it was thus several times smaller than the Jugoszów species which was definitely more than 35 mm in length. In the slightly younger Wheeler Formation of Utah, corresponding in age to *Ptychagnostus atarus* Zone, closely related *Ctenocystis colodon* Ubaghs & Robison, 1988 occurs (Ubaghs & Robison, 1988). Ctenocystoids of similar age have been reported also from Wales (Jeffries *et al.*, 1987). Another species from France, *C. smithi* Ubaghs, 1987, although dated as late Middle Cambrian, is morphologically close to *C. utahensis*, being different in its larger suborals (Ubaghs, 1987).

Even more advanced in this respect, and geologically much younger, is *Etoctenocystis bohemica* Fatka and Kordule, 1985 which occurs in the *Paradoxides gracilis* Zone of the Jince Formation in Bohemia. The Jince Formation represent time equivalents of the latest *P. paradoxissimus* Stage and the early part of the following *P. forchhammeri* Stage (Šnajdr, 1958). Its suborals have long « arms » penetrating in between plates of the dorsal surface of the theca. More than 300 specimens have been found, their maximum length is 6.0 mm.

The most advanced end-member of this morphocline is *Ctenocystis jagoi* Jell, Burrett, and Banks, 1985 from Tasmania. The Tasmanian species has still more robust appearance and, if the separate generic unit is accepted for the Bohemian ctenocystoid, *C. jagoi* should be included in it, too. The ptychoparioid *Penarosa* and agnostoids suggest medial Middle Cambrian age according to Jell *et al.* (1985). If the morphologic advancement of *C. jagoi* corresponds to geological age, it must be younger than *E. bohemica.* Only five specimens have been collected, their maximum length is 9.0 mm.

Both the stratigraphic position and anatomy of *Jugoszovia* point to its ancestral position in respect to other Ctenocystoidea. The uniform plating of the body and its apparent flexibility are undoubtedly archaic characters which have been later replaced by more and more box-shaped appearance of the theca. The number of plates in the ctenoid apparatus of *Jugoszovia*, higher than in later representatives of the group, probably reflects its relatively large size, more than 7 mm in width. It is 1.3 times wider than that of *Ctenocystis.*

The relationships of the Ctenocystoidea remain enigmatic and they are rarely considered in reviews of the early phylogeny of the echinoderms. Until the present reinterpretation of the Jugoszów material, the group was known only on the basis of highly derived, late species with massive plating of small thecae. Starting from data available then, Ubaghs (1975) pointed out similarities of *Ctenocystis* to stylophoran carpoids, namely 1) the location of mouth and anus at opposite ends of the body, 2) the occurrence of a marginal framework composed of lower and upper plates, and 3) the probable association of the right anterolateral with an opening of hydropore or gonopore. Ubaghs' phylogenetic interpretation has been followed by Sprinkle (1992), and Friedrich (1993) has extensively discussed possible relationships of the ctenocystoids with the cinctan « carpoids. »

The uniform plating of the theca in the oldest known Jugoszów ctenocystoid and the presence of the most massive plates in the youngest known species of the group convincingly show that the marginal frame of *Ctenocystis* is a derived feature. Such homology with the

Stylophora would require that its ctenoid apparatus developed independently of *Jugoszovia*, which is hard to accept.

The body plan and feeding behavior of *Jugoszovia* is comparable to that of the holothurians. Phylogenetic implications of this similarity remain to be explored. The typical ctenocystoids are anatomically too derived to be directly related to any later echinoderms but this does not necessarily apply to *Jugoszovia*. The oldest holothurians with known body organization are latest Silurian (Gilliland, 1993) and early Devonian in age (Seilacher, 1961). They show clear radial organization of the calcareous ring. Their ancestor-descendant relationships with *Jugoszovia*-like ctenocystoids would require that the pentameral organization of their tentacular apparatus and ambulacra must have developed after derivation from the ctenocystoid stock. It is unlikely that the pelmatozoans developed their pentameral symmetry independently from the holothurians. It would require the eocrinoids and edrioasteroids have developed their symmetry from the ctenocystoid-holothurian lineage after the radial symmetry already developed pelmatozoans. This may mean that the eleutherozoans were ancestral to the pelmatozoans, which is an idea hard to accept.

In any case *Jugoszovia* is the most archaic member of its class. The question of the origin of *Jugoszovia* may thus appear closely connected with the problem of the ancestry of the whole phylum Echinodermata. The most remarkable seems to be the proposed presence of oral tentacles supported by the ctenoid apparatus. In fact this is implied by Nichols' (1967) hypothesis of homology between the water-vascular system of the echinoderms and the coelomic cavities filling tentacles in the sipunculids.

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PLATE I

Jugoszovia archaeocyathoides n. gen. and sp., silicone casts (all × 3)

FIG. 1. – UWWG 2.2844, ctenoid apparatus in oral view, Jugoszów 1a.

FIG. 2. – UWWG 2.2896, ctenoid apparatuses in dorsal view, Jugoszów 1a.

FIG. 3. – UWWG 2.2843, ctenoid apparatuses in dorsal view, Jugoszów 1a.

FIG. 4. – UWWG 2.2886, ctenoid apparatus in ventral view, Jugoszów 1a.

FIG. 5. – UWWG 2.2917, ctenoid apparatus in ventral view, Jugoszów 1a.

FIG. 6. – UWWG 2.2780, ctenoid apparatuses with significant portion of the thecal « neck » in dorsal view, Usargów 19.

FIG. 7. – UWWG 2.2425, part of theca with ambulacrum possibly belonging to this species in dorsal view, Jugoszów 3.

FIG. 8. – UWWG 2.2913, theca with suboral plates of the ctenoid apparatus, Jugoszów 1a (15d).

FIG. 9. – UWWG 2.2918, set of three linearly arranged ctenoid apparatuses cut off with « necks » (coprolite or predator's gut content), Jugoszów 1a.

FIG. 10. – UWWG 2.2914, similarly associated truncated « necks », Jugoszów 1a.

PLANCHE I

Jugoszovia archaeocyathoides gen. et sp. nov., Moulages silicones (× 3)

FIG. 1. – UWWG 2.2844. Appareil ctenoïde, face orale. Jugoszów 1a.

FIG. 2. – UWWG 2.2896. Appareil ctenoïde, face dorsale. Jugoszów 1a.

FIG. 3. – UWWG 2.2843. Appareil ctenoïde, face dorsale. Jugoszów 1a.

FIG. 4. – UWWG 2.2886. Appareil ctenoïde, face ventrale. Jugoszów 1a.

FIG. 5. – UWWG 2.2917. Appareil ctenoïde, face ventrale. Jugoszów 1a.

FIG. 6. – UWWG 2.2780. Face dorsale de l'appareil ctenoïde avec une grande partie du « col » thecal. Usarzów 19.

FIG. 7. – UWWG 2.2425. Face dorsale d'un fragment de thèque avec ambulacre pouvant appartenir à la même espèce. Jugoszów 3.

FIG. 8. – UWWG 2.2913. Thèque avec les plaques suborales de l'appareil ctenoïde. Jugoszów 1a (15d).

FIG. 9. – UWWG 2.2918. Alignement de 3 appareils ctenoïdes sectionnés et pourvus d'un « col » (coprolithe ou contenu intestinal de prédateur). Jugoszów 1a.

FIG. 10. – UWWG 2.2914. Même association de « cols » coupés que sur la fig. 9. Jugoszów 1a.

PLATE II

Jugoszovia archaeocyathoides n. gen. and sp., silicone casts

FIG. 1. – UWWG 2.2908, holotype, dorsal wall of the theca exposed, numerous sclerites cover the ambulacrum, Jugoszów 1 (× 3).

FIG. 2. – Same specimen before preparation, deeper layers exposed. Note continuation between the « neck » and the theca (× 3).

FIG. 3. – Large theca from Jugoszów 3, possibly representing medially folded dorsal part of Jugoszovia archaeocyathoides n. gen. and sp. or an eocrinoid, part (× 2).

FIG. 4. – Same specimen, counterpart (× 2).

PLANCHE II

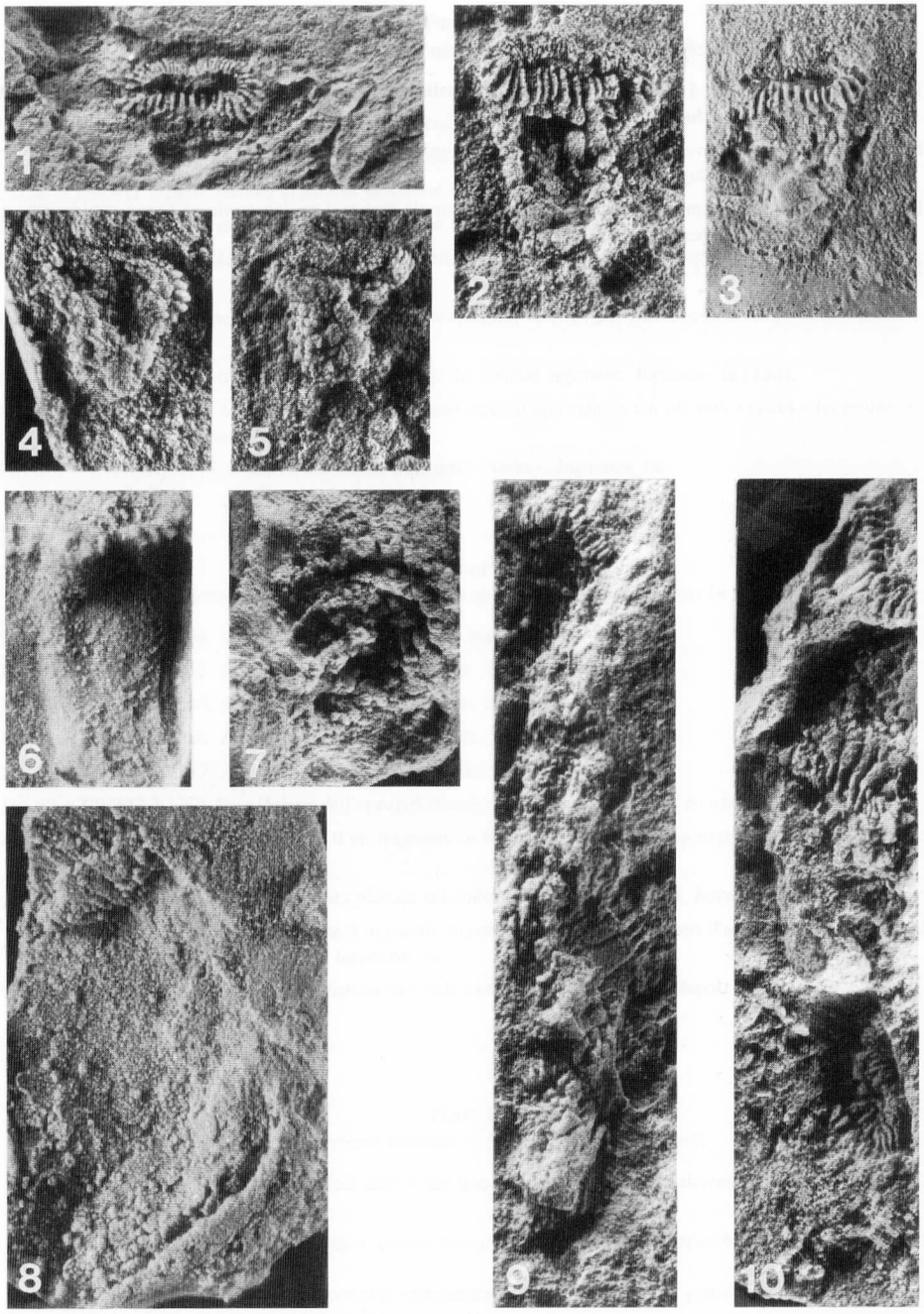
Jugoszovia archaeocyathoides gen. et sp. nov. Moulages silicones (× 3)

FIG. 1. – UWWG 2.2908. Holotype. Paroi dorsale de la thèque exposée avec de nombreux sclérites couvrant l'ambulacre. (× 3). Jugoszów 1a.

FIG. 2. – Même spécimen avant préparation montrant les couches plus profondes. Noter la continuité entre le « col » et la thèque (× 3). Jugoszów 1a.

FIG. 3. – Grande thèque représentant peut-être la partie dorsale repliée d'un *Jugoszovia archaeocyathoides* gen. et sp. nov. ou d'un Eocrinoïde (× 2). Jugoszów 3.

FIG. 4. – Même spécimen. Contre-empreinte (× 2).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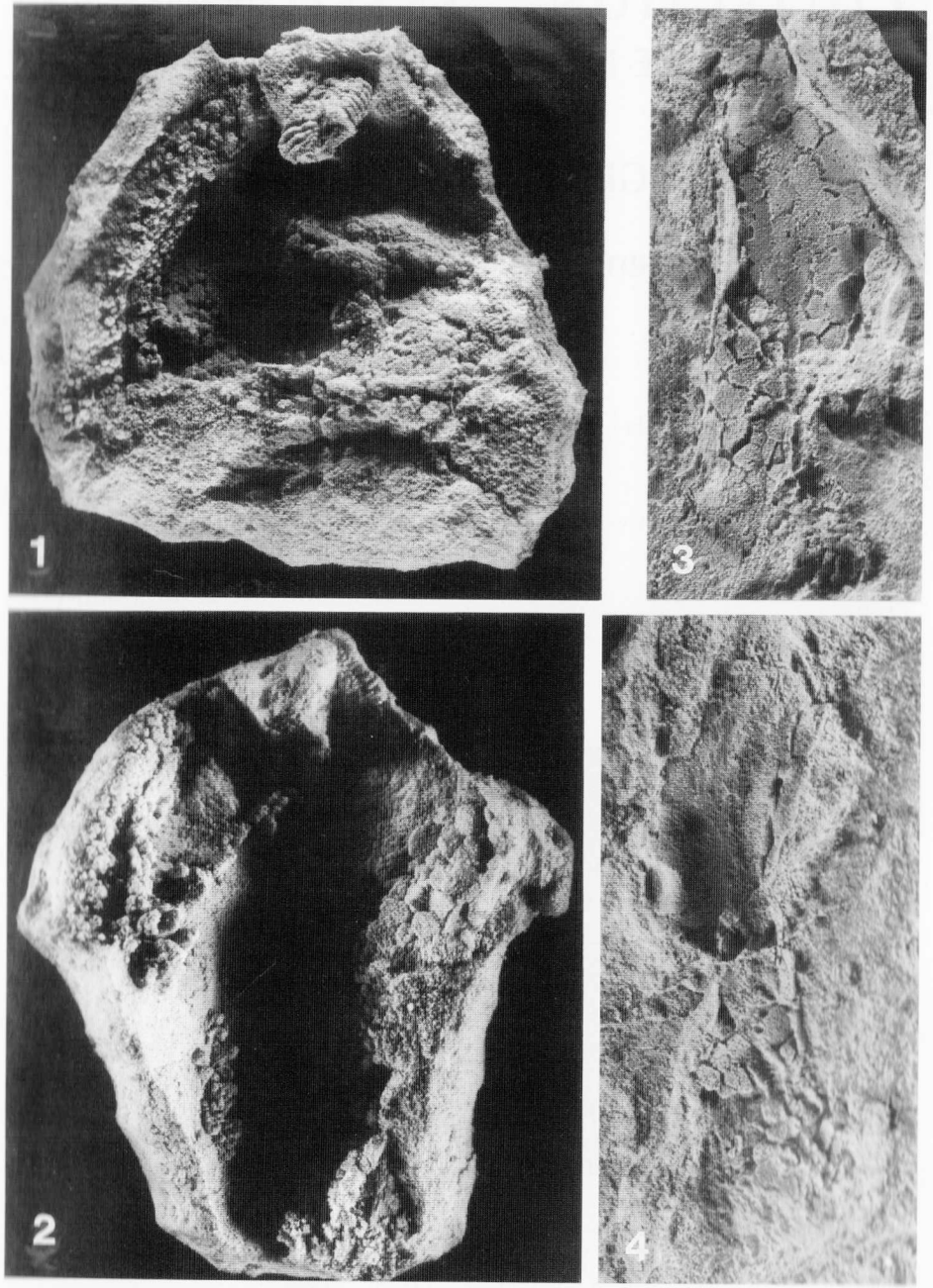
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