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ISOLATED SCLERITES OF DEVONIAN NON-PELMATOZOAN ECHINODERMS

(IZOLOWANE SKLERYTY DEWOŃSKICH SZKARŁUPNI BEZŁODYGOWYCH)

by

ANDRZEJ BOCZAROWSKI

(WITH 76 TEXT-FIGURES AND 19 PLATES)

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ISOLATED SCLERITES OF DEVONIAN NON-PELMATOZOAN ECHINODERMS

ANDRZEJ BOCZAROWSKI

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Isolated echinoderm sclerites have been obtained from carbonaceous and clayey Devonian rocks (Emsian–Frasnian) from the Holy Cross Mountains (Poland), by dissolving them in acetic acid buffered by calcium acetate or in calgone mixed with perhydrol. 60 new and 10 already known biologically understood species and 59 incomplete sklerotomes are recognised. In volume, ophiuroids form the largest component of the collection, but their taxonomic diversity is rather low, with recurrent assemblages of similar composition. Usually a single species dominates them. Sclerites of *Furcaster* comprise up to 90% of specimens and locally may be rock-forming. Described are three new genera of ophiuroids (*Umerophiura*, *Astutuaster*, *Weigeltura*), 16 new species; distinguished are 35 scleritomes of spines, scales, and other elements. The cyclocystoids are common, represented by nine new genera (*Linguacycloides*, *Neocyclocystoides*, *Smithocycloides*, *Platycycloides*, *Apparatocycloides*, *Paradoxocycloides*, *Concavocycloides*, *Brutocycloides*, *Chimaerocycloides*) and eleven new species classified in the new family Apycnodiscidae. Ophiocistioid remains are also common, their assemblages being of even lower diversity. Eight genera (three of them new: *Erisserra*, *Longiserra*, *Ornatoserra*) contain seven new and three earlier known species. Echinoid assemblages are highly differentiated, but their precise taxonomic identifications are rarely possible. Three scleritomes and numerous assemblages of pedicellariae are described (among them *Bursulella*). Holothurians are the most differentiated. Described are 30 species (25 of them new) and nine new genera (*Ballistocucumis*, *Palaeohemioedema*, *Staurocaudina*, *Priscocaudina*, *Propinquoohshimella*, *Palaeocaudina*, *Bracchiothuria*, *Gagesiniotrochus*, *Ocellothuria*), based not only on dermal sclerites, but also on calcareous rings. The new family Palaeocaudinidae and six new subfamilies, namely Devonothyoninae, Palaeohemioedemiinae, Staurocaudininae, Eocaudiniinae, Calclamninae, and Propinquoohshimellinae, including new and old genera, have been proposed.

Key words: Ophiuroidea, Ophiocistioidea, Echinoidea, Holothurioidea, evolution, fossils, stratigraphy, Devonian, Holy Cross Mountains, Poland.

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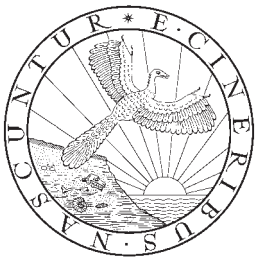

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INTRODUCTION

Most of the new data on the Devonian echinoderms presented in this paper have been extracted from fossil material collected in exposures in the Holy Cross Mountains area in central Poland. During the Mid and Late Devonian sedimentation of more or less calcareous clays and muds took place over a significant part of the present day Holy Cross Mountains. These sediments contain masses of non-pelmatozoan echinoderm skeletons: ophiuroids, asteroids, echinoids, holothurians, as well as cyclocystoids and ophiocistioids. New methods of maceration have enabled extraction of extremely rich assemblages of echinoderm sclerites from these strata. Attempts have been made to identify species in collections of isolated skeletal elements. Coeval fossil materials from elsewhere have been reinterpreted in the same way. The main aim of the present paper is the biological interpretation of the succession of soft-bottom echinoderm faunas in the Devonian.

In life, sclerites of the studied echinoderms were connected only by soft tissues, but it was occasionally possible to recover multi-sclerite assemblages. This has helped in reconstructing complete scleritomes of particular species. These reconstructions are also based on comparison with fossil species and related extant forms where sclerite composition is known precisely. Associations of sclerites thus described are defined as scleritomes. The scleritome is an association of all types of skeletal elements of one species (Bengtson 1985). If the fossil taxa are described on the basis of isolated elements, the applied palaeontological nomenclature is valid in terms of the biological taxonomy, unless explicitly defined as parataxa (Bengtson 1985). This approach has already been suggested by Haude (1992) and Gilliland (1993) who underlined the high value of natural aggregates of sclerites for anatomy and systematics of fossil echinoderms.

The sampled interval ranges from the Late Emsian (conodont *Polygnathus patulus* Zone) to the latest Frasnian (*Palmatolepis linguiformis* Zone). Particular samples represent the main transgressive pulses identified in the Holy Cross Mountains Devonian (Racki 1992). The Late Frasnian crisis resulted in a profound impoverishment and transformation of echinoderm faunas. The Famennian assemblages show more similarity with those of the Early Carboniferous rather than the Frasnian; therefore they have not been included in the present study. Descriptions of the sampling localities and sections have been given by Racki (1992).

The material is housed at the Museum of Department of Earth Sciences, Silesian University, Poland (abbreviated GIUS).

Acknowledgements. — The present monograph is a modified version of the author's Ph.D. thesis, supervised by Professor Jerzy Dzik of the Institute of Palaeobiology of the Polish Academy of Sciences in Warsaw.

Sincere thanks are given to Jan Malec, M.Sc., of the State Geological Institute, the Holy Cross Branch in Kielce, for supplying data on stratigraphy of the Łysogóry region of the Holy Cross Mountains and for giving access to his paleontological collections and samples. Advise and moral support was also given by Professor Sonia Jachowicz, head of the Chair of Palaeontology and Stratigraphy of the University of Silesia. Professor Grzegorz Racki helped in collecting samples and provided constructive criticism of my research; all the other workers of the laboratory, particularly Grażyna Rusin, M.Sc., offered much help and support that enabled me to carry out this research. Krzysztof Jasik D.Sc. and Jerzy Podsiadło M.D. of the Silesian Medical School in Katowice and Piotr Dzierżanowski D.Sc. of the Warsaw University are acknowledged for their help and taking of photographs. Enormous help and support in all stages of my investigations by my wife, Barbara is deeply appreciated.

Doctors Raimund Haude and Frank Langestrassen of the Göttingen University have kindly demonstrated the collection of German echinoderms under their care and have kindly guided the present author to some echinoderm-bearing outcrops in the Rhenish Slate Mountains and the Harz. Thanks are also due to Krzysztof Łysogórski of the Gliwice Technical University for permission of comparative studies on the unique collection of echinoderms from Hunsrück (Bundenbach Slates) and other regions.

Photographs were made with the scanning electron microscopes: Tesla BS 300 at the Institute of Geochemistry, Mineralogy and Petrography of the Warsaw University and the SEMCO Nanolab 7 of the Laboratory of Electron Microscopy of the Silesian Medical School in Katowice.

I am very thankful to Dr. Andrew B. Smith for his very thorough and helpful review and for improving the English language of the manuscript.

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MATERIAL AND METHODS

Calcareous rocks were etched in calcium acid buffered by calcium acetate. The best results were obtained using a mixture of 1/2 supersaturated acetate, 1/4 30% acetic acid, and 1/4 water. During treatment of calcareous sediments the micritic components are dissolved first, whereas sparite is relatively resistant to etching, because of its larger volume to surface ratio. Thus predominantly micritic rocks have relatively larger surface area of reaction. Loosened grains of sparite fall down to the bottom where they become covered by protective layer of clayey residue and are therefore only weakly attacked by corrosion. It was experimentally confirmed that elements 0.3–1.3 mm in diameter showed the best preservation. Larger grains commonly show visible traces of etching, significantly increasing in largest specimens. Grains 0.08–0.29 mm in diameter are relatively well preserved, with the smaller ones strongly corroded. It is advisable to wash the residue every 24 hours. With bituminous marly limestones well preserved elements smaller than 0.3 mm were obtained after adding detergents to the etching solution. The maceration was slower, but the results were better. For example Śniadka III samples yielded about 150 thousand elements per kg weight without detergents, usually of poor preservation. Particularly flat and/or elongate sclerites were rare and strongly etched. When using detergents results were worse for the thicker grains, i.e. over 0.3 mm diameter, but about ten million smaller specimens per kg were recovered. The residue was washed in water using a sieve of 0.02 mm pore size. The remaining fragments were transferred into a glass vessel and residual acids were neutralised by adding a small amount of Na_2CO_3. The organics in the macerate (if any and if accompanied by clay residue) were removed through addition of perhydrol and calgone, the only disintegration factor (peptiser) active in presence of calcium ions. The peptiser causes a change of electric charge on colloidal surfaces (clayey particles including), and results in disintegration (peptization) of their aggregates.

The porous limestones were macerated using the method of Bolli (Witwicka *et al*. 1958) using Na_2CO_3 and benzine. The method of macerating of greasy clays elaborated by C.A. Wicher (Witwicka *et al*. 1958) i.e. boiling the sample in water with addition of Na_2CO_3 was also used. Strongly compacted clays were macerated in perhydrol using the method of F.H. van Oyen (Witwicka *et al*. 1958); some modifications of the latter method were introduced, however. Firstly the rock was dried, then the hot sample was treated with perhydrol, with small admixture of Na_2CO_3, in a flume hood. The fragmented rock was then boiled for 30 minutes in water with small amounts of Na_2CO_3 and perhydrol.

Maceration of some clayey shales was only possible with benzine (method developed by N.M. Layne; Witwicka *et al*. 1958). Usually, however, the peptisation method, as adapted from pedology, was used in a slightly modified form. To obtain one litre of peptiser, 135 g of calgone hexanatrium metaphosphate ($Na_6P_6O_{12}$) and 8 g of Na_2CO_3 should be solved in distilled water, then put away for two days before use. For samples with high content of clay the amount of peptiser approximately equal to that of the sample was applied for one day. For deposits with various clay content and for cleaning the post-maceration residue, samples were boiled for about 40 minutes with peptiser amount weighing about one-tenth of the residue and added water.

To avoid internal reflections of light and flashes at margins of spar crystals specimens were coated with fine-grained silver.

SYSTEMATIC PART

Phylum **ECHINODERMATA** Klein, 1734
Subphylum **ASTEROZOA** Zittel, 1895
Class **OPHIUROIDEA** Gray, 1840

The complex structure of the skeleton of fossil Ophiuroidea is probably the reason that their dispersed remains are studied so rarely. Also scarce are descriptions of complete specimens of Palaeozoic ophiuroids (Lehmann 1957; Schöndorf 1911; Schuchert 1914, 1915; Spencer 1914–1940; Spencer and Wright 1966; Stürtz 1886a, b, 1890). The main source of information on complete Devonian ophiuroid skeletons, exceptionally well-preserved pyritised specimens of the Bundenbach Slates in the Hunsrück Mountains, do not dis-

play anatomical details (cf. Lehmann 1957). As a rule, they do not provide enough information on the morphology of the particular elements.

Nevertheless it is only the analysis of isolated sclerites which allows full understanding of the skeletal anatomy of these organisms. Their location in the scleritome can only be properly identified where complete skeletons of related species are known. Therefore, specimens which can be cast in latex are especially helpful and provide morphologic details of particular sclerites. In the Devonian such data are offered by specimens of *Encrinaster* from the Siegenian of the Rhenish area (Grabert and Grabert 1956) and Emsian of the Eifel Mountains (Strauch and Pockrandt 1985). From the Early Devonian of the latter area other genera were also described (Lehmann 1957; Schöndorf 1911; Stürtz 1890). Some fragments, assigned here to *Weigeltura* gen. n. (cf. Becker and Weigelt 1975) and other protasterid ophiuroids (Grabert and Grabert 1965) come from the Mid Devonian. The Late Devonian species were described by Paul (1939), Schmidt (1944), and Haude and Thomas (1983). In addition a few genera of ophiuroids known from the Carboniferous of the Rhenish Slate Mountains (Hahn and Brauckmann 1981; Haude 1982) occur also in the Devonian of the Holy Cross Mountains. Palaeozoic ophiuroids are known also from other areas of Europe and the North America (Jaekel 1903; Kesling 1970, 1971, 1972; Kesling and Le Vasseur 1971; Smith 1984; Schwarzbach and Zimmermann 1936; Ubaghs 1941, 1942). The taxonomic discussion and decisions presented below are based on the assumption that the morphology of particular sclerites can be used to diagnose taxa of various ranks. It is highly probable that species-level differences concerned characters which cannot be discerned in isolated sclerites material (for instance proportions in arm length or disc diameter). However, these are obvious limitations of the whole fossil record. Potentially, future discoveries of more complete material may help in developing more precise taxon diagnoses, in the same way as findings of articulated vertebrate skeletons change understanding of tooth-based taxa.

Order **Stenurida** Spencer, 1951
Suborder **Proturina** Spencer *et* Wright, 1966
Family **Pradesuridae** Spencer, 1951
Genus *Stuertzaster* Etheridge, 1899

Type species: *Stuertzaster marstoni* (Salter, 1857).

Diagnosis. — Aboral side of central disc is highly swollen, encrusted by network with radiate spicules. Arms short and wide, ambulacrals with thin, big groove. Laterals with wide, strong juncture. Very long, thin spines consist of three blades.

Remarks. — The genus has been recorded only from the Early Devonian of Germany. Some specimens of *Tetravirga* Frizzell *et* Exline, 1955 possibly belong here. The lateral plates and spicules of species described below are unlike any other described so far, having less numerous mamelons on their lateral plates than the type species, with a biserial arrangement on the proximal plates.

Stuertzaster liquidus sp. n.
(Text-fig. 1A–I)

Holotype: GIUS 4-439 Śni./877/2, Text-fig. 1B.

Type horizon: Early Givetian, *Polygnathus hemiansatus* Zone.

Type locality: Outcrop III at Śniadka, Holy Cross Mountains.

Derivation of the name: From Latin *liquidus* – distinct, certain.

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)			
Number of specimens	Features	Holotype	Minimum	Mean	Maximum
Ambulacral plates: 6	Length	–	760	950	1220
	Width	–	745	810	900
Lateral plates: 10	Length	795	320	690	930
	Height	965	475	865	1135
	Width	1170	625	1150	1490
Anchor-like spicules: 27	Length	–	475	520	565
	Height	–	200	950	1085

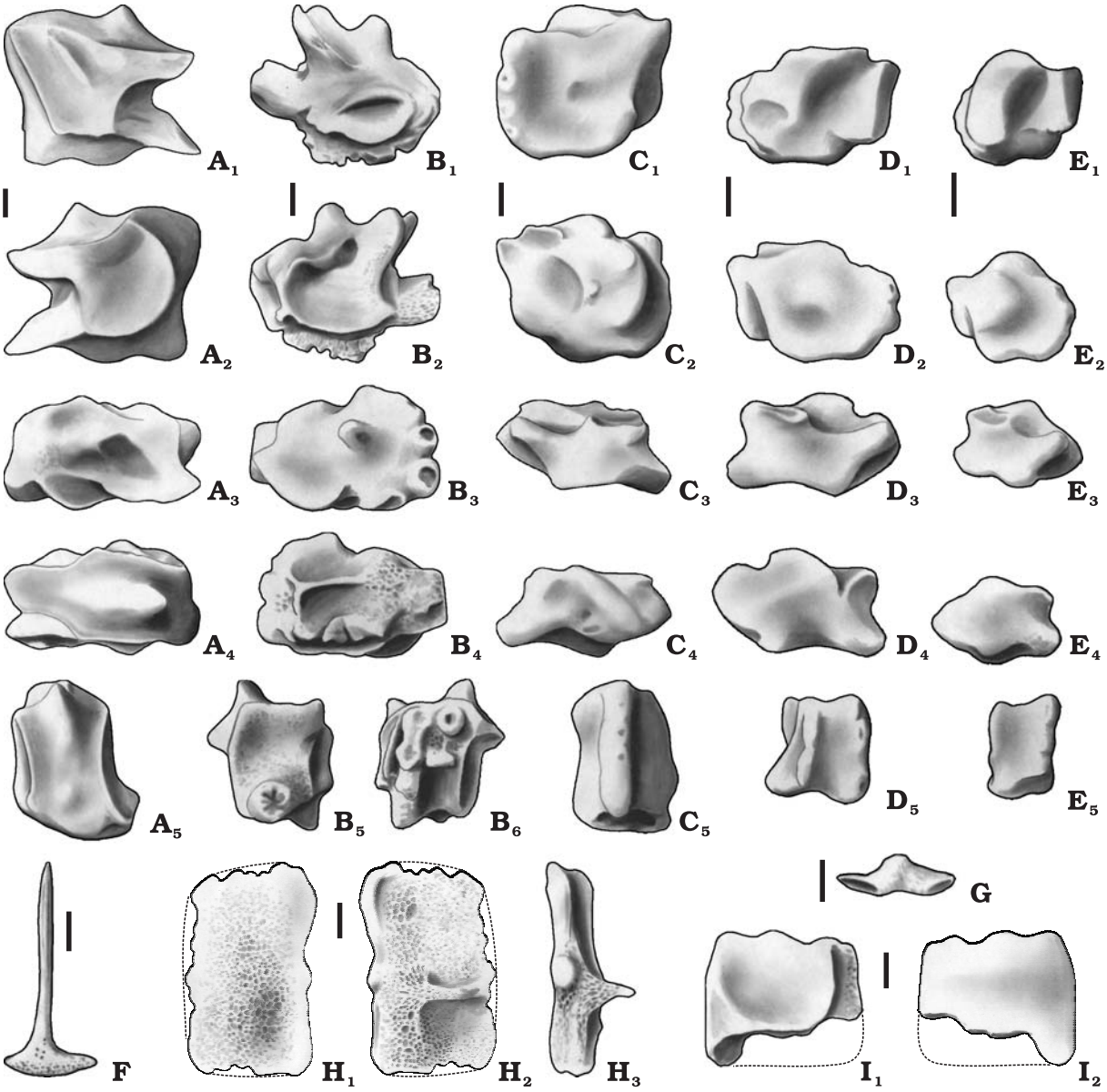

Fig. 1. Skeletal elements of the ophiuroid *Stuertzaster liquidus* sp. n. from the Early Givetian of outcrop III at Śniadka, Holy Cross Mountains. **A**. Lateral plate GIUS 4-439 Śni./877/1 from the middle part of the arm; A_1 proximal view, A_2 distal view, A_3 dorsal view, A_4 ventral view, A_5 outer view. **B**. Holotype lateral plate GIUS 4-439 Śni./877/2 from the proximal part of the arm; B_1 proximal view, B_2 distal view, B_3 dorsal view, B_4 ventral view, B_5 outer-oblique view, B_6 outer view. **C**. Lateral plate GIUS 4-439 Śni./877/3 from the middle part of the arm; C_1 proximal view, C_2 distal view, C_3 ventral view, C_4 dorsal view, C_5 outer view. **D**. Lateral plate GIUS 4-439 Śni./877/4 from the middle part of the arm; D_1 distal view, D_2 proximal view, D_3 ventral view, D_4 dorsal view, D_5 outer view. **E**. Lateral plate GIUS 4-439 Śni./877/5 from the distal part of the arm; E_1 distal view, E_2 proximal view, E_3 dorsal view, E_4 ventral view, E_5 outer view. **F**. Anchor-like spicule GIUS 4-439 Śni./916/2 lateral view. **G**. Anchor-like spicule GIUS 4-439 Śni./916/1 lateral view. **H**. Ambulacral plate GIUS 4-439 Śni./933/1 from the proximal part of the arm; H_1 dorsal view, H_2 ventral view, H_3 distal view. **I**. Ambulacral plate GIUS 4-439 Śni./933/2 from the middle part of the arm; I_1 ventral view, I_2 dorsal view. Scale bar 200 μm.

Diagnosis. — Up to five mamelons usually only weakly developed on the narrow outer lateral surface of the lateral plate. Vertical processes of the anchor-like spicules from the central disc are very long and attain up to seven-eighths of their height.

Description. — Ambulacral plates. When compared with those of the other species of the genus, the plates, of rectangular outline, are thinner and are smooth on the dorsal side; on their ventral side there occurs a groove, perpendicular to the arm axis (Text-fig. 1H–I).

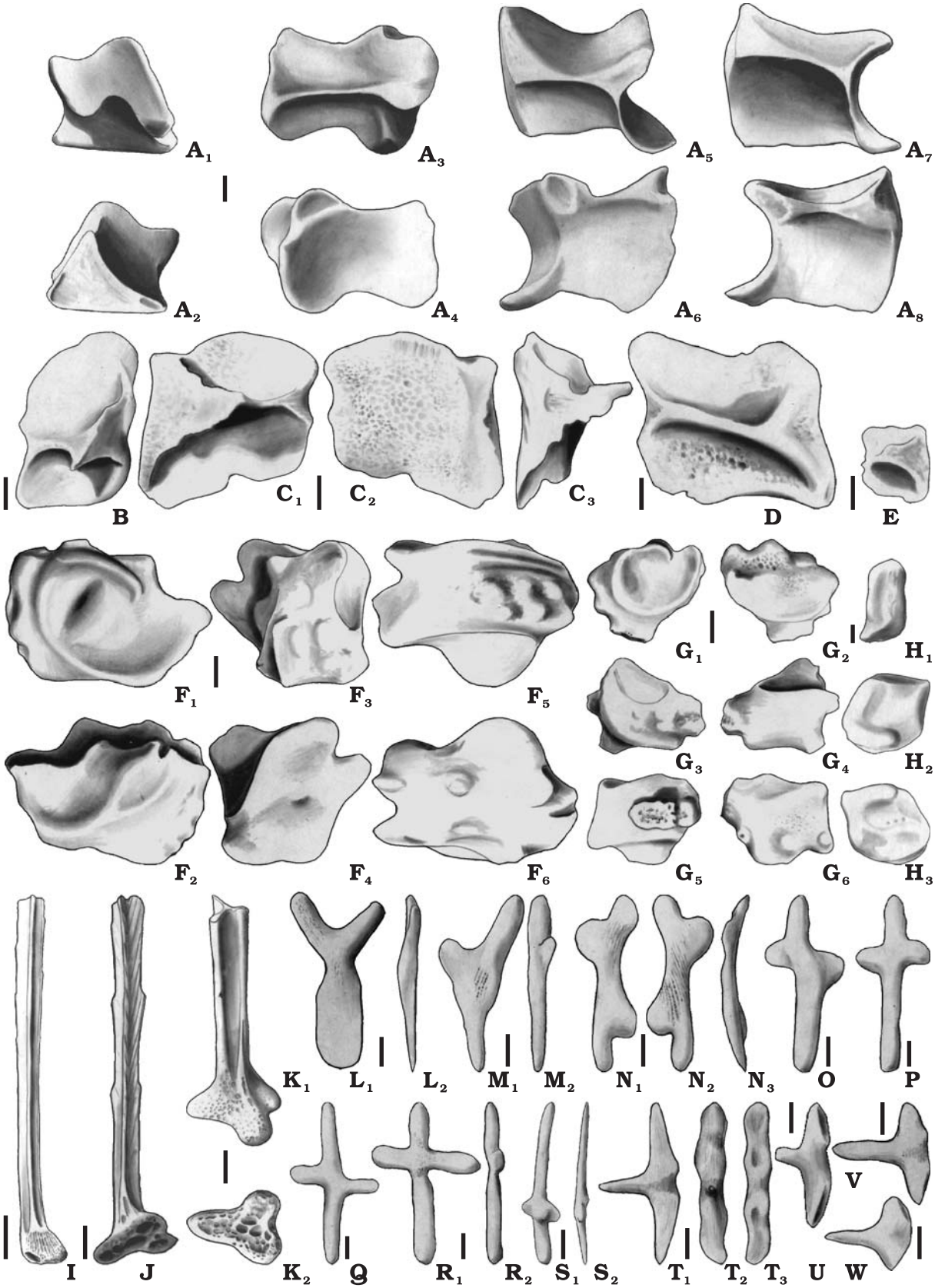

Fig. 2. Skeletal elements of the ophiuroid *Stuertzaster utroquecognitus* sp. n. from the Late Givetian of Marzysz, Holy Cross Mountains, samples Marzysz II/4 (A, C–E), Marzysz II/6 (B, L–W), Marzysz II/13 (F–K). **A**. Mouth-angle plate GIUS 4-575 Mrz./313/1; A_1 proximal view, A_2 distal view, A_3 adaxial view, A_4 abaxial view, A_5 oral-oblique view, A_6 aboral-oblique view, A_7 oral view, A_8 aboral view. **B**. First ambulacral plate from the proximal part of the arm GIUS 4-568 Mrz./976/1, oral view. ➝

Lateral plates. These plates have complicated surfaces, forming junctions with the neighbouring laterals and with the ambulacral plates. On the proximal surface there is a small ridge, corresponding to the depression at the neighbouring distal side of the next lateral plate. Closer to the distal part of the arm the articulation surfaces become more and more flat. Ventrally the lateral plate has flattened sides, so in plane of section perpendicular to the arm axis it is T-shaped, corresponding to the outer lateral edges of the ambulacral plates. Its ventral side is flat. Specimens from the distal parts of arms seem to lack mamelons. Proximal lateral plates have more distinct sculpture and, occasionally, stronger mamelons, although the latter may be lacking completely (Text-fig. 1A–E). The lateral plates from middle and distal parts of arm have a distinct elevated ring around the marginal edge. It penetrates the corresponding depression of the opposite plate. Arm spines are known from crushed fragments only, so their structure cannot be reconstructed.

Spicules from the central disc. Only anchor-shaped spicules have been recognised. The base of the spicule has a flat truncation, possibly the attachment area with the neighbouring spicules, devoid of any articulation sculpture (Text-fig. 1F–G).

Remarks. — From *Stuertzaster utroquecognitus* sp. n. the present species differs in having more elongated lateral plates with few mamelons.

Occurrence. — Only known from the type locality.

Stuertzaster utroquecognitus sp. n.
(Pl. 1: 1–14; Text-fig. 2A–W)

Holotype: GIUS 4-584 Mrz./190/1, Text-fig. 2F.

Type horizon: Late Givetian, Early *Mesotaxis falsiovalis* Zone.

Type locality: Trench II, layer 13 at Marzysz, Holy Cross Mountains.

Derivation of the name: From Latin *utroque* – at both sides, *cognitus* – recognised, due to data for the skeletal elements.

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)			
Number of specimens	Features	Holotype	Minimum	Mean	Maximum
Mouth angle plates: 3	Length	–	630	660	680
	Width	–	980	1020	1050
Ambulacral plates: 40	Length	–	820	950	1185
	Width	–	495	895	1185
Lateral plates: 34	Length	880	220	655	880
	Width	1065	305	795	1065
	Height	830	540	785	830
Anchor-like spicules: 45	Length	–	355	820	1000
	Height	–	340	450	510
Crossed spicules: 128	Length	–	1000	1315	1665
Spines: > 500	Length	–	1300	1550	1840
	Diameter of base	–	205	330	510

C. Ambulacral plate GIUS 4-575 Mrz./313/2 from the middle part of the arm; C_1 ventral view, C_2 axial-lateral view, C_3 dorsal view. **D**. Ambulacral plate GIUS 4-575 Mrz./313/4 from the middle part of the arm, ventral view. **E**. Ambulacral plate GIUS 4-575 Mrz./313/3 from the distal part of the arm, ventral view. **F**. Holotype lateral plate GIUS 4-584 Mrz./190/1 from the proximal part of the arm; F_1 distal view, F_2 proximal view, F_3 outer view, F_4 inner view, F_5 ventral view, F_6 dorsal view. **G**. Lateral plate GIUS 4-584 Mrz./190/2 from the middle part of the arm; G_1 distal view, G_2 proximal view, G_3 outer view, G_4 inner view, G_5 ventral view, G_6 dorsal view. **H**. Lateral plate GIUS 4-584 Mrz./190/3 from the distal part of the arm; H_1 ventral view, H_2 proximal view, H_3 distal view. **I**. Spine with rounded base GIUS 4-584 Mrz./1115/1, lateral view. **J**. Spine with trilobate base GIUS 4-584 Mrz./1115/2, lateral view. **K**. Spine with trilobate base GIUS 4-584 Mrz./1115/3; K_1 oblique view, K_2 view of base. **L–W**. Radiate spicules from aboral surface of the arms and highly swollen part of central disc. **L**. Symmetrical triradiate spicule GIUS 4-568 Mrz./37/1; L_1 aboral view, L_2 lateral view. **M**. Asymmetrical triradiate spicule GIUS 4-568 Mrz./37/2; M_1 aboral view, M_2 lateral view. **N**. Asymmetrical crossed spicule GIUS 4-568 Mrz./37/3; N_1 aboral view, N_2 opposite side, N_3 lateral view. **O**. Asymmetrical cruciform spicule GIUS 4-568 Mrz./37/4, aboral view. **P**. Cruciform spicule GIUS 4-568 Mrz./37/6, aboral view. **Q**. Crossed spicule GIUS 4-568 Mrz./37/8, aboral view. **R**. Cruciform spicule GIUS 4-568 Mrz./37/7; R_1 aboral view, R_2 lateral view. **S**. Elongate, crossed spicule GIUS 4-568 Mrz./37/5; S_1 aboral view, S_2 lateral view. **T**. Anchor-like spicule GIUS 4-568 Mrz./36/1; T_1 lateral view, T_2 aboral view, T_3 opposite side (oral? view). **U**. Anchor-like spicule GIUS 4-568 Mrz./36/4, lateral view. **V**. Anchor-like spicule GIUS 4-568 Mrz./36/3, lateral view. **W**. Anchor-like spicule GIUS 4-568 Mrz./36/2, lateral view. Scale bar 200 μm.

Diagnosis. — Lateral plates with up to eight, weakly developed mamelons on the narrow outer lateral surface. On the ventral side the laterals do not flatten laterally towards the arm axis and maintain a uniform width. Vertical processes of the anchor-like spicules of the central disc are short – up to half of their height.

Description. — Mouth-angle plate. On the proximal side there is a semicylindrical depression. The abaxial and aboral surfaces are flat, on the other hand the adaxial and oral surfaces have prominent ridges (Text-fig. 2A).

Ambulacral plates. They are of various shapes: rectangular, rhomboid or square (distal ones) with rounded corners (Text-fig. 3B–E). Proximal ambulacral plates have a proximal ventral area asymmetrically enlarged and expanded (Text-fig. 2B).

Lateral plates. Towards the distal part of the arm lateral plates become more and more oval (Text-fig. 2F–H). Contact between the lateral and ambulacral plates is wavy. Mamelons and pits are absent on specimens from the distal part of the arm. Proximal lateral plates have better developed sculpture and, occasionally, strong mamelons, towards the distal part of an arm, the mamelons gradually disappear. Lateral plates from the distal part of an arm have an elevated ring around the marginal edge on their proximal side and marginally near the outer and ventral edge, juxtaposed with the corresponding depression of the opposite plate. On the other hand at the distal side, the ring around the marginal edge lies along the ventral and dorsal edges.

Spines. The shaft consists of three blades converging at the axis. The blades have ocassional scarce groovelets, peripherally terminated by short splinters. The spine base is oval or trilobate when seen from the base (Pl. 1: 10–14; Text-fig. 2I–K).

Spicules from the central disc. The anchor-like basal part of the spicules on the adoral side has flat terminal truncations, possibly forming attachment areas with the neighbouring spicules, without any processes (Pl. 1: 1–4; Text-fig. 2T–W). Other spicules are strongly variable in shape (Pl. 1: 5–9, 14; Text-fig. 2L–S).

Remarks. — It differs from *Stuertzaster liquidus* sp. n. by the less elongated lateral plates, spicules with short processes, the high ventral groove and asymmetrically enlarged ventral area of its ambulacral plates.

Occurrence. — Late Givetian: trench II at Marzysz; Set B of Posłowice, Holy Cross Mountains, Poland.

Suborder **Parophiurina** Jaekel, 1923

Family **Palaeuridae** Spencer, 1951

Genus *Umerophiura* gen. n.

Type species: *Umerophiura opiparia* sp. n.

Derivation of the name: From Latin *umera* – spade, due to shape of its adambulacral plates.

Diagnosis. — Spade-shaped adambulacral plates with a single series of mamelons.

Umerophiura opiparia sp. n.

(Pl. 1: 22; Text-fig. 3E–M)

Holotype: GIUS 4-584 Mrz./175/5, Text-fig. 3E.

Type horizon: Late Givetian, Early *Mesotaxis falsiovalis* Zone.

Type locality: Trench II, layer 13 at Marzysz, Holy Cross Mountains.

Derivation of the name: From Latin *opiparia* – magnificent.

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)			
Number of specimens	Features	Holotype	Minimum	Mean	Maximum
Ambulacral plates: 39	Length	760	625	695	760
	Width	600	425	520	600
	Height	730	510	635	730
Lateral plates: 59	Length	–	900	1050	1150
	Width	–	1085	1250	1360

Diagnosis. — Adambulacral plates with broad blades and some pits on the dorsal surface. There is a deep ventral fossa for muscle attachment on the distal surface of ambulacral plates.

Description. — Ambulacral plates. On the dorsal side the podial basin bears a hemispherical cover, the latter does not form a cupola on the proximal elements, but in the ambulacral plates from the middle and distal parts of an arm the cupola may protrude slightly towards the exterior (Text-fig. 3E–I).

Adambulacral plates. The dorsal surface is smooth, but where it joins the shaft there is usually a broad pit, becoming less apparent in more distal plates. On specimens from the middle part of an arm a club-shaped process may occur, emerging from the proximal part of the base of ca. 2% of specimens (Text-fig. 3M). Shafts of the adambulacral plates from the middle and distal part of arm have multifaceted surfaces (Pl. 1: 22; Text-fig. 3J–M).

Remarks. — Differs from species of *Palaeura* Jaekel, 1903 by the presence of a single series of adambulacral plates, with a single row of mamelons, and from *Umerophiura umera* sp. n. by the linear arranged dorsal tubercles on the ambulacral plates, softer development of its ventral and distal surfaces of the ambulacral plates and by narrow, fan-shaped adambulacral plates.

Occurrence. — Only known from the type locality.

Umerophiura umera sp. n.
(Pl. 1: 20–21; Text-fig. 3A–D)

Holotype: GIUS 4-439 Śni./1117/1, Text-fig. 3A.

Type horizon: Early Givetian, *Polygnathus hemiansatus* Zone.

Type locality: Outcrop III at Śniadka, Holy Cross Mountains.

Derivation of the name: From Latin *umera* – spade, due to shape of adambulacral plates.

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)			
Number of specimens	Features	Holotype	Minimum	Mean	Maximum
Ambulacral plates: 11	Length	705	505	610	705
	Width	630	450	555	850
	Height	655	425	550	655
Adambulacral plates: 53	Length	–	380	385	390
	Width	–	610	740	850

Diagnosis. — Adambulacral plates with a narrow blade and lacking a pit on their dorsal surface. Ventral fossa for muscle attachment on the distal surface of ambulacral plate slight.

Description. — Ambulacral plates. They are massive, cube-shaped, and covered slight on their dorsal sides by well-marked tubercles. On the ventral side near the proximal edge there are two non-parallel, smooth, rectangular areas, one of them located internally, the other smaller and located externally (Text-fig. 3A). The podial basin is large and reaches up to half the height of an ambulacral plate; at its bottom is the oval aperture for the water channel. On the dorsal side the basin is covered by a cupola-shaped process. Proximal and distal surfaces are only weakly morphologically differentiated.

Adambulacral plates. Spoon-shaped adambulacral plates with up to ten tubercles in pits, arranged as an arch along the outer edge of the plate. The pits are oval in outline, the tubercles are large and protrude at the exterior. Dorsal surface smooth. From this side the tubercles are invisible and their pits form a wavy margin (Pl. 1: 20–21; Text-fig. 3B–D). The longest shaft occurs on the large plates from the middle part of the arm. On the ventral side the blade has a broad depression, passing towards the shaft. The shaft base has multifaceted surface.

Remarks. — It differs from *Umerophiura opiparia* sp. n. by the chaotic arranged dorsal tubercles on the ambulacral plates, greater development of its ventral and distal surfaces of the ambulacral plates and by narrow, spoon-shaped adambulacral plates.

Occurrence. — Only known from the type locality.

Suborder **Scalarina** Hotchkiss, 1976

Family **Klasmuridae** Spencer, 1925 emend. Hotchkiss, 1976

Genus *Pectenura* Haude, 1982

Type species: *Pectenura horni* Haude, 1982.

Remarks. — Among living ophiuroids there are numerous taxa with similar hooks (Pl. 2: 1–3), e.g. *Ophiothrix* Müller *et* Troschel, 1840 (cf. Cherbonnier and Guille 1978). Similar hooks have been noted in fossil material from the Triassic of the Alps (Mostler 1971b), the Namurian of the Rhenish Slate Mountains, and the type species of the genus.

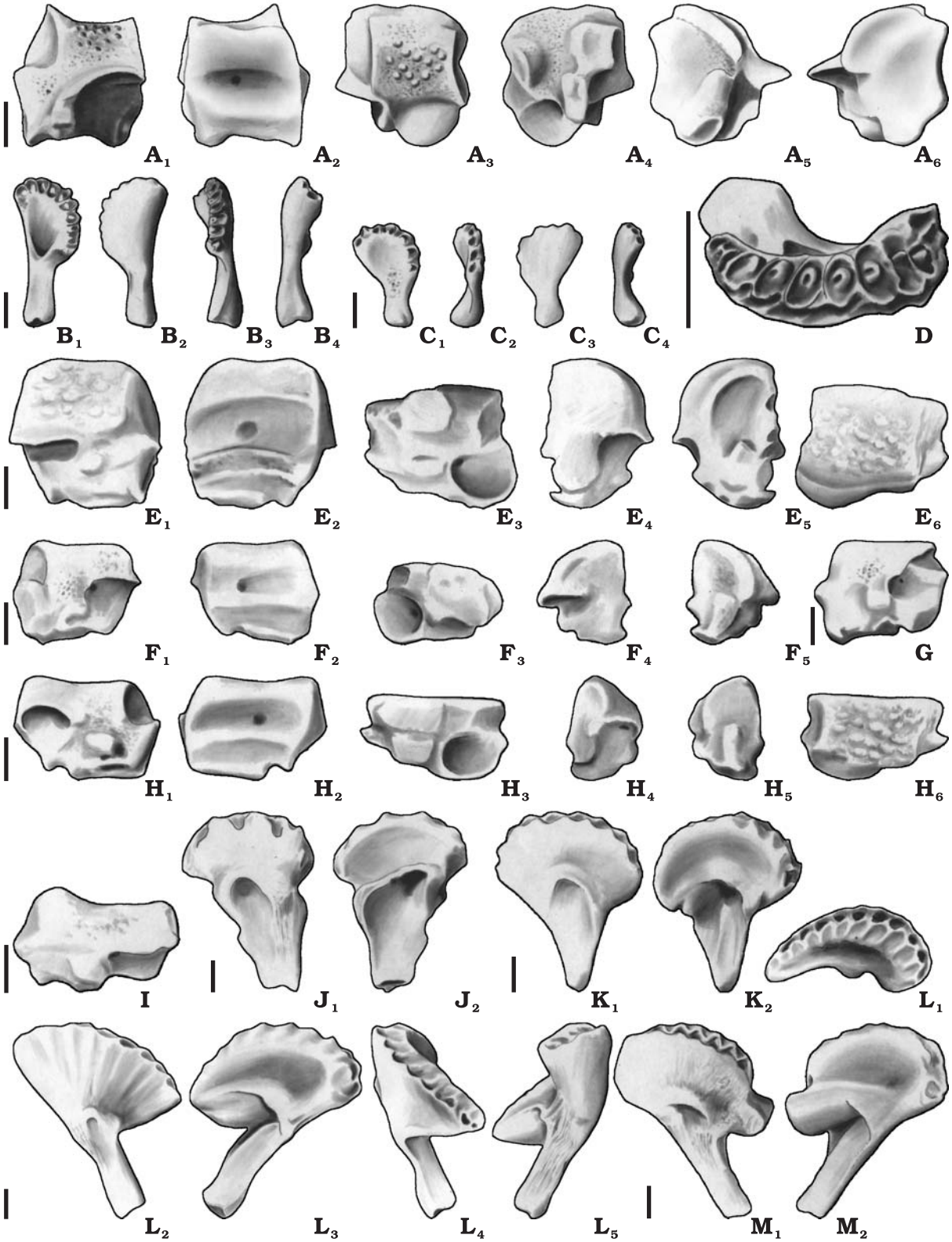

Fig. 3. Skeletal elements of the ophiuroid *Umerophiura* gen. n. from the Holy Cross Mountains. **A**–**D**. *Umerophiura umera* sp. n. from the Early Givetian of outcrop III at Śniadka. **A**. Holotype ambulacral plate GIUS 4-439 Śni./1117/1 from the proximal part of the arm; A_1 outer view, A_2 inner view, A_3 dorsal view, A_4 ventral view, A_5 proximal view, A_6 distal view. **B**. Adambulacral plate GIUS 4-439 Śni./926/2 from the middle part of the arm; B_1 inner view, B_2 outer view, B_3 ventral view, B_4 dorsal view. **C**. Adambulacral plate GIUS 4-439 Śni./926/3 from the distal part of the arm; C_1 inner view, C_2 dorsal view, C_3 outer view, C_4 ventral view. **D**. Adambulacral plate GIUS 4-439 Śni./926/1, view of the edge with tubercles for insertion of the spines. **E**–**M**. *Umerophiura opiparia* sp. n. from the Late Givetian of Marzysz II/13. **E**–**I**. Ambulacral plates. **E**. Holotype GIUS 4-584 ➝

Pectenura excubitor sp. n.
(Pl. 2: 6–9; Text-fig. 4AE–AM)

Holotype: GIUS 4–577 Mrz./47/1, Text-fig. 4AJ.

Type horizon: Late Givetian, Early *Mesotaxis falsiovalis* Zone.

Type locality: Trench II, layer 6 at Marzysz, Holy Cross Mountains.

Derivation of the name: From Latin *excubitor* – guardian, due to armament of hooks.

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)			
Number of specimens	Features	Holotype	Minimum	Mean	Maximum
Sublateral plates: 22	Length	–	140	155	175
	Width	–	480	520	540
Lateral plates: > 500	Length	–	410	440	470
	Width	–	520	540	560
Hooks: 70	Length	795	415	565	795
	Number of teeth	8	6	7	8

Diagnosis. — Hooks with grooved pennon bearing triangular teeth, elliptical in transverse section, perpendicular to the tooth slat. Along the slat there is a delicate lateral groove crossed by oblique trabeculae.

Description. — Sublateral plates. Biscuit-shaped, with curved lateral margins. Their ventral surface is smooth and slightly convex. On the dorsal side there is a flat area with broad depressions at both ends (Text-fig. 4AE).

Lateral plates. Terminally bifurcated, with the longer branch directed proximally (Pl. 2: 6–8; Text-fig. 4AH–AI). The branches were oriented along the arm axis. The elements from the proximal part of the arm have shorter branches and their shaft is narrowed. At its outer end there is a club-shaped termination, with a groove on the ventral side, bordering a hemispherical wart-like process, which is the place of attachment of hook batteries. On the dorsal side, between the branches, there is a triangular pit, corresponding to a delicate mamelon on the opposite element.

Hooks. All the hooks have pennons (Pl. 2: 9; Text-fig. 4AJ–AM). The sickle-shaped hook slat has two or three bends. The distal tooth is the largest. On the inner edge of a hook, five to seven accessory teeth, perpendicular to the teeth slat, may occur. The basal part of the shaft has a simple truncation. The pennon is also relatively flat, reaching up to the primary tooth. Its maximum width is half the length of the shaft. The grooves at the vane of a blade are delicate and parallel to each other. Accessory teeth always increase in size distally.

Remarks. — Differs from *Pectenura hamata* sp. n. by the shorter (on average) branches on lateral plates, the presence of a sculpted pennon and the lateral groove along the surface of the teeth slat. It differs from the other Devonian species by the structure of the base of the hooks; from *Pectenura horni* by the development of accessory teeth (cf. Haude 1982).

Occurrence. — Late Givetian: trench II at Marzysz; Set B of Posłowice, Holy Cross Mountains, Poland.

Pectenura formosa sp. n.
(Pl. 2: 5, 15–16)

Holotype: GIUS 4-785 Gza./1109/1, Pl. 2: 15.

Type horizon: Early Frasnian, Early *Mesotaxis falsiovalis* Zone.

Type locality: Set F of Góra Zamkowa at Chęciny, Holy Cross Mountains.

Derivation of the name: From Latin *formosus* – beautiful, due to its shape.

Mrz./175/5 from the proximal part of the arm; E_1 outer view, E_2 inner view, E_3 ventral view, E_4 distal view, E_5 proximal view, E_6 dorsal view. **F**. Specimen GIUS 4-584 Mrz./175/2 from the middle part of the arm; F_1 outer view, F_2 inner view, F_3 ventral view, F_4 distal view, F_5 proximal view. **G**. Specimen GIUS 4-584 Mrz./175/1 from the middle part of the arm, outer view. **H**. Specimen GIUS 4-584 Mrz./175/4 from the distal part of the arm; H_1 outer view, H_2 inner view, H_3 ventral view, H_4 distal view, H_5 proximal view, H_6 dorsal view. **I**. Specimen GIUS 4-584 Mrz./175/3 from the distal part of the arm, outer view. **J**–**M**. Adambulacral plates. **J**. Specimen GIUS 4-584 Mrz./182/3 from the proximal part of the arm; J_1 dorsal view, J_2 ventral view. **K**. Specimen GIUS 4-584 Mrz./182/2 from the proximal part of the arm. K_1 dorsal view, K_2 ventral view. **L**. Specimen GIUS 4-584 Mrz./182/1 from the middle part of the arm; L_1 view of the edge with tubercles for insertion of the spines, L_2 dorsal view, L_3 ventral view, L_4 distal view, L_5 proximal view. **M**. Specimen GIUS 4-584 Mrz./182/4 from the proximal(?) part of the arm; M_1 dorsal view, M_2 ventral view. Scale bar 200 μm.

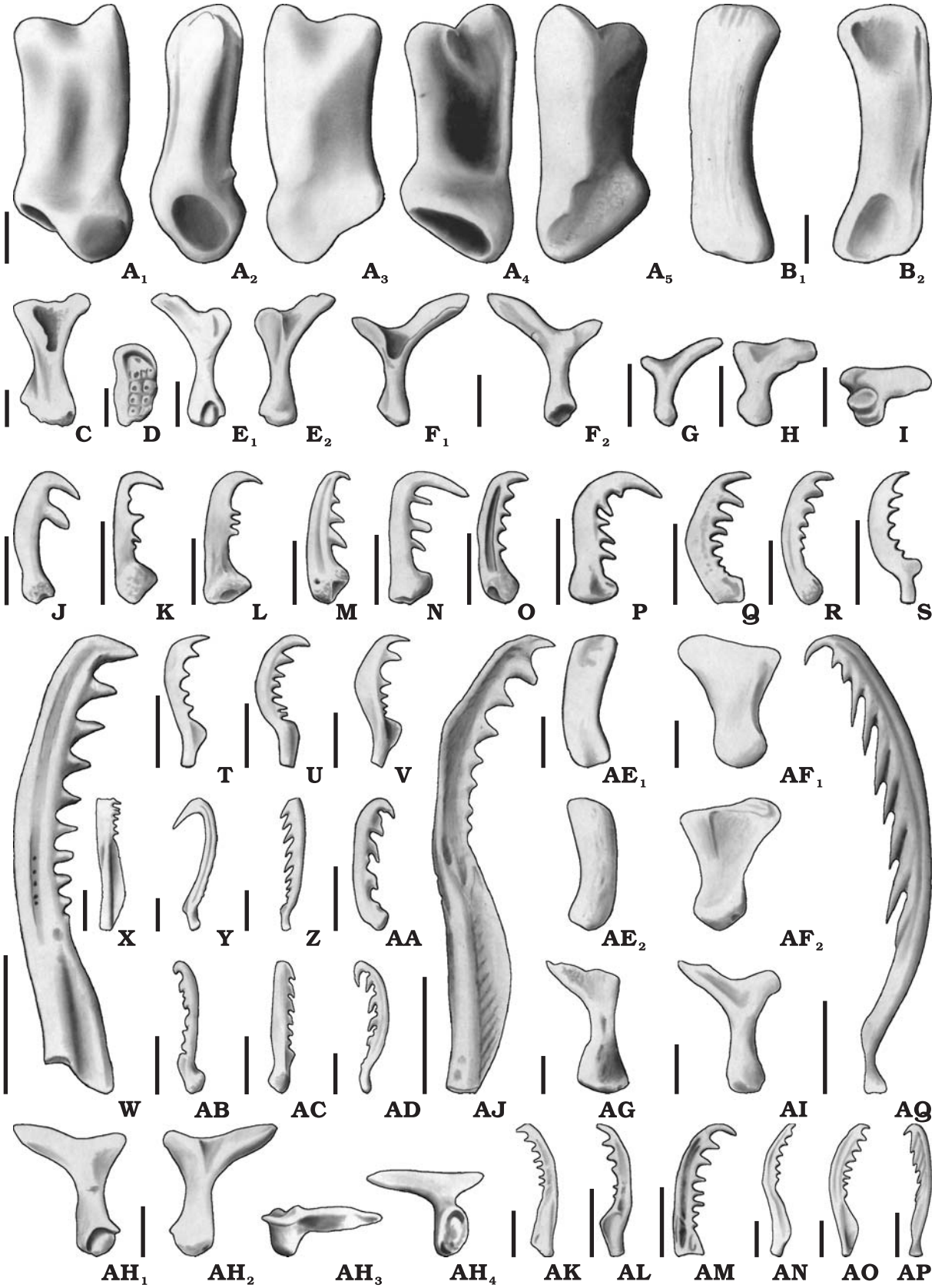

Fig. 4. Skeletal elements of the ophiuroid *Pectenura* from the Holy Cross Mountains. **A**–**AD**. *Pectenura hamata* sp. n. from the Early Givetian of outcrop III at Śniadka. **A**. Ambulacral plate GIUS 4-439 Śni./870/1 from the proximal part of the arm; A_1 ventral view, A_2 inner view, A_3 dorsal view, A_4 ventral oblique view, A_5 dorsal-oblique view. **B**. Sublateral plate GIUS 4-439 Śni./1110/1; B_1 ventral view, B_2 dorsal view. **C**. Lateral plate GIUS 4-439 Śni./914/2 from the proximal part of the arm, dorsal ➔

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)			
Number of specimens	Features	Holotype	Minimum	Mean	Maximum
Sublateral plates: 3	Length	–	150	155	160
	Width	–	465	475	485
Hooks: 17	Length	630	590	670	1010
	Number of teeth	7	6	7	7

Diagnosis. — The largest tooth among the hooks is always adjacent to the distal tooth.

Description. — Sublateral plates. These are biscuit-shaped, laterally curved, with their ventral surface slightly convex, and dorsal surface at both ends with broad depressions (Pl. 2: 5).

Hooks. The tooth slat is only weakly curved; straight in some specimens. Accessory teeth are very sharp, five or six in number, their length increasing distally. The shaft forms a short rod, oval in transverse section, its basal part simply truncated (Pl. 2: 15–16).

Remarks. — Hooks of this species are similar to those of *Pectenura pecten* sp. n. but the teeth are different, the second tooth below of distal ending being the largest. The shaft is short and wide. Pennons display some similarity to those in *Pectenura hamata* sp. n.

Occurrence. — Only known from the type locality.

Pectenura hamata sp. n.
(Pl. 2: 4, 10, 11; Text-fig. 4A–AD)

Holotype: GIUS 4-439 Śni./932/12, Text-fig. 4V.

Type horizon: Early Givetian, *Polygnathus hemiansatus* Zone.

Type locality: Outcrop III at Śniadka, Holy Cross Mountains.

Derivation of the name: From Latin *hamatus* – supplied with hooks.

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)			
Number of specimens	Features	Holotype	Minimum	Mean	Maximum
Ambulacral plates: 1	Length	–	460	–	–
	Width	–	990	–	–
Sublateral plates: 6	Length	–	330	340	350
	Width	–	970	1010	1060
Lateral plates: 80	Length	–	285	440	480
	Width	–	275	570	600
Hooks: > 500	Length	45	315	510	830
	Number of teeth	6	1	6	9

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view. **D**. Tubercles for hooks on lateral plate GIUS 4-439 Śni./914/1 from the proximal part of the arm. **E**. Lateral plate GIUS 4-439 Śni./914/3 from the proximal part of the arm; E_1 ventral view, E_2 dorsal view. **F**. Lateral plate GIUS 4-439 Śni./914/4 from the middle part of the arm; F_1 dorsal view, F_2 ventral view. **G**. Lateral plate GIUS 4-439 Śni./914/5 from the distal part of the arm, dorsal view. **H**. Lateral plate GIUS 4-439 Śni./914/6 from the distal part of the arm, dorsal view. **I**. Lateral plate GIUS 4-439 Śni./914/7 from the proximal part of the arm, oblique view from the tubercle for hook. **J**–**AD**. Various kinds of hooks. **J**. GIUS 4-439 Śni./932/7. **K**. GIUS 4-439 Śni./932/5. **L**. GIUS 4-439 Śni./932/4. **M**. GIUS 4-439 Śni./932/2. **N**. GIUS 4-439 Śni./932/15. **O**. GIUS 4-439 Śni./932/16. **P**. GIUS 4-439 Śni./932/3. **Q**. GIUS 4-439 Śni./932/6. **R**. GIUS 4-439 Śni./932/1. **S**. GIUS 4-439 Śni./932/9. **T**. GIUS 4-439 Śni./932/11. **U**. GIUS 4-439 Śni./932/10. **V**. Holotype GIUS 4-439 Śni./932/12. **W**. GIUS 4-439 Śni./932/13. **X**. GIUS 4-439 Śni./932/8. **Y**. GIUS 4-439 Śni./931/5. **Z**. GIUS 4-439 Śni./931/4. **AA**. GIUS 4-439 Śni./931/6. **AB**. GIUS 4-439 Śni./931/3. **AC**. GIUS 4-439 Śni./931/2. **AD**. GIUS 4-439 Śni./931/1. **AE**–**AM**. *Pectenura excubitor* sp. n. from the Late Givetian of Marzysz, samples Marzysz II/W/1 (AE) and Marzysz II/13 (AF–AI). **AE**. Sublateral plate GIUS 4-563 Mrz./978/1; AE_1 dorsal view, AE_2 ventral view. **AF**. Lateral plate GIUS 4-584 Mrz./169/1 from the proximal part of the arm; AF_1 ventral view, $\mathbf{AF_2}$ dorsal view. **AG**. Lateral plate GIUS 4-584 Mrz./169/4 from the proximal part of the arm, dorsal view. **AH**. Lateral plate GIUS 4-584 Mrz./169/2 from the middle part of the arm; $\mathbf{AH_1}$ ventral view, AH_2 dorsal view, AH_3 inner view, AH_4 outer view. **AI**. Lateral plate GIUS 4-584 Mrz./169/3 from the middle part of the arm, dorsal view. **AJ**–**AQ**. Various kinds of hooks from Marzysz II/6. **AJ**. Holotype GIUS 4-577 Mrz./47/1. **AK**. GIUS 4-577 Mrz./47/2. **AL**. GIUS 4-577 Mrz./47/3. **AM**. GIUS 4-577 Mrz./47/4. **AN**–**AQ**. Hooks of *Pectenura pecten* sp. n. from the Mid Givetian, set B of Laskowa Góra. **AN**. GIUS 4-604 Las./1046/3. **AO**. Holotype GIUS 4-604 Las./1046/2. **AP**. GIUS 4-604 Las./1047/2. **AQ**. GIUS 4-604 Las./1047/1. Scale bar 200 μm.

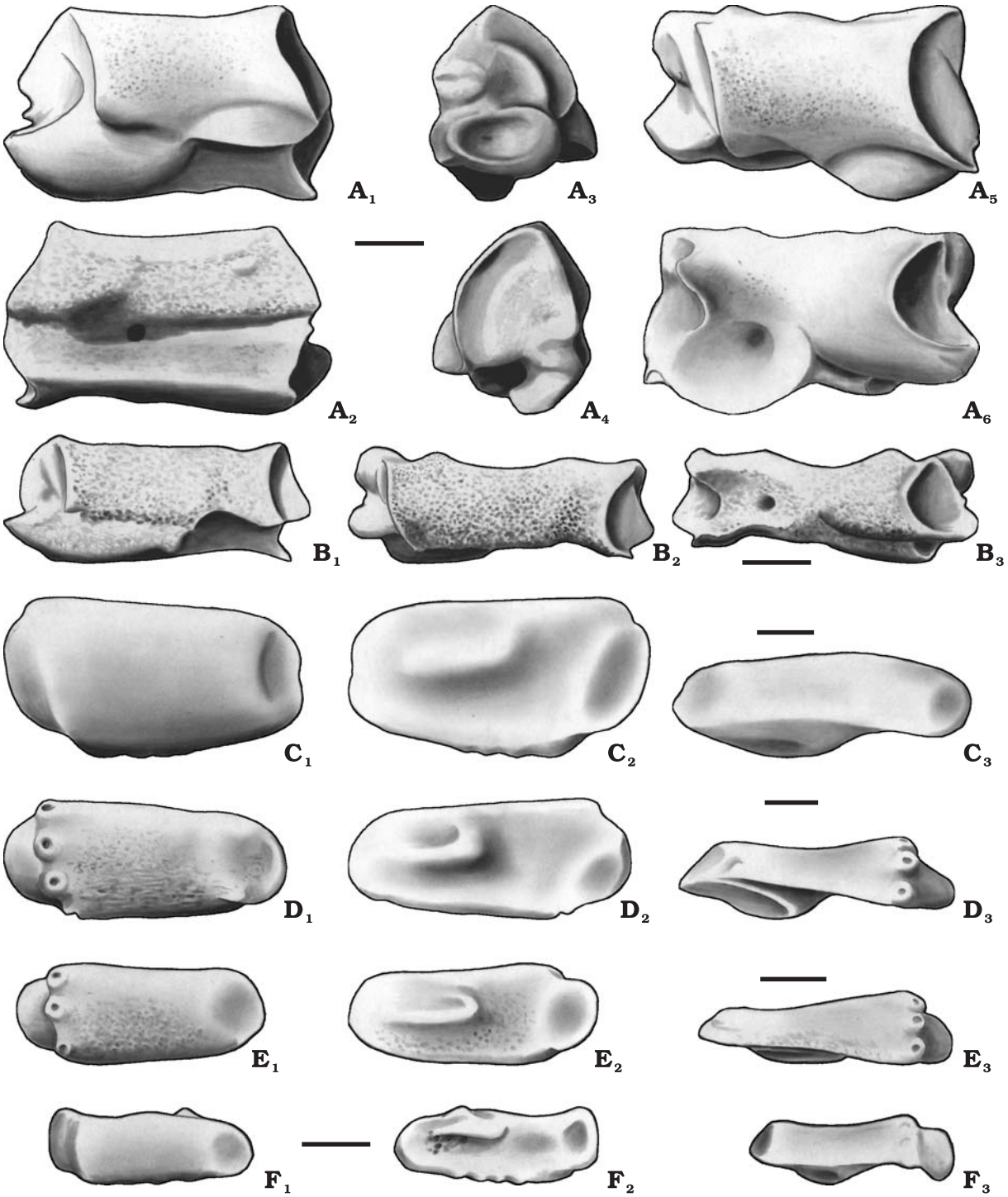

Fig. 5. Skeletal elements of the ophiuroid *Astutuaster athleta* sp. n. from the Early Givetian of outcrop III of Śniadka, Holy Cross Mountains. **A**. The holotype, ambulacral plate GIUS 4-439 Śni./918/1 from the proximal/middle part of the arm; A_1 outer view, A_2 inner view, A_3 proximal view, A_4 distal view, A_5 dorsal view, A_6 ventral view. **B**. Ambulacral plate GIUS 4-439 Śni./918/2 from the distal part of the arm; B_1 outer view, B_2 dorsal view, B_3 ventral view. **C**. Lateral plate GIUS 4-439 Śni./934/1 from the proximal part of the arm; C_1 outer view, C_2 inner view, C_3 dorsal view. **D**. Lateral plate GIUS 4-439 Śni./934/2 from the middle part of the arm; D_1 outer view, D_2 inner view, D_3 dorsal view. **E**. Lateral plate GIUS 4-439 Śni./934/3 from the distal part of the arm; E_1 outer view, E_2 inner view, E_3 dorsal view. **F**. Lateral plate GIUS 4-439 Śni./934/4 from the distal part of the arm; F_1 outer view, F_2 inner view, F_3 dorsal view. Scale bar 200 μm.

Diagnosis. — Hooks of the pennon along the shaft with flat triangular spines, perpendicular to the tooth slat, along the latter there is a delicate lateral groove, devoid of oblique trabeculae.

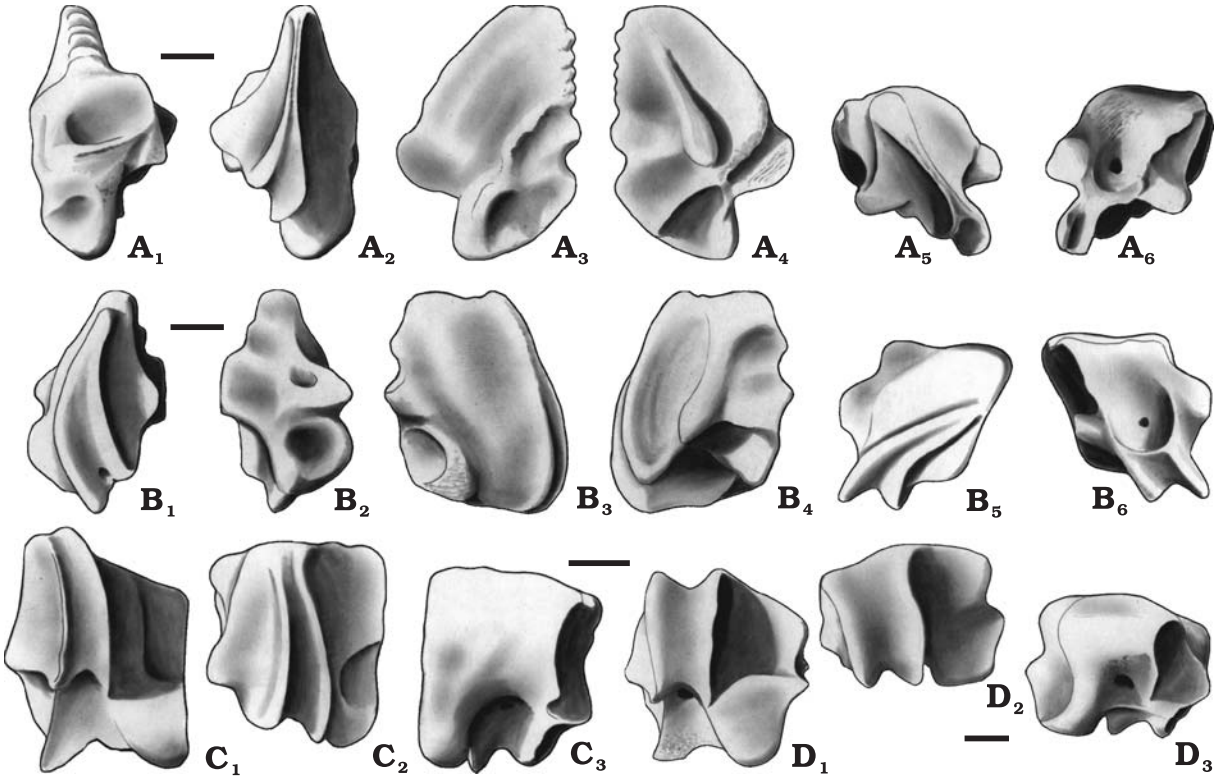

Fig. 6. Ambulacral plates of the ophiuroid *Weigeltura beckeri* sp. n. from the earliest Eifelian *Chimaerothyris dombrowiensis* horizon at Zbrza, Holy Cross Mountains. **A**. Second or third ambulacral plate GIUS 4-779 Zba./356/1; A_1 outer view, A_2 inner view, A_3 proximal view, A_4 distal view, A_5 dorsal view, A_6 ventral view. **B**. Second(?) ambulacral plate GIUS 4-779 Zba./356/2; B_1 outer view, B_2 inner view, B_3 proximal view, B_4 distal view, B_5 dorsal view, B_6 ventral view. **C**. Third(?) ambulacral plate GIUS 4-779 Zba./356/3; C_1 outer view, C_2 dorsal view, C_3 ventral view. **D**. Ambulacral plate GIUS 4-779 Zba./368/1 from the proximal part of the arm; D_1 outer view, D_2 dorsal view, D_3 ventral view. Scale bar 200 μm.

Description. — Ambulacral plates. Rectangular in shape with rounded corners. On their ventral side there is a shallow, flat groove. A tubercle, directed towards the exterior and distally from the plates, can be seen (Text-fig. 4A); this is the attachment site for the sublateral plate. Distally and visible from within is an oval depression, where the neighbouring halves of ambulacral elements abut. Proximal end somewhat bifurcated and forming a very broad V-shaped notch. Dorsal side bifaceted with a ridge where facets contact.

Sublateral plates. Their ventral surface is smooth and slightly convex with fine groovelets along the inner edge. The dorsal side is flat, but displays two broad depressions at either end. The whole plate is arched in the distal direction when seen from its flat side (Text-fig. 4B).

Lateral plates. Proximal elements may lack the shorter branch (Pl. 2: 4; Text-fig. 4C, H, I). At its outer edge a club-shaped expansion, with two grooves, borders the hemispherical ridge in the middle and two narrow ridges at the sides on the ventral side. The ridges were the place of attachment for the hook batteries. The most proximal elements have two series of such mamelons (Text-fig. 4D).

Hooks. They form morphologically differentiated assemblage (Pl. 2: 10, 11; Text-fig. 4J–AD). The hooks with a pennon on their concave side are the most diagnostic. The hook slat is sickle-shaped with the largest tooth at the distal end. On the inner edge there are up to eight accessory teeth, cone- or triangle-shaped, straight or curved adaxially. The triangular teeth always accompany the hooks with pennons. In these usually flat hooks, the part of the shaft is simply truncated, in the form of a rod. The pennon itself is also strongly flattened, reaching up to the primary tooth (Pl. 2: 11; Text-fig. 4S–Z, AB, AC). Hooks without pennons only rarely display a lateral groove. Their basal part is strongly inflated and, in or close to its centre, displays a neuropore. Accessory teeth increase in size distally in 90% of specimens.

Remarks. — The species differs from *Pectenura excubitor* sp. n. by the longer arm branches of its lateral plates, and a smooth pennon on its hooks. Transverse trabeculae are also lacking from the lateral groove on the tooth slat. From the other Devonian species it differs by lacking an expanded basal part on its hooks with pennons. *Pectenura horni* differs in the shorter hook teeth, and shorter sublateral plates (cf. Haude 1982).

Occurrence. — Late Eifelian: Set XVIII of Skały Beds at Skały. Early Givetian: outcrop III of Śniadka, Holy Cross Mountains, Poland.

Pectenura pecten sp. n.
(Pl. 2: 12–13; Text-fig. 4AN–AQ)

Holotype: GIUS 4-604 Las./1046/2, Text-fig. 4AO.
Type horizon: Mid Givetian, Early *Palmatolepis disparilis* Zone.
Type locality: Set B of Laskowa Góra, Holy Cross Mountains.
Derivation of the name: From Latin *pecten* – comb, due to its comb-shaped hooks.

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)			
Number of specimens	Features	Holotype	Minimum	Mean	Maximum
Hooks: 37	Length	750	635	775	1000
	Number of teeth	7	7	8	10

Diagnosis. — Hooks with a large, smooth pennon with two parallel lateral grooves, devoid of transverse trabeculae. The largest accessory teeth are always in the middle of the slat.

Description. — Hooks. Two types of hooks occur, both of them with pennons (Pl. 2: 12–13; Text-fig. 4AN–AQ). The first type has a sickle-shaped tooth slat, bent either twice or not at all. The distal tooth is similar in size to the others, but may be smaller (Text-fig. 4AN–AO). On the inner edge six to nine accessory teeth may occur, of similar size, perpendicular to the tooth slat. The basal part of the shaft is not expanded, but its corners are slightly rounded. The pennon is typical in structure, being smooth and broadest mid-length. The second type comprise very long and slim hooks, slightly curved, with a single median lateral groove along the tooth slat which does not pass onto a shaft. The distal tooth is large, thin and with hook-like curvature. Accessory teeth (from six to nine) are strongly curved towards the shaft. Narrow gaps occur between the teeth, so in some specimens they coalesce even at two-thirds of their length (Pl. 2: 12–13; Text-fig. 4AP–AQ). The tips of teeth are sharp. The shaft is very thin, with a trumpet-shaped, rounded basal part. Hooks of the second type have a small pennon.

Remarks. — Forms with a large pennon have a general shape similar to hooks of *Pectenura excubitor* sp. n. but its pennon has no sculpture, teeth are weakly separated and have coalesced bases.

Occurrence. — Only known from the type locality.

Pectenura senta sp. n.
(Pl. 2: 14)

Holotype: GIUS 4-607 Grn./536/20, Pl. 2: 14.
Type horizon: Mid Frasnian, *Palmatolepis punctata* Zone.
Type locality: Set C of Górno, Holy Cross Mountains.
Derivation of the name: From Latin *sentus* – thorny, due to shape of its hooks.

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)			
Number of specimens	Features	Holotype	Minimum	Mean	Maximum
Hooks: 15	Length	965	890	950	970
	Number of teeth	5	5	5	5

Diagnosis. — Flat hooks with long teeth, directed towards the basal part.

Description. — Hooks. Only hooks with small pennons are identified (Pl. 2: 14). The sickle-shaped tooth slat is totally smooth. The primary accessory tooth is intergrown with the margin of the tooth slat. Gaps between the teeth are broad. There are four or five accessory teeth. The shaft is narrow, rod-like, terminated with a trumpet-like basal part. Hooks have a very small pennon.

Remarks. — Hooks in this species are similar to those of *Pectenura pecten* sp. n. (cf. Text-fig. 4AP–AQ) but they have fewer and longer accessory teeth, devoid of a lateral groove. They are close to *Pectenura formosa* sp. n., but that species has more teeth and different dimensions.

Occurrence. — Only known from the type locality.

Order **Oegophiurida** Matsumoto, 1915
Suborder **Lysophiurina** Gregory, 1856
Family **Protasteridae** S.A. Miller, 1889
Genus *Astutuaster* gen. n.

Type species: *Astutuaster athleta* sp. n.

Derivation of the name: From Latin *astutus* – deceitful, as its remains defied classification.

Diagnosis. — Cupola, forming the podial basin extends beyond the hemicylindrical main plate and reaches its distal end.

Remarks. — From *Strataster* the new genus differs in the structure of the inner side of its ambulacral plates, the development of a cupola for the podial basin. A similar cupola structure over the podial basin occurs in *Umerophiura* gen. n., but *Astutuaster* gen. n. has the muscle attachment situated very low and mainly on the ventral side, a smooth ventral surface to ambulacral plates, and scapula-shaped lateral plates. *Weigeltura* gen. n. differs from *Astutuaster* gen. n. in lacking a cupola over the podial basin. *Astutuaster* gen. n. differs from the remaining genera of protasterid in the human foot-shape of lateral plates and presence of proximal truncation on laterals to connect with neighbouring plate.

Astutuaster athleta sp. n.
(Text-fig. 5A–F)

Holotype: GIUS 4-439 Śni./918/1, Text-fig. 5A.

Type horizon: Early Givetian, *Polygnathus hemiansatus* Zone.

Type locality: Outcrop III at Śniadka, Holy Cross Mountains.

Derivation of the name: From Latin – *athleta* – athlete, due to its heavily built ambulacral plates.

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)			
Number of specimens	Features	Holotype	Minimum	Mean	Maximum
Ambulacral plates: 14	Length	970	880	900	970
	Width	540	290	380	540
	Height	550	300	370	550
Lateral plates: 38	Length	–	600	850	1050
	Width	–	215	405	555

Diagnosis. — As for the genus.

Description. — Ambulacral plates. These plates are dorsally smooth and hemicylindrical in shape (Text-fig. 5A–B). A cupola, below which an ear-shaped podial basin forms, is present in all but the more distal plates. On the inner side of the plate there is an elongated groove that housed the radial water channel. Two convexities on the proximal surface near the inner edge, transected by a narrow groove, form an elliptical admedian articulation, where subsequent arm halves joined each other. The adoral hinge, when observed from the dorsal side, forms a triangular tooth. The attachment surface for dorsal muscles is well developed as an oval depression. The distal surface is not so strongly differentiated. Latero-ventrally a small lateral muscular fossa is seen. At mid-height there is a small aboral hinge. The attachment field of the inner muscles forms a shallow, broad fossa.

Lateral plates. The plates are in the shape of a human foot. The most proximal laterals do not have mamelons (Text-fig. 5C). Proximal lateral plates are thick, supplied with a large extension, that articulates with the ambulacral plate via a central, oval depression. Near the distal edge there are three ring-shaped mamelons (Text-fig. 5D–E). Distally the mamelons disappear (Text-fig. 5F). The plate was originally in contact with the proximal truncation of the following platelet by an elliptical protrusion. On the ventral edge there are four wavy convexities, which, most probably, did not function as mamelons, as they are devoid of channels.

Occurrence. — Only known from the type locality.

Genus *Weigeltura* gen. n.

Type species: *Weigeltura beckeri* sp. n.

Derivation of the name: From the name of H. Weigelt who, jointly with G. Becker, for the first time illustrated remains characteristic of the genus.

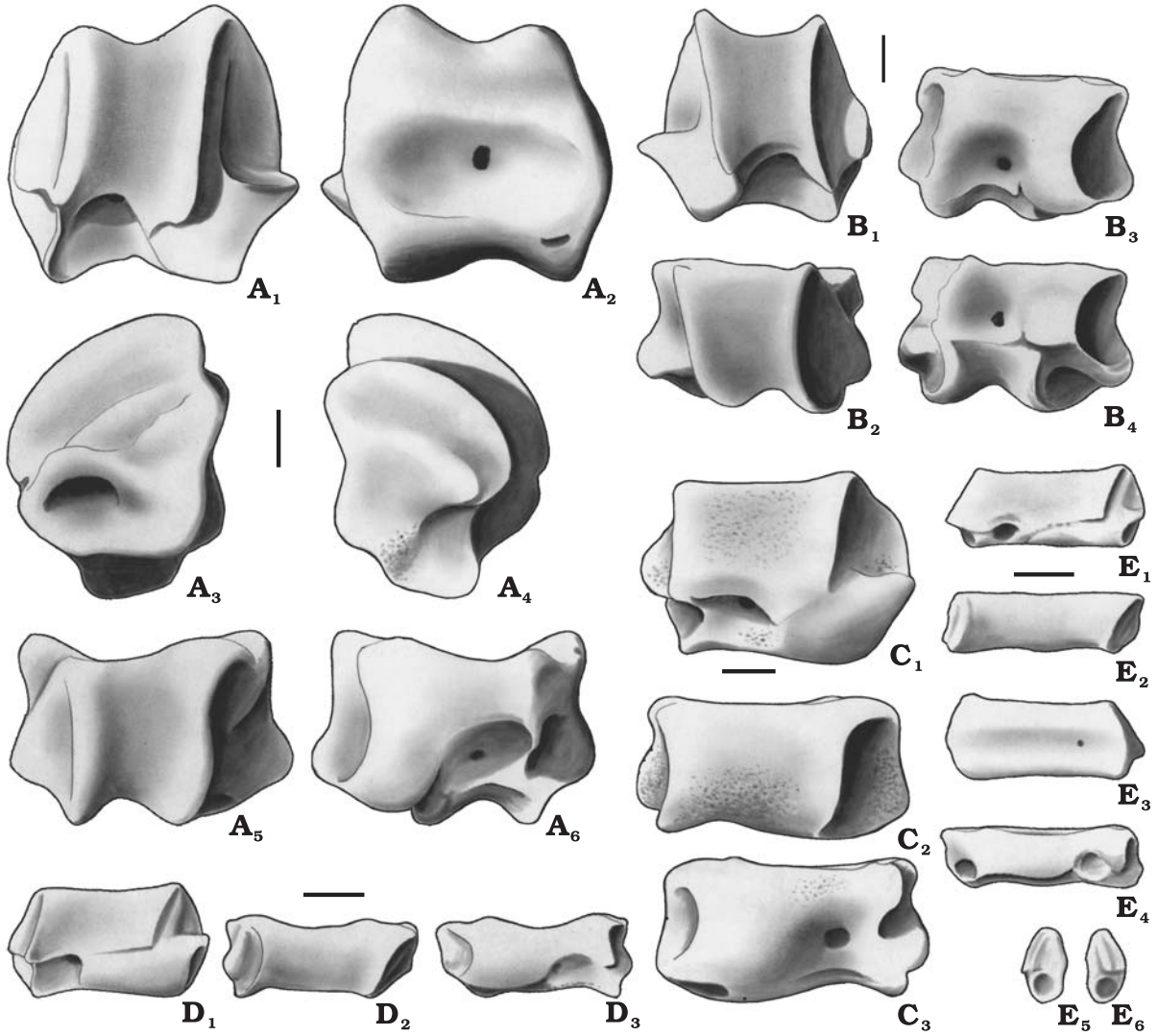

Fig. 7. Ambulacral plates of the ophiuroid *Weigeltura beckeri* sp. n. from the earliest Eifelian *Chimaerothyris dombrowiensis* horizon of Zbrza, Holy Cross Mountains. **A–E**. Ambulacral plates of *Weigeltura beckeri* sp. n. **A**. The holotype, ambulacral plate GIUS 4-779 Zba./368/2 from the middle part of the arm; A_1 outer view, A_2 inner view, A_3 proximal view, A_4 distal view, A_5 dorsal view, A_6 ventral view. **B**. Ambulacral plate GIUS 4-779 Zba./368/3 from the middle part of the arm; B_1 outer view, B_2 dorsal view, B_3 inner view, B_4 ventral view. **C**. Ambulacral plate GIUS 4-779 Zba./368/4 from the distal part of the arm; C_1 outer view, C_2 dorsal view, C_3 ventral view. **D**. Ambulacral plate GIUS 4-779 Zba./368/5 from the distal part of the arm; D_1 outer view, D_2 dorsal view, D_3 ventral view. **E**. Ambulacral plate GIUS 4-779 Zba./368/6 from the distal part of the arm; E_1 outer view, E_2 dorsal view, E_3 inner view, E_4 ventral view, E_5 proximal view, E_6 distal view. Scale bar 200 μm.

Diagnosis. — Massive ambulacrals having spacious podial basin without cupola and with large foramen for podium.

Remarks. — Sclerites of this genus were classified by Becker and Weigelt (1975) as Ambulacralia, Bautyp 1 (Amb-1, pp. 13–14, Taf. 1: 1–6; 2: 1–2; 3: 6; Abb. 2), Mundeckstücke, Bautyp 1 (ME-1: p. 19, Taf. 1: 7), Lateralplatten, Bautyp 1 (Lat-1: pp. 16–18, Taf. 2: 3–7; 3: 3–5). The genus differs from *Strataster* Kesling *et* Le Vasseur, 1971 in lacking the horizontal ridge on lateral surface of the ambulacral plate (see Kesling 1972), by a deep cavity on its internal wall; the most proximal plates are very narrow. The "boot" (see Kesling 1972) on the oral surface is strongly rounded in *Weigeltura* gen. n. and two vertical ridges are well developed on the latero-dorsal wall of ambulacral plates. Lateral plates are thicker, with a larger protrusion and without the proximo-laterally mamelon and ventral scale-shaped spines. The collection consists of two types of spines, but all the ambulacral plates are similar to each other. It differs from *Protaster* Forbes, 1849, *Aulactis* Spencer, 1930, *Bohemura* Jaekel, 1903, *Drepanaster* Whidborne, 1898,

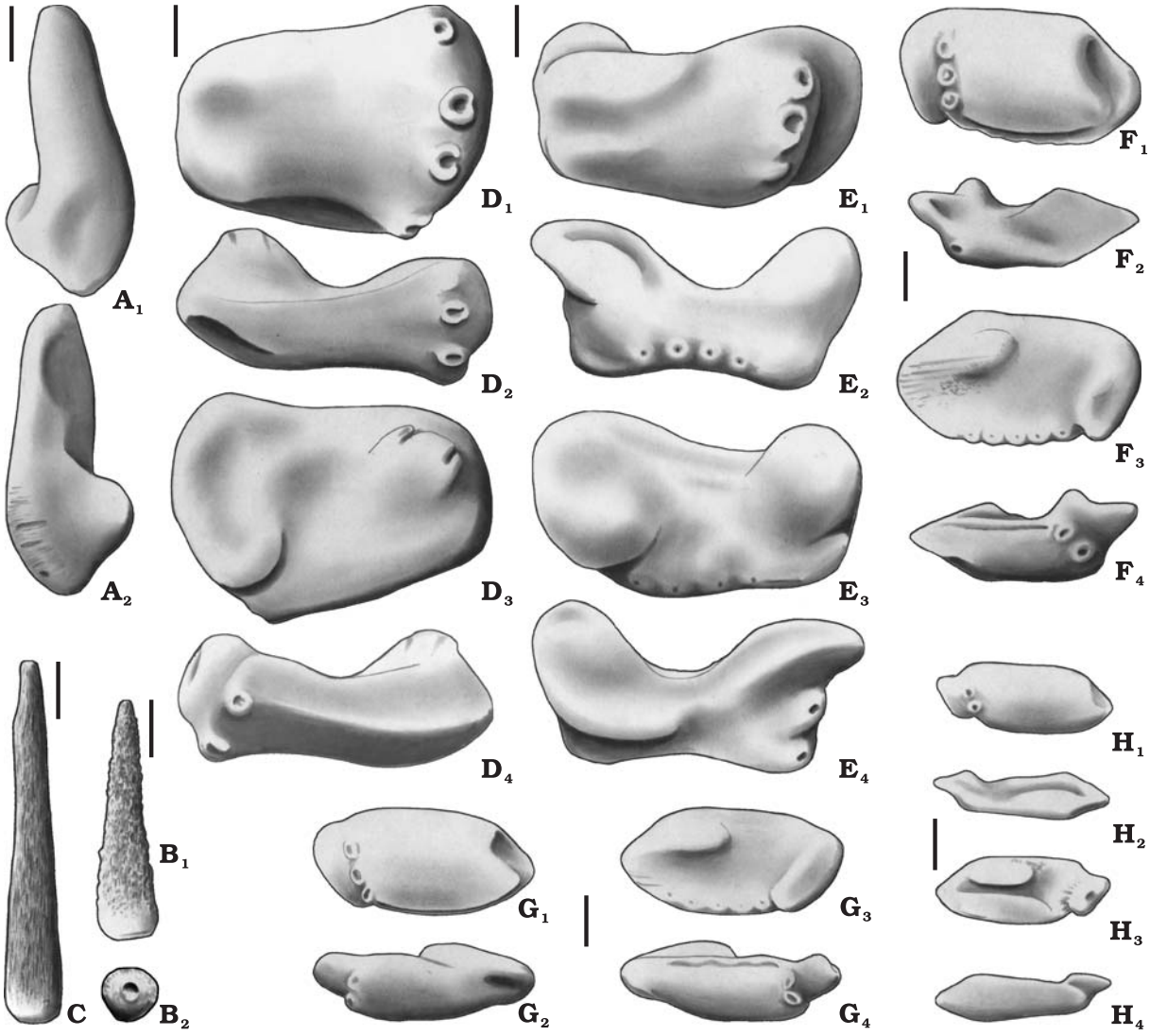

Fig. 8. Skeletal elements of the ophiuroid *Weigeltura beckeri* sp. n. from the earliest Eifelian *Chimaerothyris dombrowiensis* horizon of Zbrza, Holy Cross Mountains. **A**. First lateral plate GIUS 4-779 Zba./356/4; A_1 side view, A_2 opposite side view. **B**. Spine GIUS 4-779 Zba./361/1; B_1 lateral view, B_2 base. **C**. Spine GIUS 4-779 Zba./361/2. **D**. Lateral plate GIUS 4-779 Zba./365/4 from the proximal / middle part of the arm; D_1 outer view, D_2 dorsal view, D_3 inner view, D_4 ventral view. **E**. Lateral plate GIUS 4-779 Zba./365/5 from the proximal part of the arm; E_1 outer view, E_2 dorsal view, E_3 inner view, E_4 ventral view. **F**. Lateral plate GIUS 4-779 Zba./365/1 from the distal/middle part of the arm; F_1 outer view, F_2 dorsal view, F_3 inner view, F_4 ventral view. **G**. Lateral plate GIUS 4-779 Zba./365/2 from the distal part of the arm; G_1 outer view, G_2 dorsal view, G_3 inner view, G_4 ventral view. **H**. Lateral plate GIUS 4-779 Zba./365/3 from the distal part of the arm; H_1 outer view, H_2 dorsal view, H_3 inner view, H_4 ventral view. Scale bar 200 μm.

Mastigophiura Lehman, 1957, *Palaeophiura* Stürtz, 1890, and *Taeniaster* Billings, 1858 in its rhomboid shape and big, curved proximal truncation of its lateral plates. It differs from *Astutuaster* gen. n. by the structure of the lateral plates which in the latter genus have a pillow-shaped structure on the inner side, but it is not separated by a distinct groove. The development of a podial basin of *Astutuaster* gen. n. is also different, being covered by a cupola, which is exposed at the periphery.

Weigeltura austera sp. n.
(Text-fig. 9G–K)

Holotype: GIUS 4-578 Mrz./256/1, Text-fig. 9H.
Type horizon: Late Givetian, Early *Mesotaxis falsiovalis* Zone.

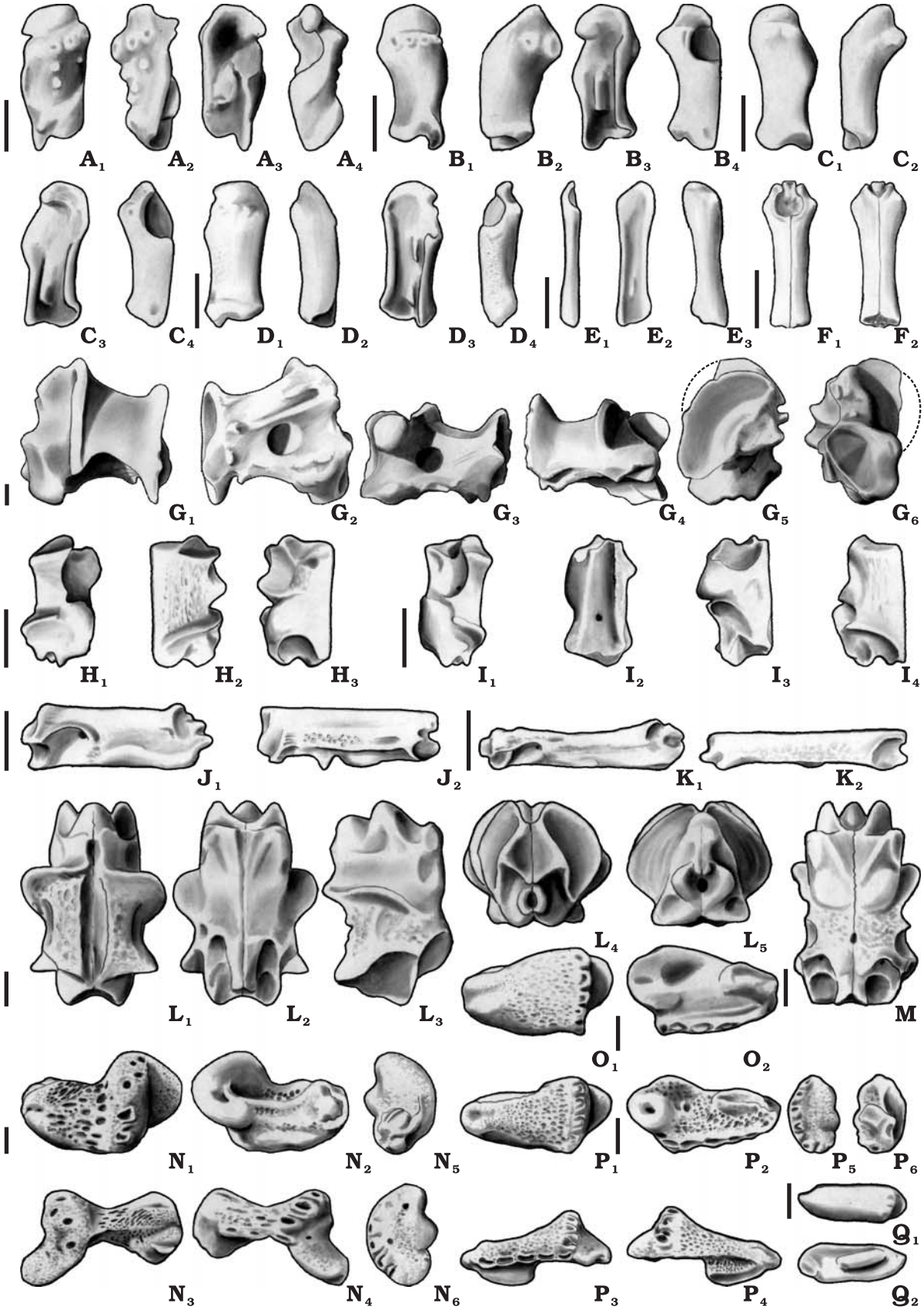

Fig. 9. Skeletal elements of the Ophiuroidea from the Devonian of the Holy Cross Mountains. **A**–**F**. *Chattaster loculus* sp. n. from the Late Givetian, sample Marzysz II/13. **A**–**E**. Lateral plates. **A**. Specimen GIUS 4-584 Mrz./159/3 from the proximal part of the arm; A_1 outer view, A_2 dorsal view, A_3 inner view, A_4 ventral view. **B**. Specimen GIUS 4-584 Mrz./159/1 from the proximal part →

Type locality: Trench II, layer 7, Marzysz, Holy Cross Mountains.

Derivation of the name: From Latin *austerus* – austere, due to simple structure of the largest ambulacral plates.

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)			
Number of specimens	Features	Holotype	Minimum	Mean	Maximum
Ambulacral plates: 17	Length	440	415	560	1440
	Width	235	120	270	1390
	Height	275	130	320	1015

Diagnosis. — Podial basins on the ambulacral plates are delimited with a ridge, exception in the most proximal plates.

Description. — Ambulacral plates. On the ventral side of the proximal plates near their distal end there is a large, spherical tubercle, which is absent from more distal plates. Lateral ridges are well-marked in proximal plates (Text-fig. 9G) becoming less prominent in distal ones (Text-fig. 9H–K). On the inner side of each plate there is a straight groove forming a half of the radial water channel. On the proximal surface there is an elliptical, voluminous, ventral proximal muscle fossa, flanked at its top by the adoral hinge. The attachment field of the dorsal muscles is small. The distal surface of typical plates has deep lateral muscular fossae in its lateral-distal corners, while posteriorly there is a kidney-shaped convexity, reaching up to half the length of an ambulacral plate. A large aboral hinge occurs more or less mid-length and is oriented obliquely towards the top. The inner muscular fossa is shallow but wide. In the more distal plates all the morphological elements are simplified, with the exception of the ridge, flanking the podial basin and the kidney-shaped process behind the lateral muscular fossa. Distally the ambulacral plates become longer, thinner and resemble a nodose twig.

Remarks. — Differs from *Weigeltura beckeri* sp. n. by having a ridge surrounding its podial basin, and by the characteristic convexities developed behind the lateral muscular fossa on the ambulacral plates.

Occurrence. — Late Givetian: trench II at Marzysz, Set B of Posłowice, Holy Cross Mountains, Poland.

Weigeltura beckeri sp. n.
(Pl. 1: 15–16; Text-figs 6A–D, 7A–E, 8A–H)

Holotype: GIUS 4-779 Zba./368/2, Text-fig. 7A.

Type horizon: Early Eifelian, *Polygnathus partitus* Zone.

Type locality: Zbrza, Holy Cross Mountains.

Derivation of the name: From the name of the co-author of the monograph of 1975 – G. Becker, where remains typical of the genus were illustrated for the first time.

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of the arm; B_1 outer view, B_2 dorsal view, B_3 inner view, B_4 ventral view. **C**. Specimen GIUS 4-584 Mrz./159/2 from the middle part of the arm; C_1 outer view, C_2 dorsal view, C_3 inner view, C_4 ventral view. **D**. Specimen GIUS 4-584 Mrz./159/4 from the distal part of the arm; D_1 outer view, D_2 dorsal view, D_3 inner view, D_4 ventral view. **E**. Specimen GIUS 4-584 Mrz./159/5 from the distal part of the arm; E_1 ventral view, E_2 inner view, E_3 outer view. **F**. Holotype segment of the arm GIUS 4-584 Mrz./974/1; F_1 ventral view, F_2 dorsal view. **G**–**K**. Ambulacral plates of *Weigeltura austera* sp. n. from the Late Givetian of Marzysz; samples Marzysz II/W/0 (G) and Marzysz II/7 (H–K). **G**. Specimen GIUS 4-562 Mrz./117/1 from the proximal part of the arm; G_1 outer view, G_2 inner view, G_3 ventral view, G_4 dorsal view, G_5 distal view, G_6 proximal view. **H**. Holotype GIUS 4-578 Mrz./256/1 from the middle part of the arm; H_1 outer view, H_2 dorsal view, H_3 ventral view. **I**. Specimen GIUS 4-578 Mrz./256/2 from the middle part of the arm; I_1 outer view, I_2 inner view, I_3 ventral view, I_4 dorsal view. **J**. Specimen GIUS 4-578 Mrz./256/3 from the distal part of the arm; J_1 outer view, J_2 dorsal view. **K**. Specimen GIUS 4-578 Mrz./256/4 from the distal part of the arm; K_1 outer view, K_2 dorsal view. **L**–**R**. *Eospondylus ingens* sp. n. from the Early Givetian of outcrop III at Śniadka. **L**–**M**. Ambulacral plates. **N**–**R**. Lateral plates. **L**. Holotype GIUS 4-439 Śni./920/1 from the middle part of the arm; L_1 dorsal view, L_2 ventral view, L_3 lateral view, L_4 distal view, L_5 proximal view. **M**. Specimen GIUS 4-439 Śni./920/2 from the middle part of the arm, ventral view. **N**. Specimen GIUS 4-439 Śni./928/2 from the proximal part of the arm; N_1 outer view, N_2 inner view, N_3 dorsal view, N_4 ventral view, N_5 proximal view, N_6 distal view. **O**. Specimen GIUS 4-439 Śni./928/4 from the middle part of the arm; O_1 outer view, O_2 inner view. **P**. Specimen GIUS 4-439 Śni./928/5 from the middle part of the arm; P_1 outer view, P_2 inner view, P_3 ventral view, P_4 dorsal view, P_5 distal view, P_6 proximal view. **Q**. Specimen GIUS 4-439 Śni./928/3 from the distal part of the arm; Q_1 outer view, Q_2 inner view. Scale bar 200 μm.

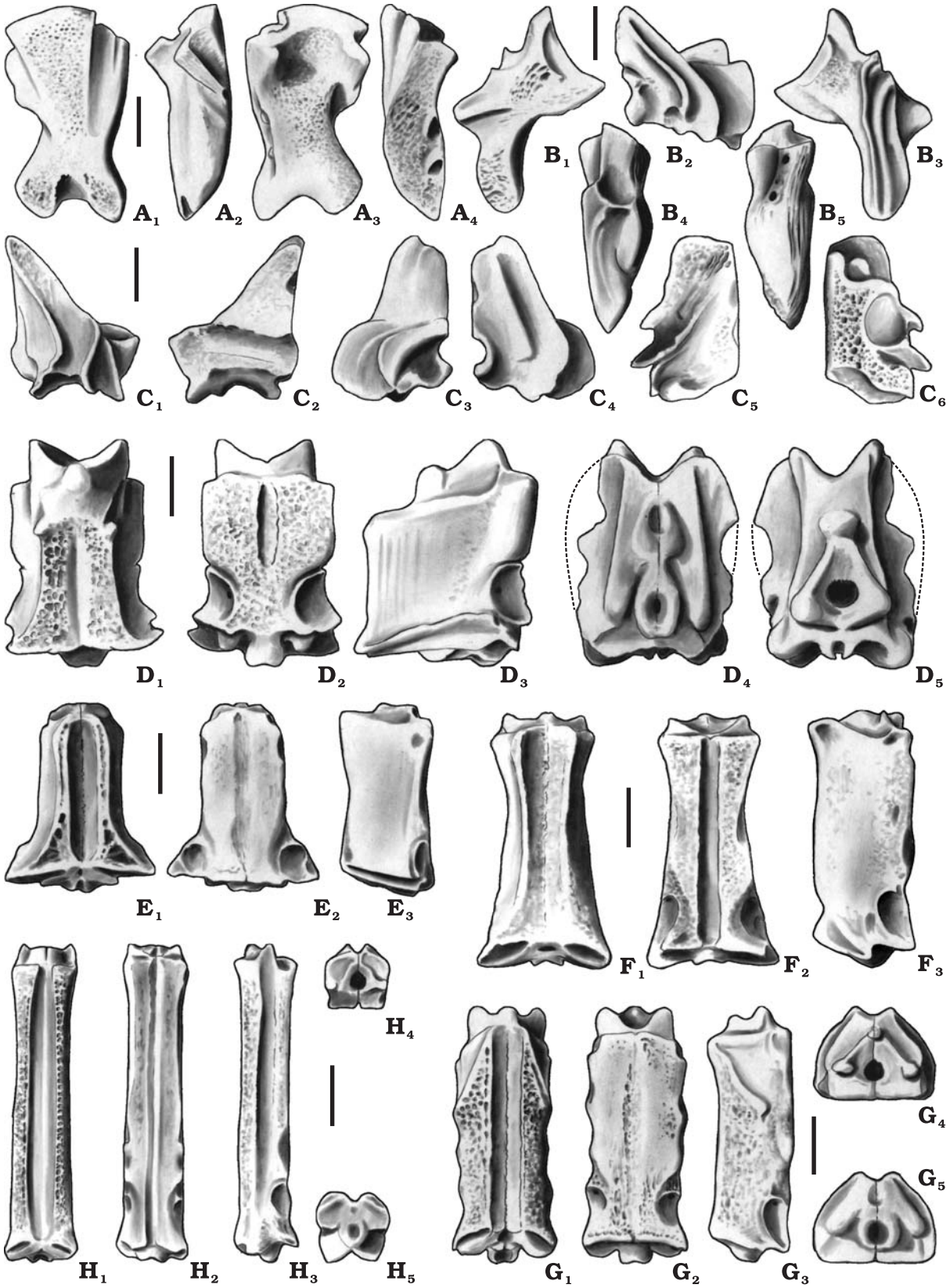

Fig. 10. Skeletal elements of the ophiuroid *Furcaster aequoreus* sp. n. from the Early Givetian of outcrop III at Śniadka, Holy Cross Mountains. **A**. Mouth-angle plate GIUS 4-439 Śni./936/1; A_1 abradial view, A_2 dorsal view, A_3 adradial view, A_4 ventral view. **B**. Half of the first ambulacral plate GIUS 4-439 Śni./935/1; B_1 inner view, ventral edge is on the top of figure, B_2 distal view, ventral edge is on the bottom of figure, B_3 outer view, ventral edge is on the top of figure, B_4 ventral view, B_5 dorsal view. **C**. Half of the second ambulacral plate GIUS 4-439 Śni./935/2; C_1 outer view, C_2 inner view, C_3 proximal view, C_4 distal view, ➝

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)			
Number of specimens	Features	Holotype	Minimum	Mean	Maximum
Ambulacral plates: 188	Length	970	685	850	970
	Width	695	125	430	695
	Height	910	235	780	1070
Lateral plates: 222	Length	–	705	1015	1325
	Width	–	255	560	890
Spines: 34	Length	–	835	1100	1265
	Diameter of base	–	205	210	215

Diagnosis. — Podial basin on the ambulacral plate poorly delimited. Lateral plates with a large posterio-internal bulge, well demarcated along almost all of its periphery by a groove.

Description. — Ambulacral plates. The most proximal ambulacral plates are narrow and high. The greatest shortening occurs in the middle part where the lateral edges are almost in contact. In side-view, the plate is obliquely truncated from the proximal side, allowing greater flexibility of arm movement especially in the adoral direction (Pl. 1: 15; Text-figs 6A–D, 7A–E). On the distal side, latero-ventrally there are deep lateral muscular fossae.

Lateral plates. The primary lateral plate is narrow and lacks mamelons (Text-fig. 8A). Proximal lateral plates are thick with a large protrusion for articulation to the ambulacral plate. Near the distal edge there are four ring-shaped mamelons (Pl. 1: 16; Text-fig. 8D–E). Distally the number of mamelons decreases to two. An elliptical bulge contacts with the proximal truncation of the next plate (Pl. 1: 16; Text-fig. 8D–H). Along the ventral edge there are four mamelons for attachment of the smaller spines. In distal elements the number of the mamelons increases to five, but the most distal elements lack ventral mamelons, and presumably their fine spines (Text-fig. 8H).

Spines. Two kinds of conical spines were found: some have fine groovelets, the others are short and have numerous thorns (Text-fig. 8B–C). The larger ones were located at the distal edge, the others on the ventral edge and directed sidewards. The basal parts of both kinds of spines are the same.

Remarks. — The species differs from *Weigeltura austera* sp. n. by the lack of a ridge surrounding the podial basin, lack the convexities developed behind the lateral muscular fossa on the ambulacral plates.

Occurrence. — Late Emsian: Set V of the Grzegorzowice Beds at Grzegorzowice. Early Eifelian: brachiopod *Chimaerothyris dombrowiensis* Zone of Zbrza, Holy Cross Mountains, Poland.

Genus *Chattaster* Hahn *et* Brauckmann, 1981

Type species: *Chattaster hueffneri* (Schöndorf, 1915).

Chattaster loculus sp. n.
(Pl. 1: 25–26; Text-fig. 9A–F)

Holotype: GIUS 4-584 Mrz./974/1, Text-fig. 9F.

Type horizon: Late Givetian, Early *Mesotaxis falsiovalis* Zone.

Type locality: Trench II, layer 13 at Marzysz, Holy Cross Mountains.

Derivation of the name: From Latin *loculus* – box, due to complete closure of ambulacrals by laterals.

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)			
Number of specimens	Features	Holotype	Minimum	Mean	Maximum
Arm fragment: 1	Length	510	–	–	–
	Width	195	–	–	–
Lateral plates: > 500	Length	–	500	520	540
	Height	–	100	240	255

C_5 dorsal view, C_6 ventral view. **D**. Holotype vertebra GIUS 4-439 Śni./917/1 from the proximal part of the arm; D_1 dorsal view, D_2 ventral view, D_3 lateral view, D_4 distal view, D_5 proximal view. **E**. Vertebra GIUS 4-439 Śni./917/2 from the middle part of the arm; E_1 dorsal view, E_2 ventral view, E_3 lateral view. **F**. Vertebra GIUS 4-439 Śni./917/3 from the middle part of the arm; F_1 dorsal view, F_2 ventral view, F_3 lateral view. **G**. Vertebra GIUS 4-439 Śni./917/4 from the distal part of the arm; G_1 dorsal view, G_2 ventral view, G_3 lateral view, G_4 proximal view, G_5 distal view. **H**. Vertebra GIUS 4-439 Śni./917/5 from the distal part of the arm; H_1 dorsal view, H_2 ventral view, H_3 lateral view, H_4 proximal view, H_5 distal view. Scale bar 200 μm.

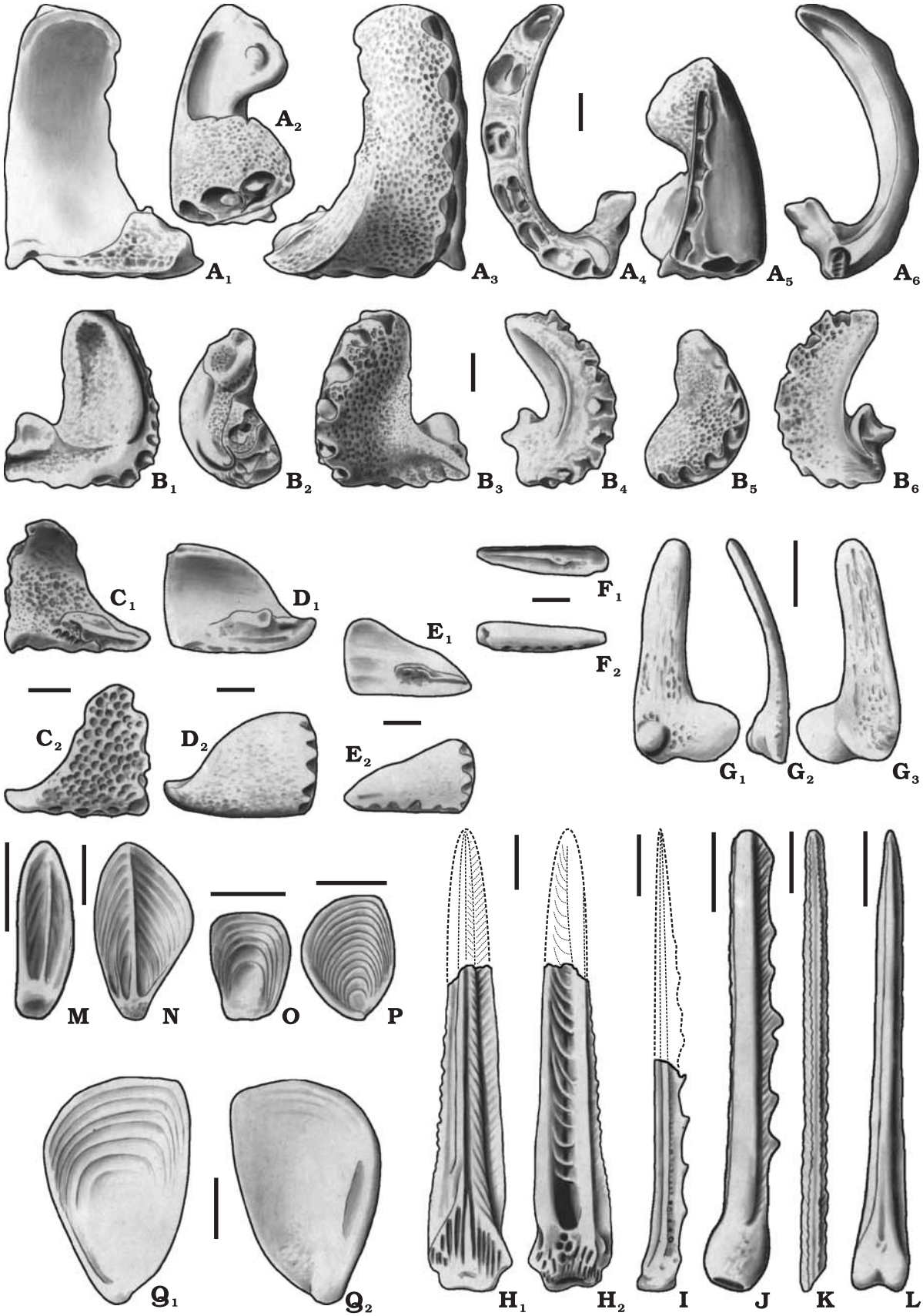

Fig. 11. Skeletal elements of the ophiuroid *Furcaster aequoreus* sp. n., from the Early Givetian of outcrop III at Śniadka, Holy Cross Mountains. **A**. Lateral plate GIUS 4-439 Śni./927/2 from the proximal part of the arm; A_1 inner view, A_2 dorsal view, A_3 outer view, A_4 distal view, A_5 ventral view, A_6 proximal view. **B**. Lateral plate GIUS 4-439 Śni./927/3 from the proximal part →

Diagnosis. — Proximal lateral plates have pustules over their outer surfaces.

Description. — Ambulacral plates. One articulated fragment has been discovered, comprising an ambulacral plate and two tightly adjoining lateral plates. Its distal end is expanded (Text-fig. 9F). On the ventral side is an oval podial opening between the lateral plates. This belongs to the more distal part of an arm, as it lacks mamelons on its lateral plates. No isolated ambulacral plates were found, possibly due to their extreme fragility.

Lateral plates. These are in the shape of a half tube with a swollen distal end bearing a ring of mamelons. The mamelons disappear on the more distal lateral plates. Up to four mamelons may occur. Behind the ring of mamelons there is a narrow tongue, protecting the median articular process. On the ventro-distal side there is a semicircular slit for a podium. Externally a protrusion can be seen, where the plate contacted the next ambulacral plate. The proximal edge has a small, circular convexity for articulation to the proximal end of an ambulacral plate.

Remarks. — Lateral plates differ from those of *Chattaster hueffneri* in having more numerous mamelons, and by the presence of pustules and lack of longitudinal incision at the proximal end.

Occurrence. — Late Givetian: trench II at Marzysz; Set C of Sowie Górki, Holy Cross Mountains, Poland.

Suborder **Zeugophiurina** Matsumoto, 1929

Family **Furcasteridae** Stürtz, 1900

Genus *Furcaster* Stürtz, 1900 (= *Calclyra* Frizzell *et* Exline, 1955)

Type species: *Furcaster palaeozoicus* Stürtz, 1886.

Remarks. — Frizzell and Exline (1955, 1966) and Spandel (1898) separated some arm spines of *Furcaster* from holothurian sclerites because of their porosity, placing these in the genus *Calclyra* Frizzell *et* Exline, 1955 (= *Prosynapta* Spandel, 1898; not *Prosynapta* Cuénot, 1891). 1975. The ambulacral plates described by Becker and Weigelt (1975; as "Bautyp" 2 Amb-2, "Wirbel", pp. 14–16 (partim), Taf. 4: 1–6 (non fig. 7); 5: 2–4, 5?) are congeneric.

The arm vertebra of these ophiuroids were formed of fused halves, whereas in more primitive forms these were separate skeletal elements (cf. Pl. 3: 10, 13; Text-fig. 10A–H). The suture between these halves remains recognisable in some Recent ophiuroids (Pl. 3: 14). Lateral plates of *Furcaster* also correspond in structure to those of some modern ophiuroids (cf. Pl. 4: 1–11; Text-figs 11A–G, 14A–R). On the other hand, the development of their mouth frame is unlike that in modern form (cf. Pl. 3: 1, 3–7; Text-figs 10A–B, 12A–E). They also lack the dorsal and ventral plates. This indicates affinity with the Phrynophiurida, although no homologue of the radial shields and the bursal plates can be recognised, unless their equivalents are the plates interpreted as the primary laterals (Text-figs 11G, 14A–B). The genus is well known because more or less complete specimens exist (Haude 1982; Haude and Thomas 1983). Reconstruction of the scleritome, based on isolated elements is quite easy; moreover the Devonian material from the Holy Cross Mountains contains numerous elements which remain articulated. Furcasteridae are one of the most important links between the Palaeozoic and post-Palaeozoic ophiuroids.

Furcaster aequoreus sp. n.

(Pl. 3: 13; Text-figs 10A–H, 11A–Q)

Holotype: GIUS 4-439 Śni./917/1, Text-fig. 10D.

Type horizon: Early Givetian, *Polygnathus hemiansatus* Zone.

Type locality: Outcrop III at Śniadka, Holy Cross Mountains.

Derivation of the name: From Latin *aequoreus* – marine.

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of the arm; B_1 inner view, B_2 dorsal view, B_3 outer view, B_4 distal view, B_5 ventral view, B_6 proximal view. **C**. Lateral plate GIUS 4-439 Śni./927/4 from the middle part of the arm; C_1 inner view, C_2 outer view. **D**. Lateral plate GIUS 4-439 Śni./927/5 from the middle part of the arm; D_1 inner view, D_2 outer view. **E**. Lateral plate GIUS 4-439 Śni./927/6 from the distal part of the arm; E_1 inner view, E_2 outer view. **F**. Lateral plate GIUS 4-439 Śni./927/7 from the distal part of the arm; F_1 inner view, F_2 outer view. **G**. First lateral plate GIUS 4-439 Śni./907/1; G_1 inner view, G_2 proximal view, G_3 outer view. **H–L**. Various kinds of spines. **H**. Big spine GIUS 4-439 Śni./922/2, probably from proximal lateral plate; H_1 side (dorsal?) view, H_2 opposite side view. **I**. GIUS 4-439 Śni./922/6. **J**. GIUS 4-439 Śni./922/3. **K**. GIUS 4-439 Śni./922/5. **L**. GIUS 4-439 Śni./922/4. **M–Q**. Various kinds of leaf-like scales. **M**. Plate intermediate in form between spines and scales from the corner of lateral plate GIUS 4-439 Śni./923/4, abradial side. **N**. Abradial side of GIUS 4-439 Śni./923/3. **O**. GIUS 4-439 Śni./923/5, abradial side. **P**. GIUS 4-439 Śni./923/1, abradial side. **Q**. GIUS 4-439 Śni./923/2; Q_1 abradial side, Q_2 adradial side. Scale bar 200 μm.

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)			
Number of specimens	Features	Holotype	Minimum	Mean	Maximum
Mouth-angle plates: 55	Length	–	520	870	1375
	Width	–	255	505	910
First ambulacrals: 60	Length	–	340	590	790
	Width	–	195	355	450
	Height	–	505	815	935
Second ambulacrals: 45	Length	–	320	560	610
	Width	–	195	320	400
	Height	–	280	430	630
Other ambulacrals: 230	Length of proximal plates	775	620	755	790
	Width of proximal plates	450	400	450	475
	Height of proximal plates	630	590	615	680
	Length of median plates	–	520	630	845
	Width of median plates	–	450	510	550
	Height of median plates	–	290	325	385
	Length of distal plates	–	730	870	1070
	Width of distal plates	–	245	345	445
	Height of distal plates	–	225	240	285
Lateral plates: 115	Length of proximal plates	–	865	1000	1135
	Height of proximal plates	–	1050	1310	1525
	Length of median plates	–	695	785	880
	Height of median plates	–	600	615	625
	Length of distal plates	–	730	735	745
	Height of distal plates	–	170	300	524
Spines: > 500	Length	–	980	1295	1785
	Diameter of base	–	130	165	335
Leaflike scales: > 500	Length	–	300	600	775
	Width	–	140	385	510

Diagnosis. — Articular surfaces of arm vertebra are rectangular, the wings are oval. Spines have frilled edges.

Description. — Mouth angle plates. These X-shaped plates have on their abradial side two ear-shaped, wrinkled processes which formed an articulation surface for the subsequent plates of mouth frame (Text-fig. 10A). On the dorsal side there are two furrows: the first one, more distal and shallower, is the circumoral water channel furrow, the other one, more proximal and more strongly curved, contained the neural ring. On the adradial surface, opposite to the auricular processes and connecting the neighbouring mouth angle plates, there is a depression above which an edge joined the first ambulacral plate.

Ambulacral plates. The structure of the first ambulacral plate is quite different from that of subsequent plates. They are formed of two separate halves, apparently connected by a more or less mobile junction during life. On the inner dorsal side is a wedge-shaped, wrinkled process; the articular junction with the opposite half of the first ambulacral plate (Text-fig. 10B). Below it there is a radial water channel. Still lower, by the junction with the mouth angle plate there are two broad fossae, containing the pores of the ambulacral canals, marking the location of the first podia. Second ambulacrals are found separately as a rule. On the ventral side there is usually only a single podial basin (Text-fig. 10C). Subsequent ambulacrals form an arm vertebra of two fused halves (Pl. 3: 13; Text-fig. 10D–H). By the vertebral edge there is an oral muscular fossa.

Lateral plates. The laterals are covered in fine, shallow, oval depressions. These pseudoperforations disappear in distal elements. The first lateral plates are in the shape of an arched, vertical blade, separated by a curved deflection from the outer side. There is an articular protrusion on the inner corner which differs from those in more distant lateral plates. Possibly the modified lateral plates are equivalents of the buccal plates (Text-fig. 11G). Proximal plates are L-shaped; in the middle part of an arm they become triangular and subsequently their height quickly decreases and their width also decreases but more slowly. Mamelons occur at the ventral and distal edges in peculiar pits of either rectangular or oval outline. The distal edge bore long spines whereas ventral edge had flat leaf-shaped scales.

Spines. Along the main ridge these have a characteristic braided pattern, with oblique lines at the lateral laminae, and numerous transverse trabeculae on the opposite side. The edges of spines are of unequal size, and have numerous thorns (Text-fig. 11H–L).

Scales. All are leaf-shaped. One side shows concentric rings, possibly reflecting their mode of growth (Text-fig. 11M–Q). The elements with a ridge at their centre do not have a pointed apex, especially in intermediate forms between the scales and spines. On the opposite side the scales are smooth. No lyre-shaped scales were recognised.

Remarks. — The species differs from *Furcaster cataphractus* sp. n. in having a large wedge-shaped convexity on the aboral surface of the mouth angle plate, an oval wing developed distally, and a cigar-shaped aboral groove on its arm vertebra. Furthermore, lateral plates are covered by circular, crescent-shaped depressions. It differs from the other species in the structural details of all the elements, chiefly of spines and scales. The spines have many thorns. In contrast to this species, scales of Carboniferous species do not have one side smooth (cf. Haude 1982; Haude and Thomas 1983). It differs from *Furcaster separatus* Haude, 1995 from the Early Devonian of the Precordillera (Argentina), by the sculpture of the lateral surface of arm vertebra and, most probably, by structure of its scales and spines; the other elements are poorly preservated (cf. Haude 1995b).

Occurrence. — Late Eifelian: outcrop I, II at Śniadka. Early Givetian: outcrop III at Śniadka; Set XXV of the Skały Beds at Skały, Holy Cross Mountains, Poland.

Furcaster cataphractus sp. n.

(Pls 3: 3–12, 15, 16, 4: 4–19, 5: 1–3, 5–23; Text-figs 12A–I, 13A–E, 14A–R, 15A–AL, AZ)

Holotype: GIUS 4-564 Mrz./999/1, Text-fig. 13A.

Type horizon: Late Givetian, Early *Mesotaxis falsiovalis* Zone.

Type locality: Trench II, layer 2 at Marzysz, Holy Cross Mountains.

Derivation of the name: From Latin *cataphractus* – armoured, due to protection of the arm vertebra by the laterals.

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)			
Number of specimens	Features	Holotype	Minimum	Mean	Maximum
Mouth-angle plates: > 500	Length	–	390	650	745
	Width	–	195	405	500
First ambulacrals: > 500	Length	–	320	490	460
	Width	–	410	490	560
	Height	–	360	590	1270
Second ambulacrals: > 500	Length	–	360	430	480
	Width	–	435	530	600
	Height	–	410	570	630
Other ambulacrals: > 15000	Length of proximal plates	745	590	650	745
	Width of proximal plates	1340	620	780	1340
	Height of proximal plates	1185	660	700	1185
	Length of median plates	–	800	840	885
	Width of median plates	–	675	680	715
	Height of median plates	–	620	635	655
	Length of distal plates	–	755	795	805
	Width of distal plates	–	235	285	325
	Height of distal plates	–	225	255	285
Lateral plates: > 15000	Length of proximal plates	–	580	640	755
	Height of proximal plates	–	775	820	970
	Length of median plates	–	550	680	825
	Height of median plates	–	560	695	845
	Length of distal plates	–	840	865	920
	Height of distal plates	–	310	335	365
Spines: > 15000	Length		980	1955	3120
	Diameter of base		170	270	335
Leaflike scales: > 15000	Length	–	380	690	845
	Width	–	150	410	510
Lyrelike scales: 253	Length	–	250	590	655
	Width	–	135	260	325

Diagnosis. — Vertebral articula and wings are triangle-shaped. Spines with straight edges.

Description. — Mouth angle plates. These are L-shaped (Pl. 3: 3–5; Text-fig. 12A). When seen from its side, the edge connecting the plate with the first ambulacral plate is C-shaped.

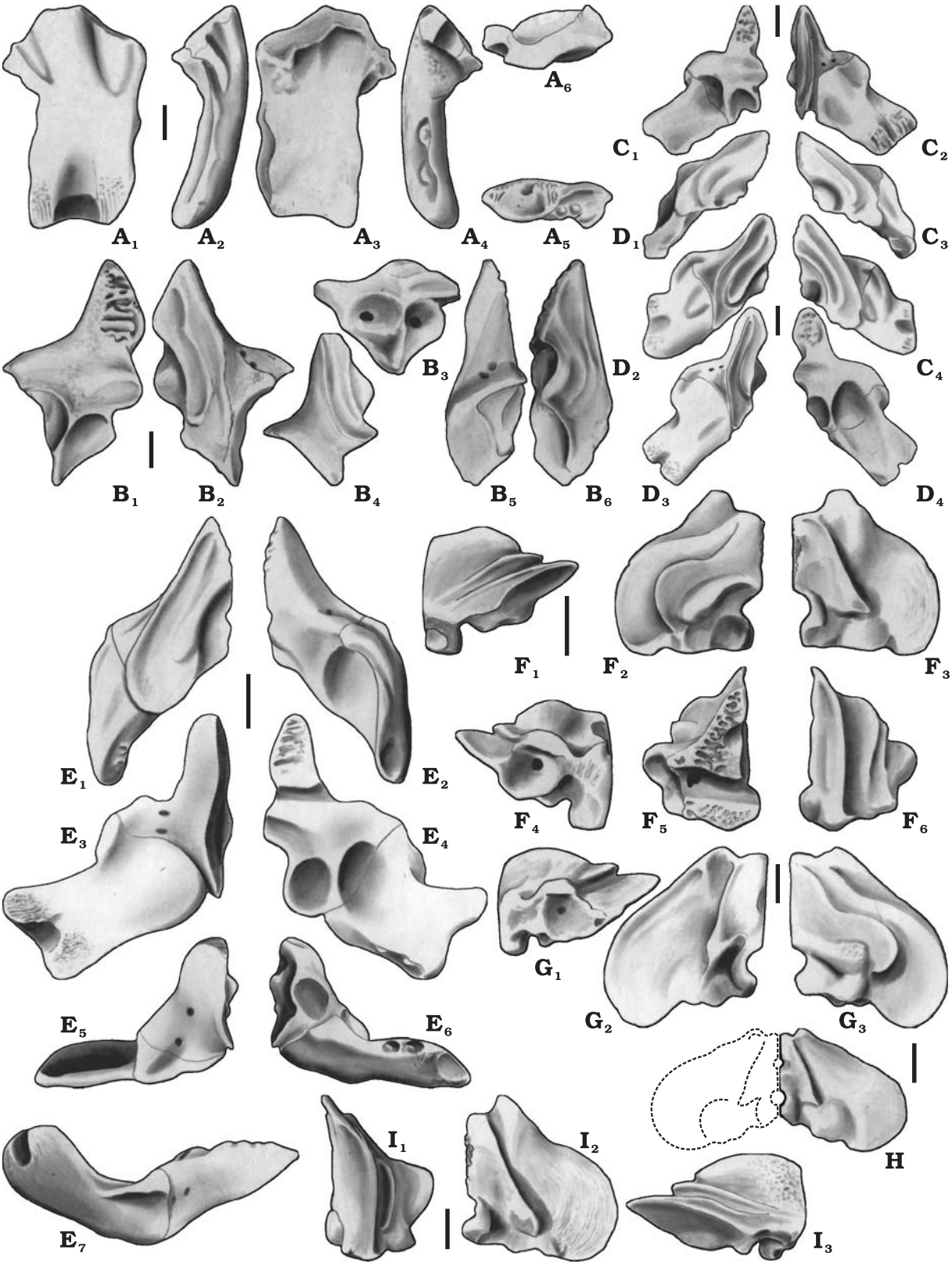

Fig. 12. Skeletal elements of the ophiuroid *Furcaster cataphractus* sp. n. from the Late Givetian of Marzysz, Holy Cross Mountains, samples Marzysz II/4 (A–B), Marzysz II/W/6 (C–D, F–I), and Marzysz II/13 (E). **A**. Mouth-angle plate GIUS 4-575 Mrz./859/3; A_1 abradial view, A_2 dorsal view, A_3 adradial view, A_4 ventral view, A_5 view of the articulation face between the two opposite mouth-angle plates, A_6 view of the articulation face with first ambulacral. **B**. Half of the first ambulacral plate GIUS 4-575 Mrz./859/1; B_1 inner view, ventral edge is on the bottom of figure, B_2 outer view, ventral edge is on the bottom of figure, B_3 view of ➝

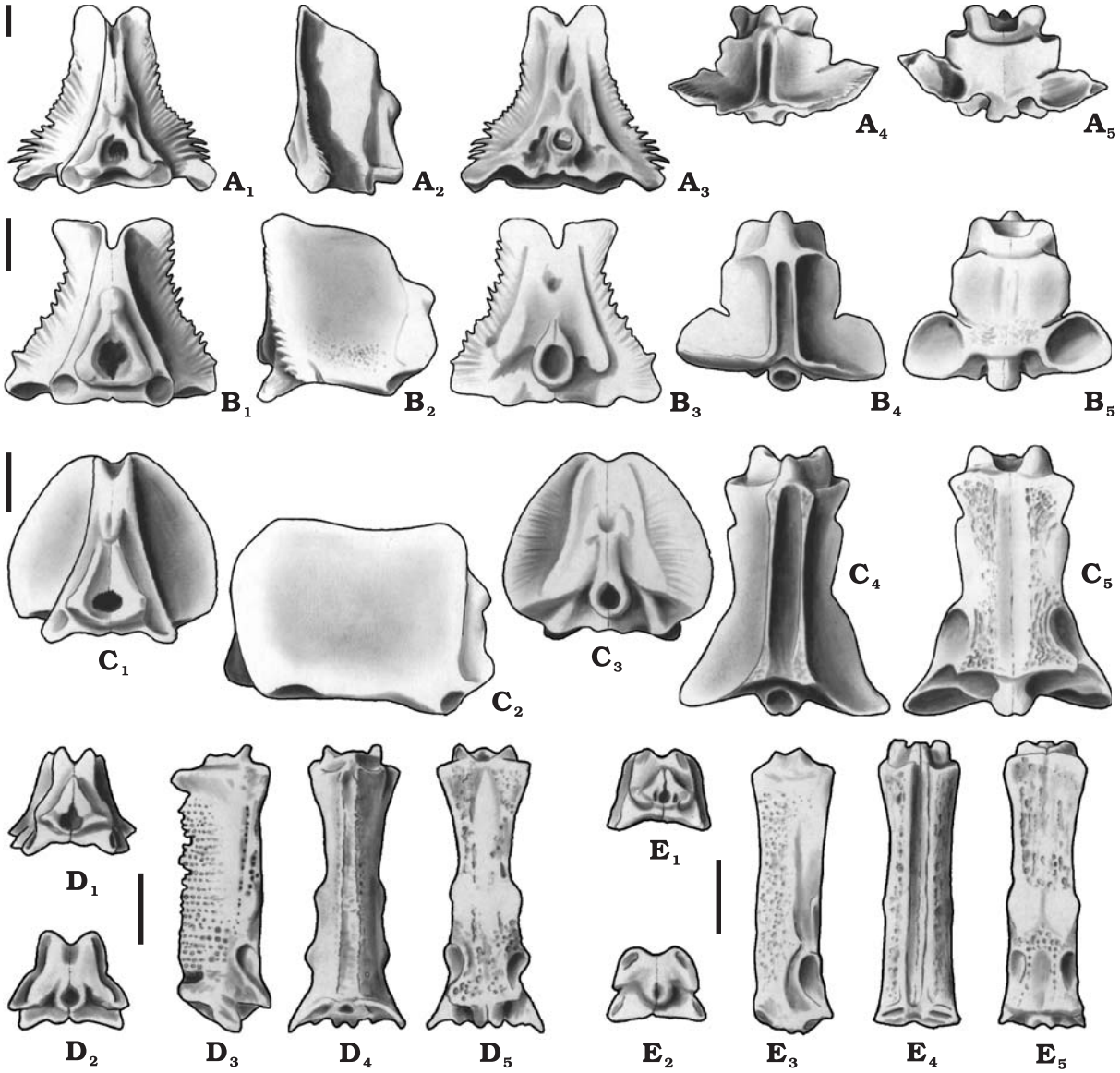

Fig. 13. Skeletal elements of the ophiuroid *Furcaster cataphractus* sp. n. from the Late Givetian of the Holy Cross Mountains. **A**. Holotype vertebra GIUS 4-564 Mrz./999/1 from the proximal part of the arm, Marzysz II/W/2; A_1 proximal view, A_2 lateral view, A_3 distal view, A_4 dorsal view, A_5 ventral view. **B**. Vertebra GIUS 4-584 Mrz./1114/3, Marzysz II/13 from the proximal part of the arm; B_1 proximal view, B_2 lateral view, B_3 distal view, B_4 dorsal view, B_5 ventral view. **C**. Vertebra GIUS 4-584 Mrz./1114/4 from the middle part of the arm, Marzysz II/13; C_1 proximal view, C_2 lateral view, C_3 distal view, C_4 dorsal view, C_5 ventral view. **D**. Vertebra GIUS 4-584 Mrz./1114/2 from the distal part of the arm, Marzysz II/13; D_1 proximal view, D_2 distal view, D_3 lateral view, D_4 dorsal view, D_5 ventral view. **E**. Vertebra GIUS 4-584 Mrz./1114/1 from the distal part of the arm, Marzysz II/13; E_1 proximal view, E_2 distal view, E_3 lateral view, E_4 dorsal view, E_5 ventral view. Scale bar 200 μm.

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the link edge with mouth-angle plate, B_4 view of the dorsal side, link edge between opposite halves of the first ambulacral, B_5 dorsal view, B_6 ventral view. **C**–**E**. Fragments of mouth frame, half of the first ambulacral plate is joined with the mouth angle plate. **C**–**E**. Fragments of mouth frame, half of the first ambulacral plate is joined with the mouth angle plate. **C**. GIUS 4-568 Mrz./11/1; C_1 adradial (inner) view, C_2 abradial (outer) view, C_3 distal-oblique view, C_4 distal view. **D**. GIUS 4-568 Mrz./11/2; D_1 distal-oblique view, D_2 distal view, D_3 abradial (outer) view, D_4 adradial (inner) view. **E**. GIUS 4-584 Mrz./177/1; E_1 distal view, E_2 proximal view, E_3 abradial (outer) view, E_4 adradial (inner) view, E_5 dorsal view, E_6 ventral view, E_7 dorsal-oblique view. **F**–**I**. Second ambulacral plates. **F**. GIUS 4-568 Mrz./34/1; F_1 dorsal view, F_2 proximal view, F_3 distal view, F_4 ventral view, F_5 inner view, F_6 outer view. **G**. GIUS 4-568 Mrz./34/2; G_1 ventral view, G_2 distal view, G_3 proximal view. **H**. Two joint halves GIUS 4-568 Mrz./13/1, reconstruction, distal view. **I**. GIUS 4-568 Mrz./34/3; I_1 outer view, I_2 distal view, I_3 dorsal view. Scale bar 200 μm.

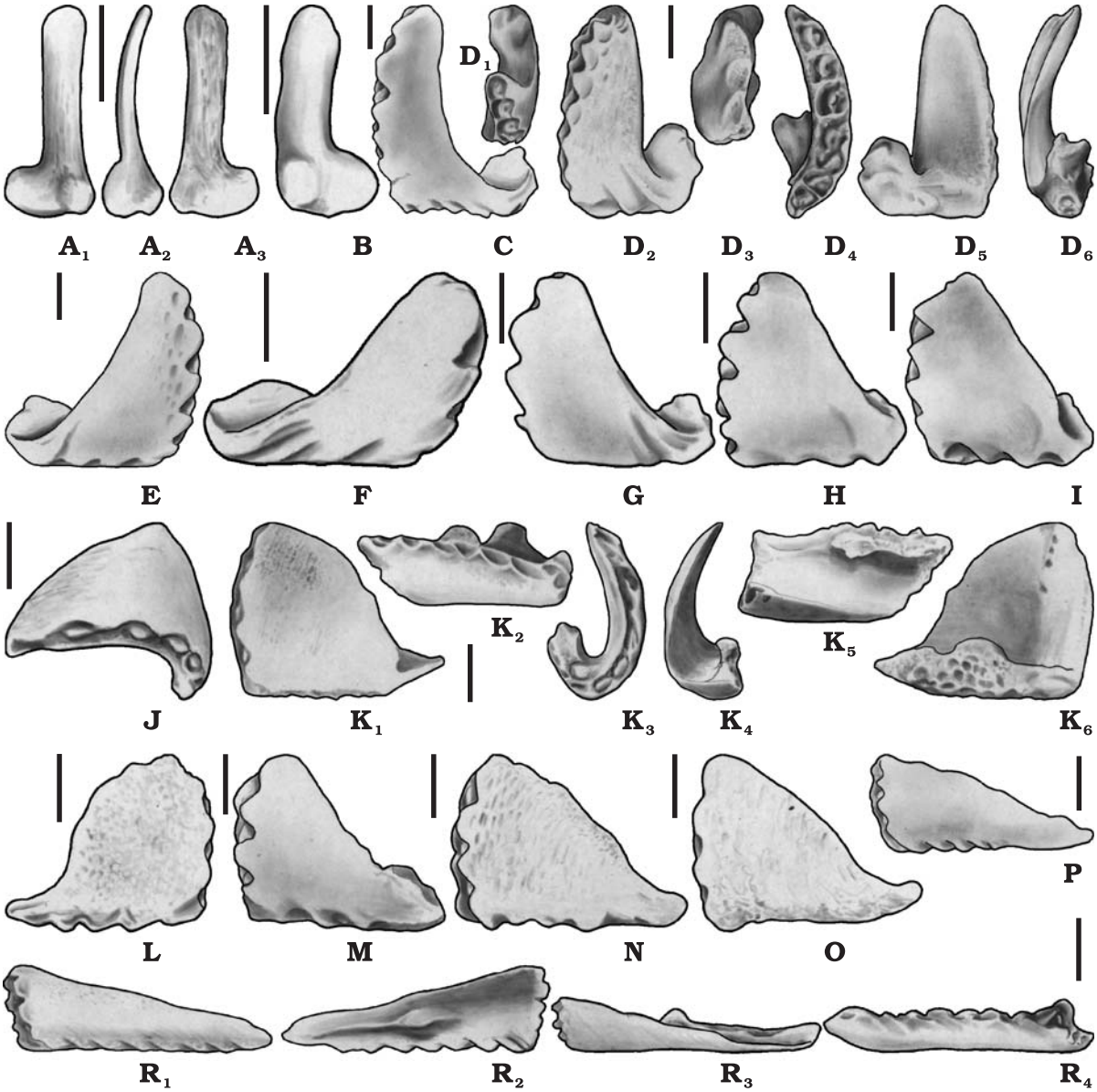


Fig. 14. Skeletal elements of the ophiuroid *Furcaster cataphractus* sp. n. from the Late Givetian of Marzysz, Holy Cross Mountains; samples Marzysz II/13 (A–B) and Marzysz II/W/6 (C–R). **A**. First lateral plate GIUS 4-584 Mrz./158/1; A_1 inner view, A_2 proximal view, A_3 outer view. **B**. First lateral plate GIUS 4-584 Mrz./158/2, inner view. **C**. Lateral plate GIUS 4-568 Mrz./74/2 from the proximal part of the arm. **D**. Lateral plate GIUS 4-568 Mrz./74/1 from the proximal part of the arm; D_1 dorsal view, D_2 outer view, D_3 ventral view, D_4 distal view, D_5 inner view, D_6 proximal view. **E**. Lateral plate GIUS 4-568 Mrz./74/3 from the middle part of the arm, outer view. **F**. Lateral plate GIUS 4-568 Mrz./74/4 from the middle part of the arm, outer view. **G**. Lateral plate GIUS 4-568 Mrz./74/6 from the middle part of the arm, outer view. **H**. Lateral plate GIUS 4-568 Mrz./74/7 from the middle part of the arm, outer view. **I**. Lateral plate GIUS 4-568 Mrz./74/5 from the middle part of the arm, outer view. **J**. Lateral plate GIUS 4-568 Mrz./74/13 from the middle part of the arm, distal-oblique view. **K**. Lateral plate GIUS 4-568 Mrz./74/10 from the middle part of the arm; K_1 outer view, K_2 ventral view, K_3 distal view, K_4 proximal view, K_5 dorsal view, K_6 inner view. **L**. Lateral plate GIUS 4-568 Mrz./74/11 from the middle part of the arm, outer view. **M**. Lateral plate GIUS 4-568 Mrz./74/8 from the middle part of the arm, outer view. **N**. Lateral plate GIUS 4-568 Mrz./74/9 from the middle part of the arm, outer view. **O**. Lateral plate GIUS 4-568 Mrz./74/12 from the middle part of the arm, outer view. **P**. Lateral plate GIUS 4-568 Mrz./74/14 from the distal part of the arm, outer view. **R**. Lateral plate GIUS 4-568 Mrz./74/15 from the distal part of the arm; R_1 outer view, R_2 inner view, R_3 dorsal view, R_4 ventral view. Scale bar 200 μm.

Ambulacral plates. The first ambulacrals have a shallow, straight radial ambulacral channel. Their distal articular surface is strongly simplified and its elements are vertically elongated (Pl. 3: 6–7; Text-fig. 12B). Mode of connection with the mouth angle plates can be seen in some articulated specimens (Pl. 3: 5; Text-fig. 12C–E). Second ambulacral plates consist of two halves, with the connecting surface covered by numerous

knobs and ribs, presumably increasing the strength of articulation (Pl. 3: 8; Text-fig. 12F–I). Ambulacrals of subsequent rows form an arm vertebra (Pl. 3: 9–12, 15, 16; Text-fig. 13A–E), have sharp-edged wall flanking the aboral groove and a triangular wings on the distal side. The proximal vertebra have a triangle-shaped proximal articular surface which becomes gradually trapezoid-shaped on distal elements.

Lateral plates. The L-shaped laterals are covered by shallow, crescent-shaped depressions (Pl. 4: 4–11; Text-fig. 14A–R). The protrusion in distal plates is translated adaxially.

Spines. Along the main ridge spines have a characteristic braided texture (Pl. 4: 12, 16; Text-fig. 15A). Spine basis are elliptical, rounded or semirectangular in outline (Pl. 4: 17–19; Text-fig. 15A–E). Occasionally the spines have longitudinal ridges, which bifurcate at the basis (Pl. 4: 12–19; Text-fig. 15A–E).

Scales. Leaf-shaped plates located in the corners are intermediate morphologically between the spines and scales. Elements with a ridge in their middle have a pointed tip, particularly so in those forms intermediate between the spines and scales. On one side the scales have concentric rings, on the other they are smooth (Pl. 5: 5–22; Text-fig. 15F–S). Lyre-like forms have numerous tear-shaped slits (two-seven) and were formerly assigned to holothurians (Frizzell and Exline 1966). More elongated forms have pointed distal ends. The basal part is trumpet-shaped with neural canal. The elements occurred most probably only on the proximal lateral plates, in their corners (the mamelons at the corners are significantly smaller in these plates, and correspond in size and shape to bases of the lyre-like plates, Pl. 5: 1–3; Text-fig. 15T–AL). Intermediate forms between the lyre-like and the leaf-like scales (Text-fig. 15T–W) and between the respective spines (Pl. 5: 1; Text-fig. 15AC–AL) can all be observed. The extreme lyre-like forms have three blades and resemble spines in structure (cf. Pl. 4: 13; and Text-fig. 14AK–AL). This type of plates is possibly connected with the so called distal tentacle scales (cf. Baker 1974 and the present paper Text-fig. 15AZ).

Remarks. — The articulation surface between the halves of the second ambulacral plate has fine ornamentation, strengthening the connection. Neither the comparable morphologies, nor the distinct oral muscular fossa on the proximal articular surface have been observed in *Furcaster aequoreus* sp. n. Moreover, *F. cataphractus* sp. n. differs from *F. aequoreus* sp. n. in having a small convexity at the aboral surface of the mouth angle plate, a triangular wings to the distal surface and an aboral groove open on one of the sides of arm vertebra. Lateral plates are covered with crescent-shaped depressions. The most significant differences however are in the morphology of spines, *F. cataphractus* sp. n. having characteristic braided texture and lacking thorns. Other species differ in details of the structure of all its elements, particularly spines and scales (*Furcaster aequoreus* sp. n.). *Furcaster separatus* Haude, 1995 from the Early Devonian of the Precordillera (Argentina), differs by having approximating proximal and distal wing-like lateral crest on the arm vertebra (Haude 1995b).

Occurrence. — Mid (Late?) Givetian: Set B of Jaźwica; Set B of Stokówka; Set A of Górno. Late Givetian: outcrop I, trench II at Marzysz; Set B of Posłowice; Sets C, G of Sowie Górki; Set C of Stokówka; Set A of Góra Zamkowa, Chęciny; Set B of Zbrza; Set B of Czarnów, Kielce; Wola Jachowa. Early Frasnian: Set D of Stokówka; Kowala I; Set K of Góra Zamkowa, Chęciny. Early/Mid Frasnian: Sets B, C of the Kowala railroad cut. Mid Frasnian: Szczukowskie Górki; Set G of Dębska Wola. Set D of the Kowala railroad cut; Set D of Górno, Holy Cross Mountains, Poland.

Furcaster sp. A
(Pl. 5: 4; Text-fig. 15AM–AN)

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)		
Number of specimens	Features	Minimum	Mean	Maximum
Lyre-like scales: 17	Length	405	445	490
	Width	215	230	250

Description. — Lyre-like scales with only two tear-shaped, elongated slits. The trabeculae are thick. When seen from the side they are flexed and shovel-like. The basal part is trumpet-shaped (Pl. 5: 4; Text-fig. 15AM–AN).

Remarks. — Similar to *Calclyra eiseliana* (Spandel, 1898), which was formerly assigned to Holothuroidea.

Occurrence. — Mid Frasnian: Set C of Górno, Holy Cross Mountains, Poland.

Furcaster sp. B
(Text-fig. 15AO–AP)

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)		
Number of specimens	Features	Minimum	Mean	Maximum
Spines: 1	Length	?	–	–
	Diameter of base	255 (?)	–	–
Lyre–like scales: 1	Length	405	–	–
	Width	220	–	–

Description. — Spines with a very narrow and smooth main ridge, with thin, broad lateral laminae, and covered by obliquely set ribs (Text-fig. 15AP). Scales are either leaf- or lyre-shaped with a distinct and corrugated axis. Lateral lobes are densely crossed by thin slits, eight on each side. The margin is wavy and the basal part trumpet-shaped (Text-fig. 15AO).

Occurrence. — Mid Frasnian: Set F of Psie Górki, Kielce, Holy Cross Mountains, Poland.

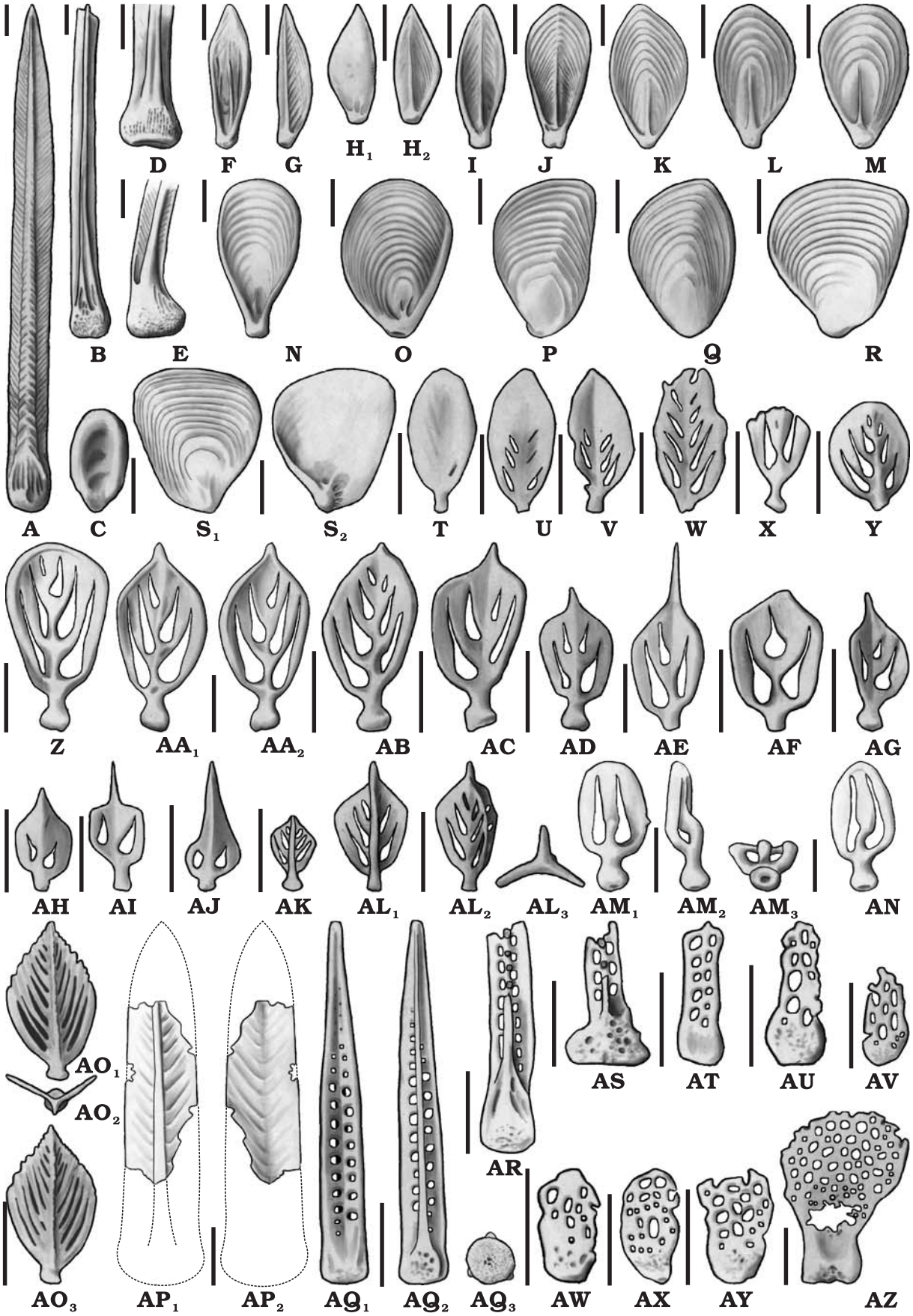
Furcaster sp. C
(Text-fig. 15AQ–AY)

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)		
Number of specimens	Features	Minimum	Mean	Maximum
Spines: 21	Length	305	600	895
	Diameter of base	120	125	130
Lyre-like scales: 45	Length	195	215	260
	Width	100	150	165

Description. — Spines have a narrow and smooth main ridge, perforated laterally. Lateral laminae are also perforated by circular pores. The basal part of the spine is rounded and has a shallow depression with

Fig. 15. Skeletal elements of the ophiuroid *Furcaster* from the Holy Cross Mountains. **A**–**AL**. Skeletal elements of *F. cataphractus* sp. n. from the Late Givetian of Marzysz, samples Marzysz II/13 (A–S, V, X–AB, AE, AG–AJ) and Marzysz II/W/6 (T–U, W, Y, AC–AD, AF, AK–AL). **A**. Spine GIUS 4-584 Mrz./163/4. **B**. Spine GIUS 4-584 Mrz./163/2. **C**. Base GIUS 4-584 Mrz./163/7. **D**. Base GIUS 4-584 Mrz./163/1. **E**. Base GIUS 4-584 Mrz./163/3. **F**–**S**. Various kinds of leaf-like scales. **F**. Plate intermediate between spine and scale GIUS 4-584 Mrz./162/12, abradial side. **G**. Plate intermediate between spine and scale GIUS 4-584 Mrz./162/14, abradial side. **H**. GIUS 4-584 Mrz./162/13; H_1 adradial side, H_2 abradial side. **I**. GIUS 4-584 Mrz./162/11, abradial side. **J**. GIUS 4-584 Mrz./162/10, abradial side. **K**. GIUS 4-584 Mrz./162/8, abradial side. **L**. GIUS 4-584 Mrz./162/7, abradial side. **M**. GIUS 4-584 Mrz./162/6, abradial side. **N**. GIUS 4-584 Mrz./162/9, abradial side. **O**. GIUS 4-584 Mrz./162/5, abradial side. **P**. GIUS 4-584 Mrz./162/3, abradial side. **Q**. GIUS 4-584 Mrz./162/4, abradial side. **R**. GIUS 4-584 Mrz./162/2, abradial side. **S**. GIUS 4-584 Mrz./162/1; S_1 abradial side, S_2 adradial side. **T**–**AL**. Various kinds of lyre-like scales. **T**. Form intermediate between leaf-like and lyre-like scale GIUS 4-568 Mrz./30/1. **U**. Same type scale GIUS 4-568 Mrz./30/3. **V**. Same type scale GIUS 4-584 Mrz./172/1. **W**. Same type scale GIUS 4-568 Mrz./30/2. **X**. Underdeveloped plate GIUS 4-584 Mrz./170/2. **Y**. GIUS 4-584 Mrz./30/4. **Z**. GIUS 4-584 Mrz./170/1. **AA**. GIUS 4-584 Mrz./170/9; AA_1 side view, AA_2 opposite side view. **AB**. GIUS 4-584 Mrz./170/7. **AC**. GIUS 4-568 Mrz./43/2. **AD**. GIUS 4-568 Mrz./43/3. **AE**. GIUS 4-584 Mrz./170/8. **AF**. Underdeveloped plate GIUS 4-568 Mrz./43/1. **AG**. Underdeveloped plate GIUS 4-584 Mrz./170/6. **AH**. Underdeveloped plate GIUS 4-584 Mrz./170/5. **AI**. Underdeveloped plate GIUS 4-584 Mrz./170/10. **AJ**. Underdeveloped plate GIUS 4-584 Mrz./170/4. **AK**. Trifoliate specimen GIUS 4-568 Mrz./38/1. **AL**. Trifoliate specimen GIUS 4-568 Mrz./38/2; AL_1 side view, AL_2 opposite side view, AL_3 top view. **AM**–**AN**. Lyre-like scales of *Furcaster* sp. A from the Middle Frasnian set C of Górno. **AM**. GIUS 4-607 Grn./1112/2; AM_1 side view, AM_2 lateral view, AM_3 view of the base. **AN**. GIUS 4-607 Grn./1112/1, side view. **AO**–**AP**. Skeletal elements of *Furcaster* sp. B from the Late Frasnian, set F of Psie Górki. **AO**. Bifoliate lyre like scale with edge GIUS 4-599 Psi./511/1; AO_1 side view, AO_2 top view, AO_3 opposite side view. **AP**. Fragment of spine GIUS 4-599 Psi./511/3 and its reconstruction; AP_1 side view, AP_2 opposite side view. **AQ**–**AY**. Skeletal elements of *Furcaster* sp. C from the Late Frasnian set F of Psie Górki. **AQ**. Long spine, GIUS 4-599 Psi./509/2 with holes; AQ_1 side view, AQ_2 opposite side view, AQ_3 base. **AR**. Fragment of spine GIUS 4-599 Psi./509/4 with holes, side view. **AS**. Fragment of spine GIUS 4-599 Psi./509/5 with holes, side view. **AT**. Short spine GIUS 4-599 Psi./510/4 with holes, side view. **AU**. Short spine GIUS 4-599 Psi./510/2 with holes, side view. **AV**. Leaf-like scales GIUS 4-599 Psi./510/6 with holes, side view. **AW**. Leaf-like scales GIUS 4-599 Psi./510/3 with holes, side view. **AX**. Leaf-like scales GIUS 4-599 Psi./510/1 with holes, side view. **AY**. Fragment of leaf-like scales GIUS 4-599 Psi./510/5 with holes, side view. **AZ**. Leaf-like scale with holes from the Late Givetian sample Marzysz II/13, GIUS 4-584 Mrz./213/1; possibly tentacle scale of *Furcaster cataphractus*, side view. Scale bar 200 μm.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three triangular pores at its bottom (Text-fig. 15AQ–AS). Scales are leaf-shaped (Text-fig. 15AU–AY) but with forms intermediate in shape to spines (Text-fig. 14AT). The axis of an element is distinct only in intermediate forms. All the scales are perforated, and with the exception of "intermediate" forms the pattern of perforation is chaotic. The basal part is flattened.

Remarks. — Scales resemble the distal tentacle scales of some modern ophiuroids (e.g. *Astrodendrum* Döderlein, 1911, cf. Baker 1974) although the latter are imperforate.

Occurrence. — Middle Frasnian: Set F of Psie Górki, Kielce, Holy Cross Mountains, Poland.

Order **Phrynophiurida** Matsumoto, 1915
Suborder **Euryalina** Lamarck, 1816
Family **Eospondylidae** Spencer *et* Wright, 1966
Genus *Eospondylus* Gregory, 1897

Type species: *Eospondylus primigenius* (Stürtz, 1886).

Eospondylus ingens sp. n.
(Pl. 1: 17–19; Text-fig. 9L–Q)

Holotype: GIUS 4-439 Śni./920/1, Text-fig. 9L.
Type horizon: Early Givetian, *Polygnathus hemiansatus* Zone.
Type locality: Outcrop III at Śniadka, Holy Cross Mountains.
Derivation of the name: From Latin *ingens* – extraordinary.

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)			
Number of specimens	Features	Holotype	Minimum	Mean	Maximum
Ambulacral plates: 3	Length	1235	1050	1140	1235
	Width	830	645	735	830
	Height	680	650	675	680
Lateral plates: 7	Length	–	630	865	930
	Width	–	220	490	580

Diagnosis. — On the lateral surface of the ambulacral plate there are two ridges, flanking the strongly expanded articular parts on both sides.

Description. — Ambulacral plates. Ambulacrals form an arm vertebra of two fused halves (Pl. 1: 17; Text-fig. 9L–M). The dorsal surface is sculpted by numerous fine depressions. The aboral groove is broadest in its median part. Lateral ridges extend up to the dorsal side where they disappear close to the aboral groove. The lateral space between the ridges shows the same sculpture as on the dorsal side (Pl. 1: 17; Text-fig. 9L–M). By the ventral edge the ridges converge without actually touching. Oral articular processes form two expanded lobes, symmetrical in respect to the aperture of the central channel. Fulcral ridges are weakly marked and flank above and on both sides, small and circular oral muscular fossae. On the distal articular surface, the fulcral ridge is still in contact with the aboral articular processes. The median articular process is ring-shaped and is perforated by the central water vessel channel. This is no median saddle, in its place two ridges diverge obliquely towards the dorsal surface from the median articular process to two ridges join the aboral articular process. Oral articular surfaces are flat and surround the proximal process. The oral notch narrows on both sides in the axial direction.

Lateral plates. The laterals are strongly perforated (Pl. 1: 18–19; Text-fig. 9N–Q) although perforation disappears in distal elements. When seen from the dorsal side the plates are characteristically saddle-shaped. The distal tongue is in shape of a pillow. It is large and internally displays an oval depression. Mamelons (from three to five) form a prominent ridge. Along proximal plates the pores of the mamelons are large and are surrounded by a narrow ring, whereas on large plates from the middle part of the arm mamelons are flanked by a rectangular ring. Similarly the mamelons at the ventral edge are surrounded by a ring with a large kidney-shaped pore, where the mamelon proper is located. There can be up to five ventral mamelons. On the outer lateral surface, proximally, there may occur a small thickening with a depression in its centre; on the inner lateral surface is a prominent protrusion, connecting the plate to the kidney-shaped or oval depression of the arm

vertebrum. The protrusion of proximal plates is connected by a strong ridge with a pillow-shaped tongue. Plates from the middle part of the arm lack the latter structure. Plates become more simplified in structure distally.

Remarks. — The Early Devonian *Eospondylus primigenius* has less complicated lateral plates, the articulation surfaces of its ambulacral plates are not so strongly expanded beyond the lateral ridges nor so strongly developed, and the oral notch on its vertebra is broader.

Occurrence. — Early Givetian: outcrop III at Śniadka; Set XXV of the Skały Beds at Skały, Holy Cross Mountains, Poland.

Ophiuroidea *incertae sedis*

Disc stumps

These skeletal elements within the dermis of ophiuroids protect the aboral side of the central disc. They are known from the Ordovician onwards but have been rarely described due to their minute size. Their shapes are so diverse that they represent a potentially valuable source of taxonomic data. Mostler (1971b) demonstrated that elements from the central disc of ophiuroids lack the perforated vertical processes present in the morphologically similar holothurian sclerites. In fact ophiuroids may display such a perforation (cf. Pls 6: 1; 7: 22) but the Holothuroidea most commonly lack the smooth vertical processes to their sclerites, and horizontal processes of sclerites are usually smooth.

Type A-1

(Pl. 6: 2; Text-fig. 16A–F)

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)		
Number of specimens	Features	Minimum	Mean	Maximum
Disc stumps: 19	Height	100	105	115
	Diameter	80	125	175

Description. — These are oval, perforated plates with skewer-shaped clavate process or rod-like process at their centre. Clavate processes and skewers have numerous walls.

Occurrence. — Early Givetian: outcrop III at Śniadka; Set XXV of the Skały Beds at Skały, Holy Cross Mountains, Poland.

Type A-2

(Pl. 6: 3–7; Text-fig. 16G–M)

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)		
Number of specimens	Features	Minimum	Mean	Maximum
Disc stumps: 150	Height	30	60	100
	Diameter	30	40	70

Description. — These oval, perforated plates bear trilamellate processes at their centre. In the corners of the adjoining blades of a plate the largest usually have three pores.

Occurrence. — Middle (Late?) Givetian: Set B of Jaźwica. Late Givetian: trench II at Marzysz, Holy Cross Mountains, Poland.

Type B-1

(Pl. 6: 9–10)

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)		
Number of specimens	Features	Minimum	Mean	Maximum
Disc stumps: 25	Height	195	305	355
	Diameter	65	315	400

Description. — This perforated plate is arched, thin, and resembles the grids of *Eocaudina*. The process is a short, clavate tubercle, with an expanded termination whose top is densely perforated by closed

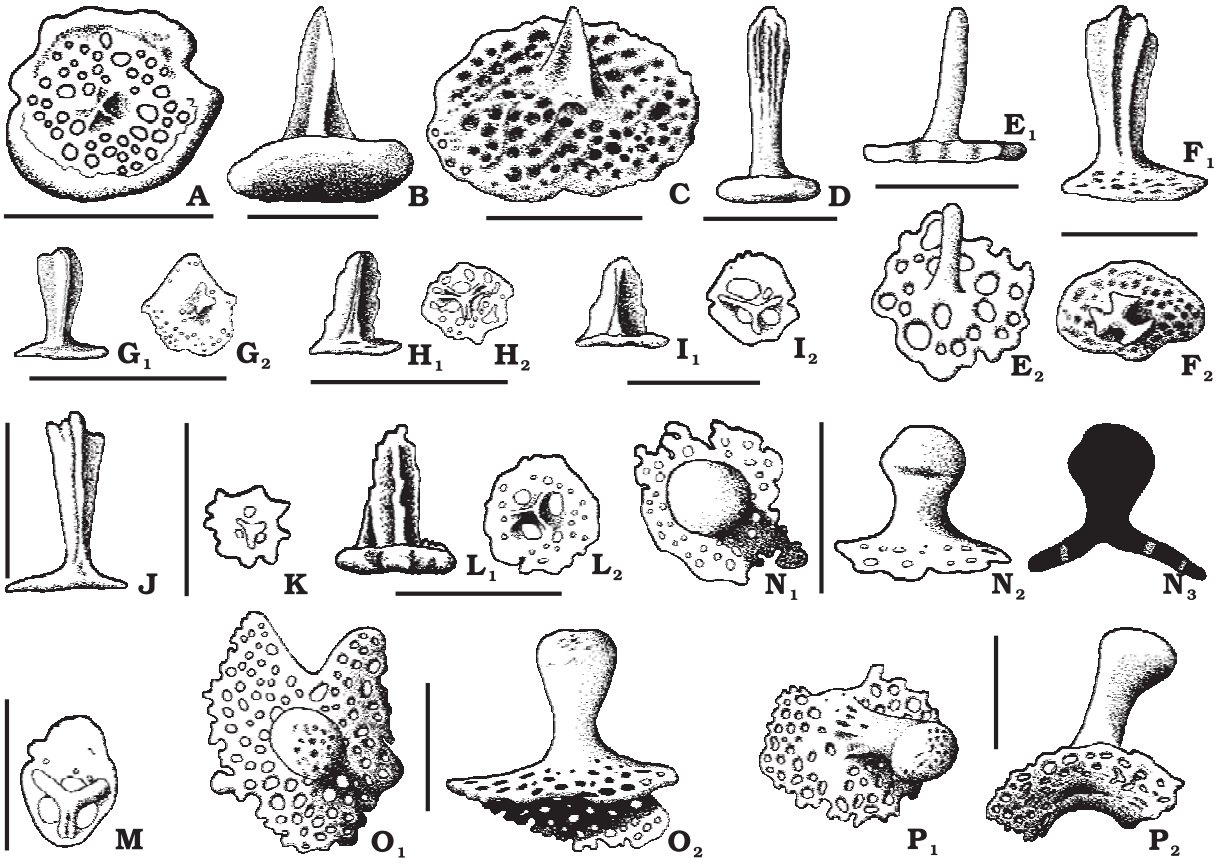

Fig. 16. Skeletal elements of Ophiuroidea from the Devonian of the Holy Cross Mountains. **A**–**F**. Various kinds of disc stumps of type A-1 from the Early Givetian of outcrop III at Śniadka. **A**–**C**. Rounded form with skewer. **A**. GIUS 4-439 Śni./954/3, aboral view. **B**. GIUS 4-439 Śni./953/2, lateral-oblique view. **C**. GIUS 4-439 Śni./953/3, aboral-oblique view. **D**. Ovate form with multilamellate clavate process, GIUS 4-439 Śni./954/2, lateral view. **E**. Lobate form with rodlike process, GIUS 4-439 Śni./954/5; E_1 lateral view, E_2 aboral view. **F**. Ovate form with the trilamellate clavate process, GIUS 4-439 Śni./954/4; F_1 lateral view, F_2 aboral view. **G**–**M**. Different kinds of the disc stumps with trilamellate processes, type A-2 from the Late Givetian of Marzysz, samples Marzysz II/13 (G–I, N), Marzysz II/W/6 (J–K, M), and Marzysz II/W/2 (P), Mid (Late?) Givetian, set B of Jaźwica (L), and Mid Frasnian set C of Górno (O). **G**. GIUS 4-584 Mrz./447/3; G_1 lateral view, G_2 aboral view. **H**. GIUS 4-584 Mrz./447/1; H_1 lateral view, H_2 aboral view. **I**. GIUS 4-584 Mrz./447/2; I_1 lateral view, I_2 aboral view. **J**. GIUS 4-568 Mrz./90/2, lateral view. **K**. GIUS 4-568 Mrz./90/1, aboral view. **L**. GIUS 4-764 Jaź./1019/1; L_1 lateral view, L_2 aboral view. **M**. GIUS 4-568 Mrz./90/36, aboral view. **N**–**P**. Retiform disc stumps with the smooth clavate processes. **N**. GIUS 4-584 Mrz./219/15; N_1 aboral view, N_2 lateral view, N_3 cross section. **O**. GIUS 4-607 Grn./539/1; O_1 aboral view, O_2 lateral view. **P**. GIUS 4-564 Mrz./475/1; P_1 aboral view, P_2 lateral view. Scale bar 100 μm.

depressions. Marginal pores are the largest. The whole structure somewhat resembles the paxillae of asteroids.

Occurrence. — Late Eifelian: Set XVIII of the Skały Beds at Skały, Holy Cross Mountains, Poland.

Type B-2
(Pl. 6: 11–13; Text-fig. 16N–P)

Material		Dimensions (μm)		
Number of specimens	Features	Minimum	Mean	Maximum
Disc stumps: 79	Height	90	125	160
	Diameter	100	170	215

Description. — This plate has an arched surface; its perforation is similar to the sieve plates of *Eocaudina*. On one of its sides the sieve plate has a thickened edge, at the opposite side there is a U-shaped incision. The process is in the shape of a smooth club, with an expanded end. The hemispherical area terminating the club is densely perforated by blind pores.

Occurrence. — Early Givetian: outcrop III at Śniadka. Middle (Late?) Givetian: Set B of Jaźwica. Late Givetian: trench II at Marzysz. Middle Frasnian: Set C of Górno, Holy Cross Mountains, Poland.

Type C-1
(Pl. 6: 8)

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)		
Number of specimens	Features	Minimum	Mean	Maximum
Disc stumps: 4	Height	110	135	150
	Diameter	105	125	145

Description. — The base is circular and perforated, with uneven margins. The process is in the shape of a crocus flower with the conical depression within it and the vertical ribs outside.

Occurrence. — Early Givetian: Set XXV of the Skały Beds at Skały, Holy Cross Mountains, Poland.

Type C-2
(Pl. 6: 14–17; Text-fig. 17AC–AD)

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)		
Number of specimens	Features	Minimum	Mean	Maximum
Disc stumps: > 500	Height	275	510	610
	Diameter	450	690	735

Description. — The base is perforated by blind pores and have two or three processes. The margin of the crocus calyx is zig-zagged.

Occurrence. — Late Givetian: trench II at Marzysz; Set C of Sowie Górki; Set B of Posłowice, Holy Cross Mountains, Poland.

Type C-3
(Text-fig. 17Z–AB)

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)		
Number of specimens	Features	Minimum	Mean	Maximum
Disc stumps: 51	Height	400	580	1070
	Diameter	200	360	395

Description. — The base is a plate, irregular or crescent-shaped with a smooth calice growing from it; the calice is commonly partitioned in one place (Text-fig. 17AA). There is a pore at the calice bottom. They could be two separate hemicylindrical plates. The margins of these plates imbricated during life (Text-fig. 17Z, AB).

Occurrence. — Late Givetian: trench II at Marzysz; Set C of Sowie Górki; Set B of Posłowice, Holy Cross Mountains, Poland.

Type D
(Pl. 7: 5)

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)		
Number of specimens	Features	Minimum	Mean	Maximum
Disc plates: 4	Height	45	60	70
	Diameter	220	320	380

Description. — The base is a large, almost elliptical, and strongly perforated plate with a short and smooth protruding cusp.

Occurrence. — Early Givetian: outcrop III at Śniadka, Holy Cross Mountains, Poland.

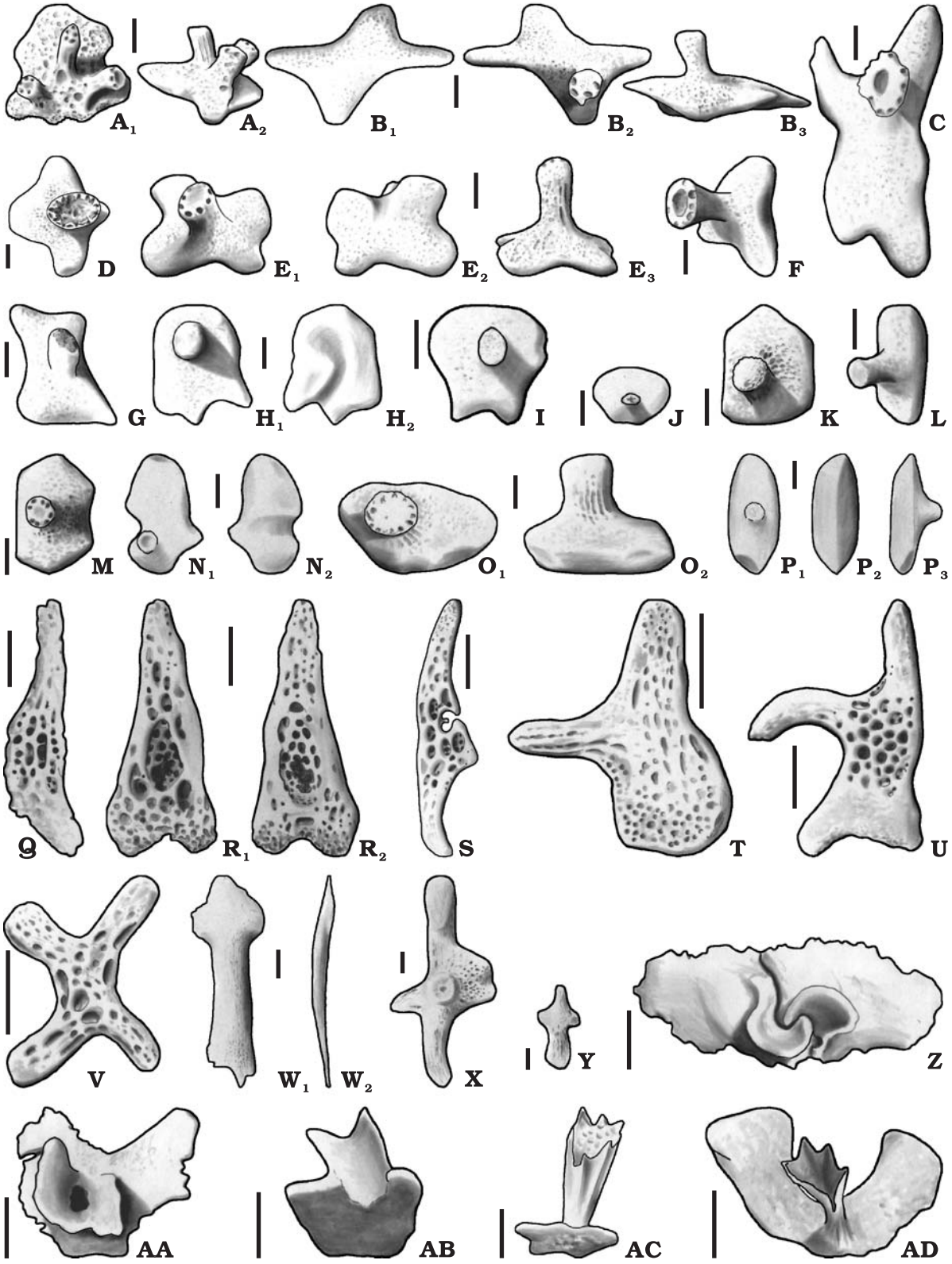

Fig. 17. Skeletal elements of Ophiuroidea from the Late Givetian of Marzysz, samples Marzysz II/13 (A–B, D–H, K–M, O, Q–T, V, AB), Marzysz II/7 (C), Marzysz II/4 (I–J, N, P, Z–AA, AC–AD), Marzysz II/W/6 (U), and Marzysz II/15 (W) and the Middle Frasnian set D of Wietrznia II in Kielce (X–Y), Holy Cross Mountains. **A–P**. Various kinds of marginal ossicles, type A. **A**. Plate with three processes, GIUS 4-584 Mrz./189/3; A_1 aboral view, A_2 lateral view. **B**. GIUS 4-584 Mrz./189/1; B_1 adoral view, B_2 aboral view, B_3 lateral view. **C**. GIUS 4-578 Mrz./271/1, aboral view. **D**. GIUS 4-584 Mrz./189/5, aboral view. **E**. GIUS 4-584 Mrz./189/4; E_1 aboral view, E_2 adoral view, E_3 lateral view. **F**. GIUS 4-584 Mrz./189/10, oblique view. **G**. GIUS 4-584 Mrz./189/2, aboral view. **H**. GIUS 4-584 Mrz./189/11; H_1 aboral view, H_2 adoral view. **I**. GIUS 4-575 Mrz./312/3, aboral view. ➔

Type E-1
(Pl. 7: 6–9)

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)		
Number of specimens	Features	Minimum	Mean	Maximum
Disc plates 77:	Diameter	480	750	900

Description. — Thick, pseudoperforated plates with rough surfaces. Their margin is flanked by a thin frame.

Remarks. — The plates most probably represent the central disc of *Weigeltura beckeri* sp. n., as this is the only species of brittle-star found accompanying the present form.

Occurrence. — Early Eifelian: Zbrza, Holy Cross Mountains, Poland.

Type E-2
(Pl. 7: 10–11)

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)		
Number of specimens	Features	Minimum	Mean	Maximum
Disc plates: > 500	Diameter	190	325	410

Description. — Thin plates, perforated throughout, with rough surfaces; pores are largest at one end and gradually decrease in size towards the opposite side. The margin is flanked by a thin frame.

Occurrence. — Early Givetian: outcrop III at Śniadka, Holy Cross Mountains, Poland.

Type E-3
(Pl. 7: 13–17)

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)		
Number of specimens	Features	Minimum	Mean	Maximum
Disc plates: 124	Diameter	290 (?)	335 (?)	930 (?)

Description. — Single- or multi-layered grids. In many specimens subsequent pore overgrowth has led to the development of a multi-layered structure (Pl. 7: 13–17). The pores in a grid are commonly hexagonal in outline; mostly only fragments of them are present.

Remarks. — Hexagonal pore shape is a result of geometric packing on a plane. Such structures, both as mono- and as multi-layered plates, have been recognised in complete specimens of fossil and modern Ophiuroidea (Pl. 7: 18–19, 22). During maceration the elements commonly disintegrate into single layers. Similar specimens were assigned to the Holothuroidea as *Eocaudina subhexagona* Gutschick, Canis, *et* Brill, 1967 and *Eocaudina marginata* (Langenheim *et* Epis, 1957). Close to the forms described above are some

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J. GIUS 4-575 Mrz./312/4, aboral view. **K**. GIUS 4-584 Mrz./189/6, aboral view. **L**. GIUS 4-584 Mrz./189/8, oblique view. **M**. GIUS 4-584 Mrz./189/9, aboral view. **N**. GIUS 4-575 Mrz./312/2; N_1 aboral view, N_2 adoral view. **O**. GIUS 4-584 Mrz./189/7; O_1 aboral view, O_2 lateral view. **P**. GIUS 4-575 Mrz./312/1; P_1 aboral view, P_2 adoral view, P_3 lateral view, aboral view. **Q–Y**. Perforate ossicles from aboral central disc. **Q**. Lamellar ossicle type F-2, GIUS 4-584 Mrz./212/1, side view. **R**. Knife-like ossicle type F-2, GIUS 4-584 Mrz./213/2; R_1 side view, R_2 opposite side view. **S**. Knife-like ossicle type F-2, GIUS 4-584 Mrz./224/2. **T**. Triangular ossicle with process type F-2, GIUS 4-584 Mrz./224/3, side view. **U**. Triangular ossicle with process type F-2, GIUS 4-568 Mrz./77/1, side view. **V**. Cross-shaped ossicle type F-2, GIUS 4-584 Mrz./224/1, side view, Late Givetian sample Marzysz II/13. **W**. Cruciform ossicle type F-3, GIUS 4-587 Mrz./481/1; W_1 side view, W_2 lateral view. **X**. Cross-shaped ossicle with the tubercle type F-4, GIUS 4-793 Wie./530/1, aboral view. **Y**. Cross-shaped ossicle type F-4, GIUS 4-793 Wie./530/2, aboral view. **Z–AD**. Ossicles from central disc. **Z**. Double ossicles with collar type C-3, GIUS 4-575 Mrz./450/3, natural position, aboral view. **AA**. Ossicle with calyx type C-3, GIUS 4-575 Mrz./450/4, aboral view. **AB**. Single ossicle with collar type C-3, GIUS 4-584 Mrz./186/1, oblique view. **AC**. Ossicle with crocus-shaped calyx type C-2, GIUS 4-575 Mrz./450/1, lateral view. **AD**. Ossicle with crocus-shaped calyx type C-2, GIUS 4-575 Mrz./450/2, aboral view. Scale bar 200 μm.

specimens described as *E. marginata* and *E. subhexagona* by Matyja *et al*. (1973), Mostler (1968a, b), and Zawidzka (1971). Similar grid-like structures can be observed in the walls of the digestive tract of living ophiuroids, but they are significantly smaller (Irimura 1988).

Occurrence. — Early Eifelian: Set VIII of the Grzegorzowice Beds at Grzegorzowice, Holy Cross Mountains, Poland.

Type F-1
(Pl. 7: 12)

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)		
Number of specimens	Features	Minimum	Mean	Maximum
Disc plates: 4	Diameter	750	885	900

Description. — These are five-armed, perforated plates thinnest at the ends of the arms.

Occurrence. — Early Eifelian: Set VIII of the Grzegorzowice Beds at Grzegorzowice, Holy Cross Mountains, Poland.

Type F-2
(Text-fig. 17Q–V)

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)		
Number of specimens	Features	Minimum	Mean	Maximum
Disc plates: 28	Diameter	545	695	950

Description. — These are triangular, knife-shaped and cross-shaped forms with imperforate margins (Text-fig. 17Q–V). Through the surface pores internal stereom is visible. All plates are of uniform thickness.

Remarks. — Cross-shaped forms are usually described as holothurian sclerites belonging to the genus *Tetravirga* (cf. Frizzell and Exline 1955, 1966), but holothuroid elements of such a type are unknown. They more closely resemble sclerites of the Asterozoa.

Occurrence. — Late Givetian: trench II at Marzysz; Set C of Sowie Górki; Set B of Posłowice, Holy Cross Mountains, Poland.

Type F-3
(Text-fig. 17W)

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)		
Number of specimens	Features	Minimum	Mean	Maximum
Disc plates: 6	Diameter	1200	1255	1440

Description. — These are very flat plates of a crucifix shape, perforated with fine pores.

Occurrence. — Late Givetian: trench II at Marzysz, Holy Cross Mountains, Poland.

Type F-4
(Text-fig. 17X–Y)

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)		
Number of specimens	Features	Minimum	Mean	Maximum
Disc plates: 5	Diameter	800	1640	2030

Description. — These are flat plates in the shape of a deformed cross, with one of its arms broader, the remaining ones of similar width. Clear bilateral symmetry can be observed. In a centre there may be a flat tubercle. Plates are perforated by fine pores.

Occurrence. — Mid Frasnian: Set D of Wietrznia II, Kielce, Holy Cross Mountains, Poland.

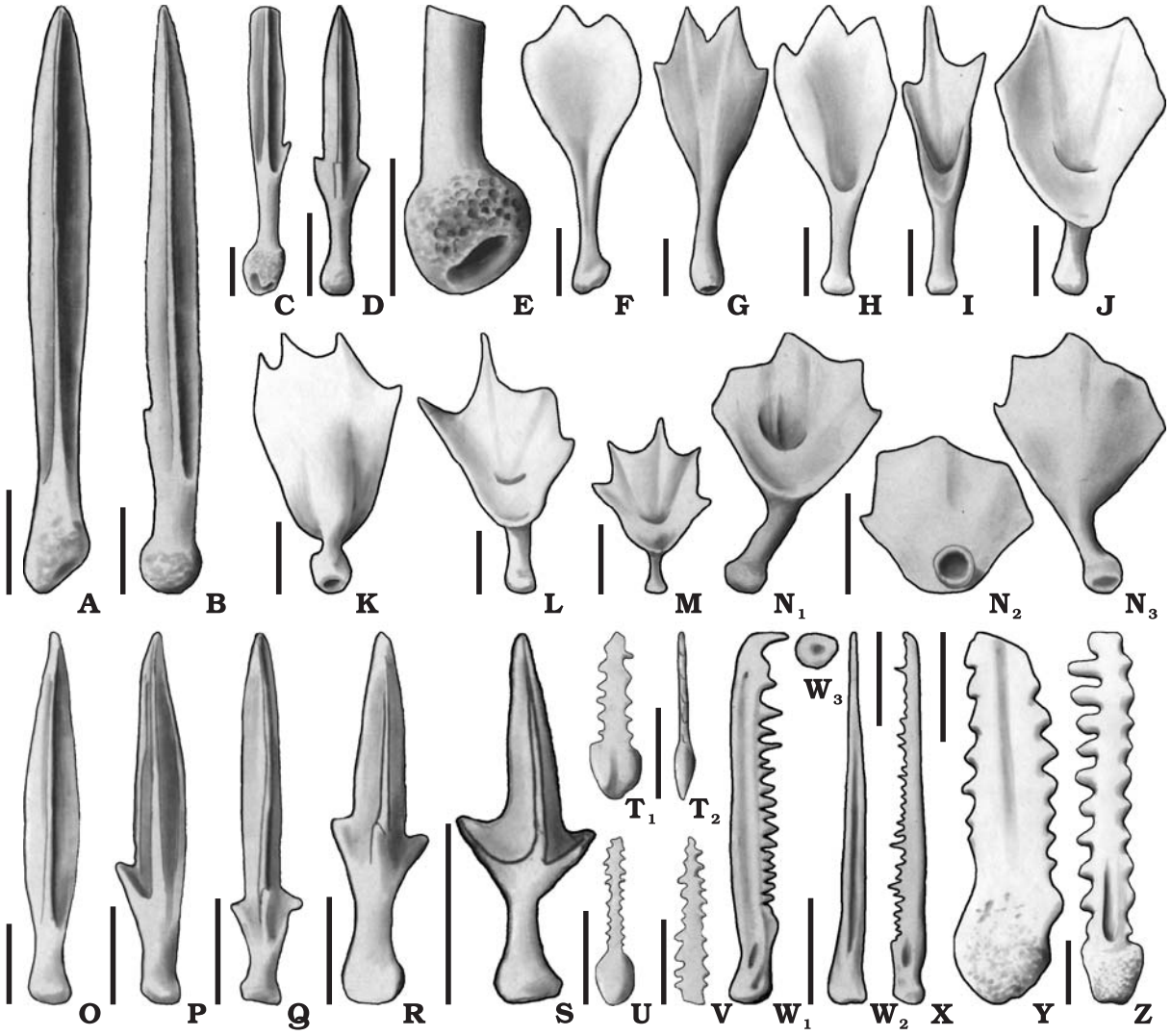


Fig. 18. Skeletal elements of Ophiuroidea from the Devonian of the Holy Cross Mountains. **A**–**E**. Fluke-shaped spines of set A-1 from the Early Givetian of outcrop III at Śniadka, lateral views. **A**. GIUS 4-439 Śni./924/1. **B**. GIUS 4-439 Śni./924/2. **C**. GIUS 4-439 Śni./924/3. **D**. GIUS 4-439 Śni./924/4. **E**. GIUS 4-439 Śni./924/5, base. **F**–**N**. Lateral views of webbed spines of set A-1, same sample. **F**. GIUS 4-439 Śni./921/6. **G**. GIUS 4-439 Śni./921/7. **H**. GIUS 4-439 Śni./921/5. **I**. GIUS 4-439 Śni./921/8. **J**. GIUS 4-439 Śni./921/4. **K**. GIUS 4-439 Śni./921/3. **L**. GIUS 4-439 Śni./921/2. **M**. GIUS 4-439 Śni./921/1. **N**. Webbed spine of set A-2 from the Late Givetian, Marzysz II/W/6, GIUS 4-568 Mrz./39/1; N_1 side view, N_2 base, N_3 opposite side view. **O**–**S**. Fluke-shaped spines of set A-2 from the Late Givetian, Marzysz II/13, lateral views. **O**. GIUS 4-584 Mrz./160/3. **P**. GIUS 4-584 Mrz./160/5. **Q**. GIUS 4-584 Mrz./160/4. **R**. GIUS 4-584 Mrz./160/1. **S**. GIUS 4-584 Mrz./160/2. **T**–**V**. Pectinated hooks of set A-2 from the Late Givetian, Marzysz II/W/6. **T**. Short pecten GIUS 4-568 Mrz./42/2; T_1 side view, T_2 lateral view. **U**. Short pecten GIUS 4-568 Mrz./42/1, side view. **V**. Shaft GIUS 4-568 Mrz./42/3, side view. **W**–**X**. Pectinated hooks of set B from the Late Givetian, Marzysz II/W/6. **W**. GIUS 4-568 Mrz./84/1; W_1 side view, W_2 lateral view, W_3 base. **X**. GIUS 4-568 Mrz./84/2, side view. **Y**–**Z**. Pectinated hooks of set A-1 from the Early Givetian of outcrop III at Śniadka. **Y**. GIUS 4-439 Śni./930/1, side view. **Z**. GIUS 4-439 Śni./930/2, side view. Scale bar 200 μm. Except for figure AN where it is 100 μm.

Type G
(Pl. 7: 20–21)

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)		
Number of specimens	Features	Minimum	Mean	Maximum
Disc plates: 68	Diameter	480	510	540

Description. — Flat plates shaped like the edge of a guillotine. At one side there is a thick rod, at the other densely perforated lamellae.

Occurrence. — Early Givetian: Set XXV of the Skały Beds at Skały, Holy Cross Mountains, Poland.

Marginal plates from the border of central disc – Type A
(Pl. 7: 1–4; Text-fig. 17A–P)

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)		
Number of specimens	Features	Minimum	Mean	Maximum
Disc plates: 132	Height	390	520	660
	Length	440	895	1490

Description. — Thick, cross-shaped, polygonal or oval plates, with a short, thick spine at their centre, terminated by an oval head. At the centre there may be a depression, surrounded by a marginal ring of pores. Plates have thinned margins, and may have curved furrows underneath (Text-fig. 17H).

Remarks. — The corresponding truncations of the margins of some of these elements indicates they occurred in series (Pl. 7: 3; Text-fig. 17H–P), or grids (Text-fig. 17B–G). Still others were situated centrally or terminally, at the margin (Text-fig. 17A).

Such plates are common in the orders Stenurida and Oegophiurida, e.g. *Encrinaster* Haeckel, 1866 (cf. Spencer 1914–1940; Spencer and Wright 1966). Particularly significant is the apex of the process, which indicates that some finer elements attached. Such a pattern, though not uncommon in Palaeozoic ophiuroids (e.g. *Taeniaster* Billings, 1858, see Spencer 1927: text-fig. 246) was more typical among the asteroids (e.g. paxillae).

Occurrence. — Early Givetian: Set XXV of the Skały Beds at Skały. Late Givetian: trench II at Marzysz, Holy Cross Mountains, Poland.

Bursal plates
(Text-fig. 20G)

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)		
Number of specimens	Features	Minimum	Mean	Maximum
Bursal plates: 54	Length	920	1115	1245

Description. — Crescent-shaped, laterally-flattened plates. At one end they display a saddle-shaped thickening, i.e. an area of anatomical contact.

Occurrence. — Late Givetian: trench II at Marzysz, Holy Cross Mountains, Poland.

Spines and scales

Remarks. — The diagnostic feature, allowing spines of various morphology to be assigned to a given set is their co-occurrence and the presence of the same kind of basal part.

Set A-1
(Pl. 8: 12, 16–17; Text-figs 18A–M, Y–Z, 19H–M)

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)		
Number of specimens	Features	Minimum	Mean	Maximum
Fluke-shaped spines: 114	Length	690	975	1335
	Diameter of base	85	105	185
"Webbed" spines: 89	Length	510	880	1020
	Diameter of base	70	95	115
Pectinated hooks: 8	Length	675	750	1090
	Diameter of base	180	185	195
Turban-shaped spines: 19	Length	765	?	805 (?)
	Diameter of base	130	145	150

Description. — Fluke-shaped spines. Three smooth blades, tapering along the axis to a sharp point (Text-fig. 18A–E). At ca. quarter to one-third of its height there may be one to three distally oriented thorns. Basal part trumpet-shaped with rounded margins, or spherical central depression.

"Webbed" spines. Arched lamella with three to six spiny processes at its distal edge extending from the blade (Pl. 8: 12; Text-fig. 18F–M). There may be a pocket, bordered by an arched additional blade with a curved incision on the concave side. The shaft is of the same type as above but the basal part is smaller and more spherical.

Pectinated hooks. The crests are apparently serial homologues of hooks in the other sets. Teeth occur on both sides, but are usually more prominent on one (Text-fig. 18Y–Z). On one side is a groove, deepest immediately by the basal part, which is as in the fluke-shaped spines.

Turban-shaped spines. These very small complicated elements always co-occur with the other spines of the group (Pl. 8: 16–17; Text-fig. 19H–M). Their shaft is only a narrow segment and the basal part is similar to that of "webbed" spines. Specimens with three, instead of the typical one pore at the centre occur, but this is only apparent, as these are only the lumina between the arms of a crown. The crown has a central axis and three peripheral blades symmetrically arranged, all of which coalesce at the apex. The whole element is in the shape of a closed flower or turban. The voluminous interstices between the arms distinguish the present morphotype from others.

Remarks. — This set of spines is clearly analogous to those seen in *Furcaster*: "flukes" correspond to the long spines, "webbed" the scales, "turbans" lyre-like scales and only lacking are the hooks, though it is by no means certain.

Occurrence. — Early Givetian: outcrop III at Śniadka, Holy Cross Mountains, Poland.

Set A-2

(Pl. 8: 10–11, 14–15; Text-figs 18N–V, 19N)

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)		
Number of specimens	Features	Minimum	Mean	Maximum
Fluke-shaped spines: > 500	Length	420	725	930
	Diameter of base	75	100	120
"Webbed" spines: > 500	Length	410	495	530
	Diameter of base	75	95	110
Pectinated hooks: 6	Length	370	395	425
	Diameter of base	95	115	120
Turban-shaped spines: 22	Length	145	155	160
	Diameter of base	20	22	25

Description. — Fluke-shaped spines and "Webbed" spines. Differing only from set A-1 in having slightly smaller basal parts (Pl. 8: 10–11; Text-fig. 18N–V). Webbed spines also have smaller cusps.

Pectinated hooks. Their basal part is enlarged proportional to the blade, flat, and, in its middle part, divided by a furrow parallel to the axis. The side spines are short (Text-fig. 18T–V).

Turban-shaped spines. Very small elements (Pl. 8: 14–15; Text-fig. 19N) with a thin central axis, circular in transverse section. There are three blades, converging at the axis apically. Proximal parts of blades are rod-like. The basal part is the same as in fluke-shaped and "webbed" spines.

Remarks. — Only the pectinated hooks have a different basal morphology, but they are the only hooks that always co-occur with the other elements of this set. In comparison to set A-1, these turban-shaped spines and pectinated hooks are significantly smaller. Fragments of blades of these pectinated hooks were formerly described as holothurian sclerites of the genus *Parvispina* Kornicker *et* Imbrie, 1958.

Occurrence. — Late Givetian: trench II at Marzysz, Holy Cross Mountains, Poland.

Set A-3

(Text-fig. 19E)

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)		
Number of specimens	Features	Minimum	Mean	Maximum
Columnar spines: 1	Length	815 (?)	–	–
	Diameter of base	95	–	–

Description. — Columnar spines. Smooth column-shaped thorns with a trumpet-shaped base plainly truncated. Along the blade there are numerous leaf-like processes, arranged in rows (Text-fig. 19E).

Occurrence. — Mid Frasnian: Set F of Psie Górki, Kielce, Holy Cross Mountains, Poland.

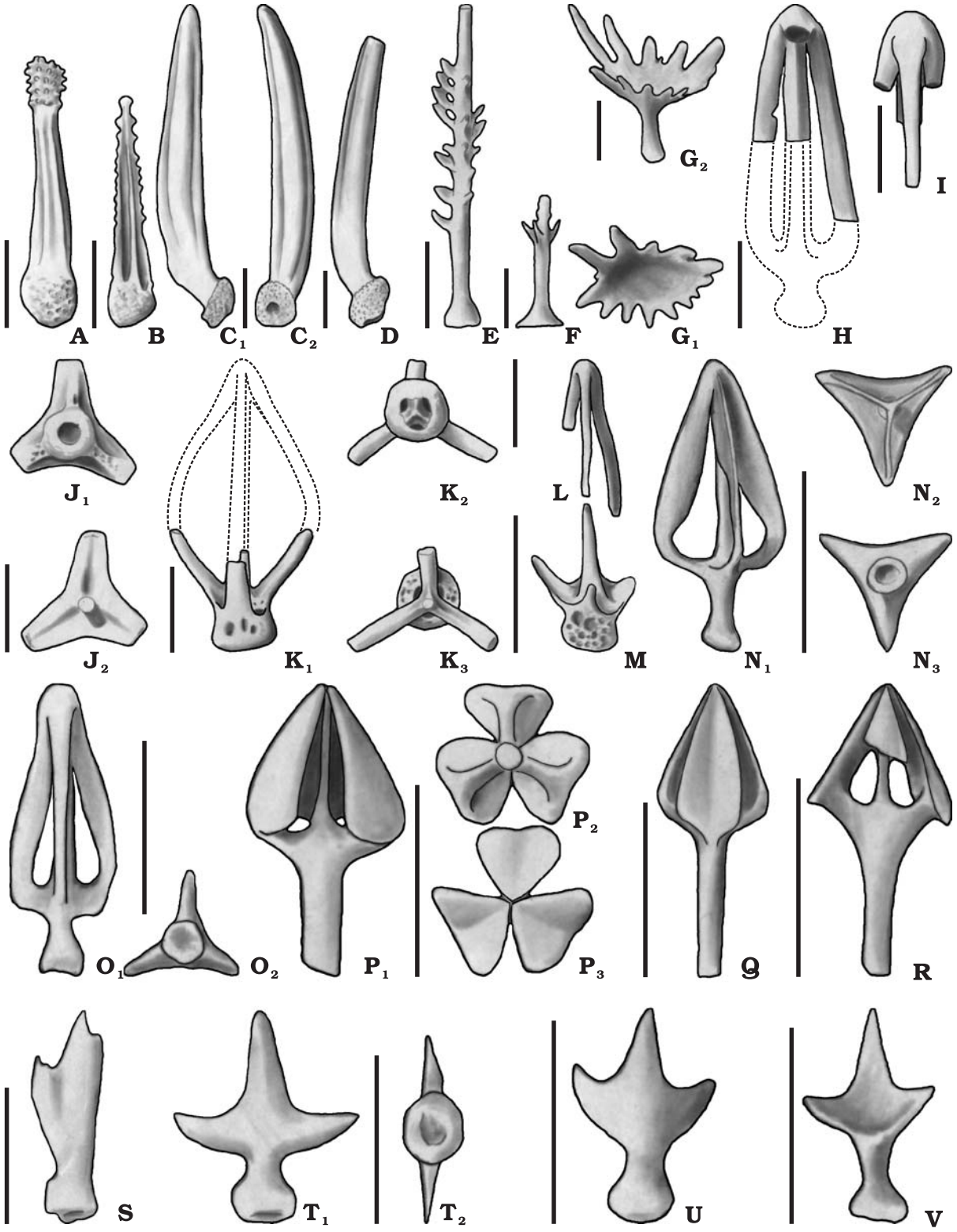


Fig. 19. Skeletal elements of Ophiuroidea from the Devonian of the Holy Cross Mountains. **A**–**B**. Spines of set C from the Early Givetian of outcrop III at Śniadka. **A**. Clavate spine GIUS 4-439 Śni./906/1. **B**. Spiky spine GIUS 4-439 Śni./906/2. **C**–**D**. Spines of set D from the Early Givetian of outcrop III at Śniadka. **C**. GIUS 4-439 Śni./905/2; C_1 lateral view, C_2 side view. **D**. GIUS 4-439 Śni./905/3, lateral view. **E**. Columnar spine of set A-3 from the Late Frasnian set F of Psie Górki in Kielce, GIUS 4-599 Psi./511/2. **F**. Columnar spine of set A-4 from the Early Givetian of outcrop III at Śniadka, GIUS 4-439 Śni./909/10. **G**. Umbrella-shaped spine of set A-4 from the Early Givetian of outcrop III at Śniadka, GIUS 4-439 Śni./911/1; G_1top view, G_2lateral view. **H**–**M**. Turban-shaped spines of set A-1 from the Early Givetian of outcrop III at Śniadka. **H**. Distal part of broken spine GIUS 4-439 Śni./929/2, lateral view. **I**. Distal part of broken spine GIUS 4-439 Śni./929/3, lateral view. **J**. Proximal part of broken spine GIUS ➝

Set A-4
(Pl. 8: 5; Text-fig. 19F–G, P–R)

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)		
Number of specimens	Features	Minimum	Mean	Maximum
Columnar spines: 1	Length	450	–	–
	Diameter of base	175	–	–
Umbrella-shaped spines: 1	Length	530	–	–
	Diameter of base	90	–	–
Turban-shaped spines: 4	Length	305 (?)	?	335 (?)
	Diameter of base	?	?	?

Description. — Columnar spines. Their basal part is trumpet-shaped and plainly truncated. Along the rod-like blade, proximally, there are three thorns (Text-fig. 19F).

Umbrella-shaped spines. Basal part trumpet-shaped, with plain truncation. The blade forms a broad, distally concave umbrella, with finger-like processes its margins with finger-like processes (Text-fig. 19G).

Turban-shaped spines. Shaft smooth and narrow; basal part unknown. The head has a thin rod-like axis medially, three leaf-like blades laterally contacting each other at the apex. Seen from the distal side the turban-shaped spine looks like a trefoil leaf (Pl. 8: 5; Text-fig. 19P–R).

Remarks. — The spines are a strongly modified version of set A. Spines with three thorns correspond to the fluke-shaped spines, umbrella-shaped spines to the webbed spines. Moreover, the turban-shaped spines are also strongly modified.

Occurrence. — Early Givetian: outcrop III at Śniadka, Holy Cross Mountains, Poland.

Set A-5
(Pl. 8: 13, 18; Text-fig. 19O, S–V)

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)		
Number of specimens	Features	Minimum	Mean	Maximum
Fluke-shaped spines: 9	Length	240	260	310
	Diameter of base	75	75	75
"Webbed" spines: 4	Length	210	215	220
	Diameter of base	60	65	70
Turban-shaped spines: 18	Length	295	335	340
	Diameter of base	55	55	55

Description. — Fluke-shaped spines. Their basal part is trumpet-shaped and their short neck is connected to a blade resembling a halberd tip (Pl. 8: 13; Text-fig. 19S–T).

"Webbed" spines. These spines differ from the fluke-shaped ones only in that they are flattened on both sides and have a small pocket, without an additional blade (Text-fig. 19U–V).

Turban-shaped spines. The basal part is trumpet-shaped and the apex, formed by connected axis and side arms, is rounded. The neck of shaft is ribbed distinguishing it from the other "turbans" (Pl. 8: 18; Text-fig. 19O).

Remarks. — These spines are the smallest and the most complex of all varieties described here.

Occurrence. — Mid Frasnian: Set C of Górno; Set L of Jaźwica, Holy Cross Mountains, Poland.

4-439 Śni./929/, base; J_1 basal view, J_2 opposite side view. **K**. Proximal part of broken spine GIUS 4-439 Śni./905/4, base; K_1 lateral view, K_2 basal view, K_3 opposite side view. **L**. Distal part of broken spine GIUS 4-439 Śni./905/5, lateral view. **M**. Proximal part of broken spine GIUS 4-439 Śni./905/1, lateral-oblique view. **N**. Turban-shaped spine of set A-2 from the Late Givetian, Marzysz II/W/6, GIUS 4-568 Mrz./29/1; N_1 lateral view, N_2 top view, N_3 basal view. **O**. Turban-shaped spine of set A-5 from the Middle Frasnian, set C of Górno, GIUS 4-607 Grn./1062/3; O_1 lateral view, O_2 basal view. **P**–**R**. Proximal part of broken turban-shaped spines of set A-4 from the Early Givetian of outcrop III at Śniadka. **P**. GIUS 4-439 Śni./913/1; P_1 lateral view, P_2 basal view, P_3 top view. **Q**. GIUS 4-439 Śni./913/3, lateral view. **R**. GIUS 4-439 Śni./913/2, lateral view. **S**–**V**. Spine set A-5 from the Middle Frasnian set C of Górno. **S**. Webbed spine GIUS 4-607 Grn./1061/4, side view. **T**. Fluke-shaped spine GIUS 4-607 Grn./1061/1; T_1 side view, T_2 basal view. **U**. Webbed spine GIUS 4-607 Grn./1061/2, side view. **V**. Webbed spine GIUS 4-607 Grn./1061/3, lateral view. Scale bar 200 μm, except for AN where it is 100 μm.

Set B
(Text-fig. 18W–X)

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)		
Number of specimens	Features	Minimum	Mean	Maximum
Pectinated hooks: 2	Length	705	755	805
	Diameter of base	70	75	80

Description. — Pectinated hooks. Basal part oval with a basal depression and lateral furrows. Isolated grooves occur laterally and dorsally. The distal tooth is the largest while along the blade there are up to 29 accessory teeth of various size (Text-fig. 18W–X).

Occurrence. — Late Givetian: trench II at Marzysz, Holy Cross Mountains, Poland.

Set C
(Text-fig. 19A–B)

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)		
Number of specimens	Features	Minimum	Mean	Maximum
Clavate spines: 1	Length	630	–	–
	Diameter of base	130	–	–
Spiky spines: 2	Length	490	510	530
	Diameter of base	120	120	120

Description. — Clavate spines. Basal part broad, club-shaped. The blade has a few smooth, thick ribs. On the top there is a pommel with numerous short spines (Text-fig. 19A).

Spiky spines. Basal part club-shaped, as above. Along the blade there are four or five thorny ribs whose size increases towards the apex (Text-fig. 19B).

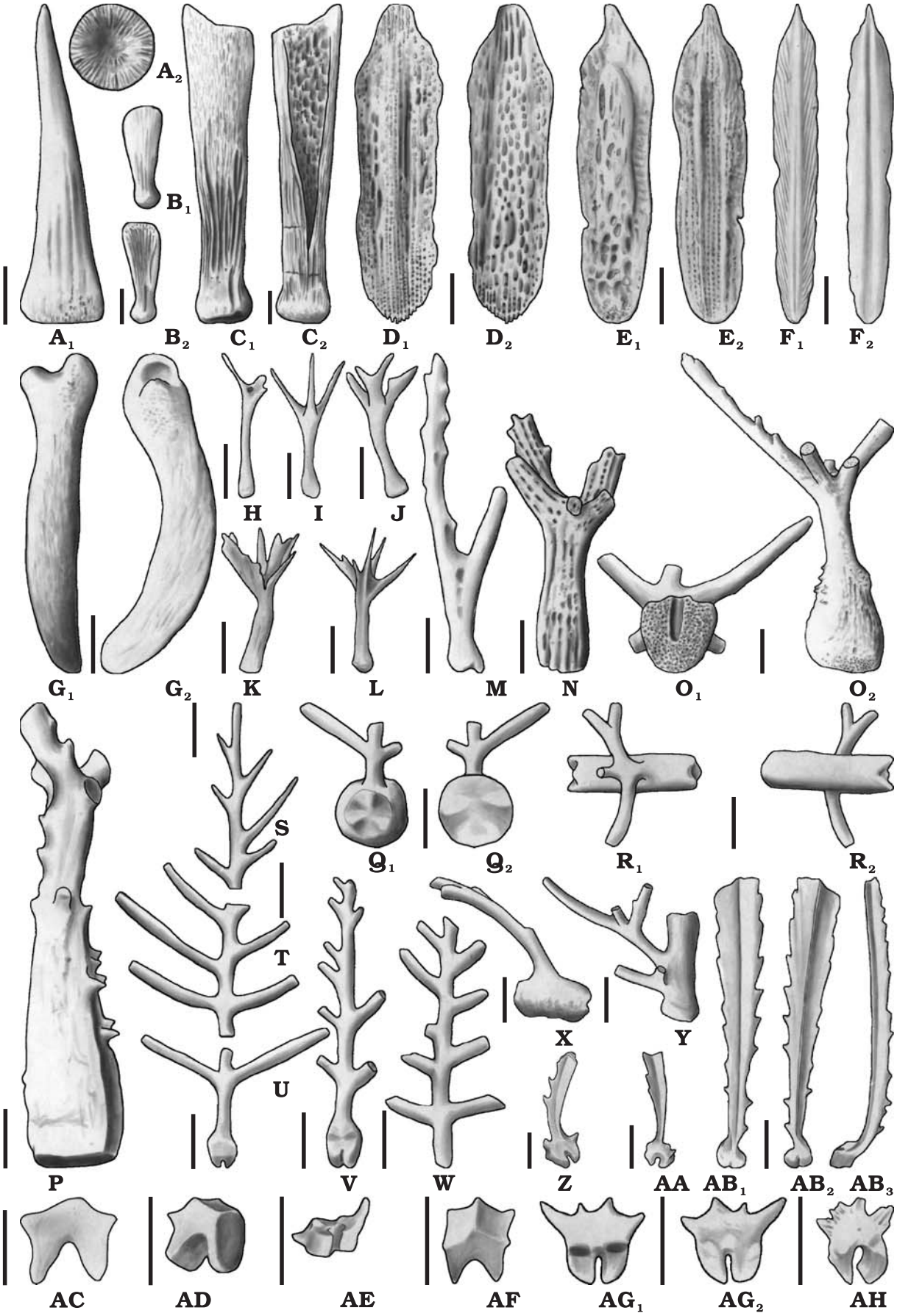
Occurrence. — Early Givetian: outcrop III at Śniadka, Holy Cross Mountains, Poland.

Set D
(Text-fig. 19C–D)

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)		
Number of specimens	Features	Minimum	Mean	Maximum
Banana-like spines: 4	Length	1000	1020	1030
	Diameter of base	140	140	140

Fig. 20. Skeletal elements of Ophiuroidea from the Holy Cross Mountains. **A**. Thorny spine of set E from the Late Givetian sample Marzysz Ic/5, GIUS 4-561 Mrz./995/1; A_1 lateral view, A_2 basal view. **B–F**. Spines of set F from the Late Givetian of Marzysz, samples Marzysz II/13 (B–D, F), Marzysz II/W/6 (E), and Marzysz II/7 (G). **B**. Chisel-shaped spine GIUS 4-584 Mrz./174/2; B_1 side view, B_2 opposite side view. **C**. Chisel-shaped spine GIUS 4-584 Mrz./174/1; C_1 side view, C_2 opposite side view. **D**. Slat-shaped spine GIUS 4-584 Mrz./1142/1; D_1 side view, D_2 opposite side view. **E**. Slat-shaped spine GIUS 4-568 Mrz./41/1; E_1 side view, E_2 opposite side view. **F**. Slat-shaped spine, GIUS 4-584 Mrz./1142/2; F_1 side view, F_2 opposite side view. **G**. Bursal plate GIUS 4-578 Mrz./280/1; G_1 aboral view, G_2 lateral view. **H–P**. Bushy spines of set H from the Early Givetian of outcrop III at Śniadka. **H**. GIUS 4-439 Śni./909/7, lateral view. **I**. GIUS 4-439 Śni./909/9, lateral view. **J**. GIUS 4-439 Śni./909/6, lateral view. **K**. GIUS 4-439 Śni./909/5, lateral view. **L**. GIUS 4-439 Śni./909/8, lateral view. **M**. GIUS 4-439 Śni./909/2, lateral view **N**. GIUS 4-439 Śni./909/3, lateral view. **O**. GIUS 4-439 Śni./909/13; O_1 view from base, O_2 lateral view. **P**. GIUS 4-439 Śni./909/4, lateral view. **Q–AH**. Ophiuroid or crinoid spine(?) from the Early Givetian of outcrop III at Śniadka. **Q–Y**. Feathery element, set I. **Q**. GIUS 4-439 Śni./912/9; Q_1 side view of basic element, Q_2 opposite side view. **R**. GIUS 4-439 Śni./912/8; R_1 top view, R_2 basal view. **S**. Fragment of distal part GIUS 4-439 Śni./912/4. **T**. Fragment of middle part GIUS 4-439 Śni./912/3. **U**. Fragment of proximal part GIUS 4-439 Śni./912/2. **V**. Whole spine with broken lateral processes, GIUS 4-439 Śni./912/1. **W**. Specimen without the basic part GIUS 4-439 Śni./912/5. **X**. GIUS 4-439 Śni./912/6, lateral view. **Y**. GIUS 4-439 Śni./912/7, oblique view. **Z–AB**. Sclerites similar to segments of crinoid arms with fan-shaped processes, set I. **Z**. Specimen with broken fan GIUS 4-439 Śni./910/2. **AA**. Specimen with broken fan GIUS 4-439 Śni./910/3. **AB**. Specimen with whole fan GIUS 4-439 Śni./910/1; AB_1 side view, AB_2 opposite side view, AB_3 lateral view. **AC–AH**. Sclerites similar to segments of crinoid arms with or without short processes, set I. **AC**. GIUS 4-439 Śni./910/4, side view. **AD**. GIUS 4-439 Śni./910/5, oblique view. **AE**. GIUS 4-439 Śni./910/8, oral(?) view. **AF**. GIUS 4-439 Śni./910/9, oblique view. **AG**. GIUS 4-439 Śni./910/7; AG_1 side view, AG_2 opposite side view. **AH**. Specimen with small processes, GIUS 4-439 Śni./910/6, side view. Scale bar 200 μm. →


A2
B1
A1
B2
C1
C2
D1
D2
E1
E2
F1
F2
H
I
J
G1
G2
K
L
M
N
O1
O2
S
Q1
Q2
R1
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U
X
Y
P
V
W
Z
AA
AB1
AB2
AB3
AC
AD
AE
AF
AG1
AG2
AH

Description. — Banana-like spines. Smooth spines in the shape of a banana. Its basal part is mushroom-shaped with a proximal pore. The neck is always inclined abaxially. The blade is partitioned by four furrows, parallel to the axis (Text-fig. 19C–D).

Occurrence. — Early Givetian: outcrop III at Śniadka, Holy Cross Mountains, Poland.

Set E

(Text-fig. 20A)

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)		
Number of specimens	Features	Minimum	Mean	Maximum
Thorny spines: 2	Length	1100	1120	1140
	Diameter of base	305	305	305

Description. — Thorny spines. These are delicately grooved. The basal part passes smoothly into the shaft of the spine. On the proximal side there is a crater-shaped depression covered by numerous radially arranged ribs.

Occurrence. — Late Givetian: trench II at Marzysz, Holy Cross Mountains, Poland.

Set F

(Pl. 8: 7–9; Text-fig. 20B–F)

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)		
Number of specimens	Features	Minimum	Mean	Maximum
Chisel-shaped spines: 48	Length	595	1905	2205
	Diameter of base	170	235	370
Slat-shaped spines: 183	Length	900	1150	1370
	Diameter of base	195	285	360

Description. — Chisel-shaped spines. Basal part large and mushroom-shaped. The convex surface of the blade is covered by furrows, which disappear distally. The opposite, concave side has numerous thorns and depressions (Pl. 8: 9; Text-fig. 20B–C).

Slat-shaped spines. The thicker variety (Pl. 8: 8; Text-fig. 20D–E) at one end is rounded with a narrow, tongue-shaped arch and at the opposite end there is a broader arch. The latter is interpreted as basal. On one side there is a shallow axial furrow, on the opposite side an axial convexity. The surface is covered in numerous furrows formed of rows of pores. The thinner and more delicate variety (Pl. 8: 7; Text-fig. 20F) is pointed at one end, while other (basal part) ends in a wide arch. One side of the spine is smooth with a shallow axial groove, the other has a smooth ridge with a longitudinal partition. On this side the blade has very numerous fine ribs converging proximally.

Occurrence. — Late Givetian: trench II at Marzysz, Holy Cross Mountains, Poland.

Set G

(Pl. 8: 2)

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)		
Number of specimens	Features	Minimum	Mean	Maximum
Prickly spines: 2	Length	710	720	730
	Diameter of base	115	115	115

Description. — Prickly spines. Basal part club-shaped, with a central depression. The curved blade is thorned on both sides.

Remarks. — Thorny or prickly spines can also be found among modern ophiuroids (cf. Pl. 8: 1). These spines for a long time were known only from broken fragments, and are similar in their structure to the pectinate type.

Occurrence. — Early Eifelian: Set VIII of the Grzegorzowice Beds at Grzegorzowice, Holy Cross Mountains, Poland.

Set H
(Pl. 8: 4; Text-fig. 20H–P)

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)		
Number of specimens	Features	Minimum	Mean	Maximum
Bushy spines: 115	Length	570	630	1660
	Diameter of base	60	85	380

Description. — Bushy spines. Typical basal parts are club-shaped, with a central depression (Pl. 8: 4; Text-fig. 20H–N). Forms with horseshoe-like bases also occur (Text-fig. 20P). Sides of the neck may display fine thorns or the entire spine is covered by linear pores.

Occurrence. — Early Givetian: outcrop III at Śniadka, Holy Cross Mountains, Poland.

Set I (Ophiuroid spines or elements of crinoid arms)
(Pl. 8: 6; Text-fig. 20Q–AH)

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)		
Number of specimens	Features	Minimum	Mean	Maximum
Feathery elements: 67	Length	1140 (?)	?	1630
Elements with a-shaped process: 33	Length	560 (?)	?	1245

Description. — Feathery elements. Basal part in shape of a horse-shoe or cylindrical, both displaying different surfaces at their opposite ends (articula?). A long axis with lateral branches projects from the element (Text-fig. 20Q–Y).

Elements with the fan-shaped process. Basal part of these elements as above. A very thin fan-shaped lamella with central axis and frilled margin arises from the base (Pl. 8: 6; Text-fig. 20Z–AB).

Remarks. These elements co-occurs with set H ophiuroid spines (Text-fig. 20O). They are very similar to crinoid arm elements but no crinoid is known with such processes which are more characteristic of ophiuroid elements. A series of horse-shoe plates with and without initial stages of such processes are also found (Text-fig. 20AC–AH), typical of crinoids. It is not certain, however, if they are conspecific with the elements with long processes.

Occurrence. — Early Givetian: outcrop III at Śniadka, Holy Cross Mountains, Poland.

Class **CYCLOCYSTOIDEA** Miller *et* Gurley, 1895

The first author who described and illustrated these fossil animals was Hall (1851); his specimens came from the Ordovician limestone of Trenton (Late Caradoc–Edenian) and Hall identified them as crinoids. In 1858 Salter and Billings introduced the generic name *Cyclocystoides* with new species from the Silurian of Canada. The latter species were placed into a new class by Miller and Gurley (1895). Subsequently, various authors have sporadically described cyclocystoids. This research has been summarised in a monograph by Smith and Paul (1982) who made a revision of all the species then known, discussed the anatomy of the group and its affinities. According to their opinion all the Devonian forms of Prokop (1980) and Sieverts-Doreck (1951) are to be classified in the genus *Sievertsia*, with *Sievertsia tartas* (Prokop, 1980) from the Pragian of Bohemia (Praha-Smichov), *Sievertsia concava* Smith *et* Paul, 1982 from the Late Emsian of Belgium (the Ardennes), Germany, and Bohemia (Praha-Zlichov), *Sievertsia gotus* (Prokop, 1980) from the Emsian of Bohemia (Praha-Zlichov, Klukovice), and *Sievertsia devonica* (Sieverts-Doreck, 1951) from the Early Eifelian of Germany (Rhineland).

Fleuegeman and Orr (1990) reported the occurrence of poorly preserved remains of *Sievertsia* and *Polytryphocycloides* Smith *et* Paul, 1982 in the Frasnian Ithaca Formation and Givetian (Cazenovian) of Logansport, Indiana. The Givetian specimen is preserved as an imprint of the dorsal surface and its generic classification is uncertainel. Wl preserved specimens of *Polytryphocycloides* are known from the Silurian (Regnéll 1945, 1973). Isolated plates of cyclocystoids (Frest in Smith and Paul 1982) are known also from the Frasnian State Quarry Formation, Iowa. Haude and Thomas (1994) described *Minicycloides carbonicus* Haude *et* Thomas, 1994 from the Early Carboniferous of Germany, which is the latest occurrence of cyclocystoids.

Relationships of the cyclocystoids remain unknown.

Functional anatomy. — Nichols (1972) believed that the cupule zones of cyclocystoids housed large locomotory tube-feet. In his opinion the feet lacked large ampullae as the majority of cyclocystoids had tube-feet arranged in pairs. Retraction of one might supply the extra fluid to the radial canal, increase pressure, and thereby straighten and expand the neighbouring tube-foot, as observed in some modern holothurians. The tube-feet were possibly connected, since grooves between the radial canal openings at the duplicature from distal side are present in some Devonian species (Text-fig. $24I_2$). Smith and Paul (1982) thought that the cupule zones on the plates of cyclocystoids might have been the location of food uptake by ciliate epithelium. Through the radial ducts of the marginal ring and radial channels of the central disc the food might be transported to the mouth. This seems improbable as the radial canal openings on the marginals are too narrow to allow for food uptake in some species, e.g. *Neocyclocystoides neocyclocystoides* sp. n.

The only living echinoderm analogous to Cyclocystoidea is *Xyloplax* (Concentricycloidea), discovered living on sunken and rotten tree stumps at depths of ca. 1000 m in the coastal waters of New Zealand (Baker *et al.* 1986). In both cases the skeleton consists of a rim of ossicles and a central disc. *Xyloplax* with two circumferential canals has interradials and marginalia connected through a marginal ring with the water system and one row of interradial tube-feet (Baker *et al*. 1986). It resorbs the products of bacterial decay of wood through its ventral membrane. After the discovery of *Xyloplax* Nichols (1986) concluded that the cyclocystoid cupule zones had tubercles and that they lacked connection with the ambulacral system, so could not be associated with tube-feet or filtration organs. On the other hand Rowe (1988) who thought that the water system was connected with the cupule zone and that cyclocystoids, like *Xyloplax,* had two circumferential water canals – the first outer circumferential canal and the second circumoral water canal. According to Kesling (1963, 1966) the soft parts of cyclocystoids were placed above the cupule zone. It is hard to agree with this interpretation, as the anus is on the other side, dorsally and centrally (Smith and Paul 1982). Due to a very limited inner space, bordering the inner organs and small mouth and anal openings (Smith and Paul 1982), the cyclocystoids certainly were hardly predators, and could not evert their stomach; also they could not have been mud-feeders.

Rowe (1988) derived the cyclocystoids from primitive Asterozoa. In his opinion an equivalent of the circumoral water canal might have existed in cyclocystoids in the internal cavity below the crest in marginals, where it was connected with the facet canals, and thereby with the coeloms. A connection between the circumoral water canal and the outer circumferential canal existed via the radial duct. In the opinion of Smith (1988a) Recent Concentricycloidea are related rather with Caymanostellidae among the Asteroidea than with the Cyclocystoidea.

Rowe (1988), following Nichols (1972), suggested that the ampullae of the cyclocystoid tube-feet occurred outside the skeleton. The cupule zone might have been the location of the large tube-feet but, as Nichols (1972) stated, there was no place for their ampullae. The presence of tubercles on the cupule zone in older forms not only did not hinder the action of the tube-feet, but also provided an excellent location for their attachment. The subsequent evolutionary disappearance of tubercles coincided with the loss of annular plates. It formed a primitive dorsal skeletal membrane, which made the body flat and diminished the contact between the marginals. All of this faciliated a change of shape. Therefore one might expect that the increase in mobility would be correlated with an enlargement of the tube-feet.

The main problem with accepting asterozoan affinities of the cyclocystoids is an apparent lack of a hydropore. Specimens from the Devonian of Poland display some interesting structures on the dorsal side of marginals. Early stages of the evolution of these structures can be observed in the Emsian *Sievertsia concava* (Text-fig. 23AG). The role of the facet canals is also uncertain (Text-fig. 21). In primitive forms they simply opened along the proximal edge of the dorsal surface of the marginal ossicles and were covered by the corresponding radial plates of the disc, abutting with the crescentic facet. In more specialised forms, e.g. *Concavocycloides* gen. n., the canals were assembled into special structures, herein called crowns. The crowns strongly resemble the hydropores of other echinoderms. The facet canals penetrate from the ventral side of the plate and are not continuous through to the dorsal side but open in the crown. In *Sievertsia concava*, similar labyrinthic structures can be observed, but located at sites of typical pores of the crescentic facet. Further evolution of the Devonian forms resulted in migration of the whole structure to the centre of the marginals.

The scarce data published so far apparently suggested that the Devonian witnessed the decline of cyclocystoids. Contrary to this picture the material from Poland demonstrates that this was the period of diversification of the cyclocystoids. The particular sklerotomes were reconstructed on the basis of frequency analysis as for ophiuroids.

Family **Apycnodiscidae** fam. n.

Diagnosis. — Marginal ring consists of (16?) 18 to 33 marginals each with one to seven cupules (specific to the genus) or varying around the circle. On the dorsal side the neighbouring plates do not contact, even partially, along their lateral edges.

Remarks. — Erection of this new family requires emendation of the diagnosis of Cyclocystoididae S.A. Miller, 1882 which is here restricted to include forms having a marginal ring composed of 28 to 45 ossicles, typically with two cupules, rarely with one or three. The marginal ring has limited flexibility because neighbouring marginals contact along the whole or larger part of their length. The oldest specimens of *Cyclocystoides* are from the Llanvirn of Ontario (Chazyan, Beatrica Beds, Carden; Raymond 1913), the youngest ones (Kolata 1975; Smith and Paul 1982) from the Ashgill of Wyoming (Upper Bighorn Formation, Hunt Mountain). *Actinodiscus* Smith *et* Paul, 1982 occurs in the Ashgill of Scotland and Norway.

Polytryphocycloides is derived from *Actinodiscus,* as both have predominantly two cupules all with tubercles. It differs from *Actinodiscus* in that dorsal contact of neighbouring marginals, occurs in the distal part only (but without the complete isolation), giving *Polytryphocycloides* a more flexible disc.

The most important evolutionary trend within the family is the increasing flexibility of the disc attained by decreasing lateral contact between neighbouring marginals. This eventually led to their almost complete separation in *Paradoxocycloides* gen. n., where marginals contact only at the strongly expanded crest. Evolutionary parallelism can be observed in respect to the independent lineage of *Zygocycloides* Smith *et* Paul, 1982 – *Diastocycloides* Smith *et* Paul, 1982. Other important trends are the gradual flattening of the body, development of saddle-shaped axial part of the crest, disappearance of sculpture on the ventral side, and probably also the loss of the dorsal skeletal membrane. Cupules are without tubercles and by *Concavocycloides* gen. n., they occur as single elements only. Decrease of the total body size can be observed, as in other groups of Frasnian echinoderms, although the reasons for this trend are not clear (Boczarowski 1992). The Early Carboniferous forms are also devoid of cupule tubercles and have narrow saddle-shaped crests. *Minicycloides carbonicus* Haude *et* Thomas, 1994 (cu $IIIa_1$ – Germany), with its large number (two to six) of cupules, full lateral contact of the marginals, and very broad radial processes, transformed into broad and thin blades, is a distinctive species, with part of its characters resembling *Smithocycloides* gen. n. on one hand, the other suggesting derivation of *M. carbonicus* from *Sievertsia.* Decrease of size, narrowing of the crest and flattening of the body continues during the Carboniferous period. *Apycnodiscus* most probably developed from *Polytryphocycloides* and not directly from *Cyclocystoides* (cf. Smith and Paul 1982), as suggested by the similarities of the two genera such as: tetraradial symmetry of the disc and similar development of the dorsal surface. There is a gradual increase in the number of cupules in subsequent species, starting with *Apycnodiscus salteri* (Hall, 1866). The Devonian diversification of the family commenced possibly from the Emsian *Sievertsia*.

A separate evolutionary lineage is formed by *Diastocycloides* and *Zygocycloides*. This line is characterised by the lack of contact along the dorsal edge of marginals or a point of contact through expanded fragments of the lateral surface in *Diastocycloides*. The genus *Zygocycloides* is also distinguished by the presence of interseptal plates. The dorsal surface is trapezoidal. Representatives of the family are derived from *Apycnodiscus* (Text-fig. 26). *Diastocycloides* developed from *Zygocycloides* and it was the first form with maximum flexibility of its body.

The oldest specimens of the *Polytryphocycloides depressus* (Billings, 1858) evolutionary lineage come from the Late Caradoc of Canada (Trenton Limestone, Ottawa). The presumably youngest specimen of the genus comes from the erratic mudstone fragment of the Quaternary fluvioglacial deposits, its origin is probably in the Late Devonian (Senecan) of Ithaca Formation of the Genese Group, New York (Fluegeman and Orr 1990; Heaslip 1969). The other records of the genus are from the Frasnian of Lime Creek and State Quarry Formations (Iowa; Smith and Paul 1982). The oldest representatives of the lineage leading to *Apycnodiscus salteri* (Hall, 1866) are from the Late Caradoc of the Snake Hill Formation, top of Trenton Limestone (New York) and from Michigan. The most abundant specimens belong to the assemblage of cyclocystoids from the Frasnian of the Holy Cross Mountains. The youngest representatives of the lineage come from the Early Carboniferous (cu $IIIa_1$) of Germany. The oldest specimens of *Zygocycloides* sp. (Kolata, 1975) are from the Caradoc (Rocklandian) of U.S.A. (Decorah Group, Illinois), the youngest ones, i.e. *Diastocycloides nitidus* (Faber, 1886) from the Late Ashgill (Richmondian) of U.S.A. (Late Cincinnatian, Hudson River Group, Ohio, Morrow, Ohio) and *Diastocycloides* sp. (Smith *et* Paul, 1982) from shales of the Wenlock Edge (Dudley, Worcestershire, Great Britain).

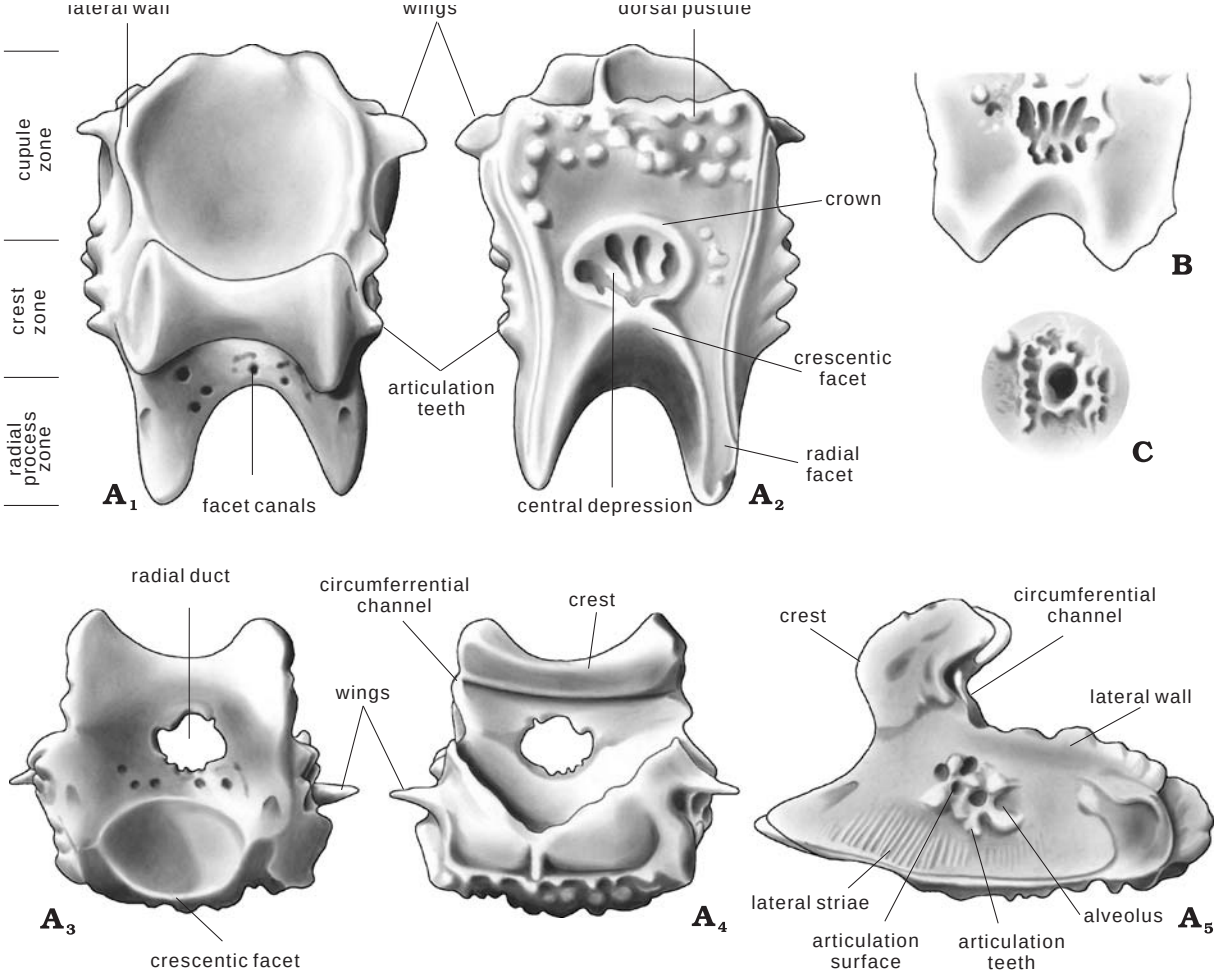

Fig. 21. Terminology of the morphologic features of marginal ossicles of cyclocystoids. $\mathbf{A_1}$ ventral view, $\mathbf{A_2}$ dorsal view, $\mathbf{A_3}$ poximal face view, $\mathbf{A_4}$ distal face view, $\mathbf{A_5}$ lateral face view. **B**. Fragment of dorsal face with crown. **C**. Another crown type. Not to scale.

Included genera. — *Apycnodiscus* Smith *et* Paul, 1982; *Apparatocycloides* gen. n.; *Brutocycloides* gen. n.; *Chimaerocycloides* gen. n.; *Concavocycloides* gen. n.; *Diastocycloides* Smith *et* Paul, 1982; *Linguacycloides* gen. n.; *Minicycloides* Haude *et* Thomas, 1994; *Narrawayella* Foerste, 1920; *Neocyclocystoides* gen. n.; *Paradoxocycloides* gen. n.; *Platycycloides* gen. n.; *Polytryphocycloides* Smith *et* Paul, 1982; *Sievertsia* Smith *et* Paul, 1982; *Smithocycloides* gen. n.; *Zygocycloides* Smith *et* Paul, 1982.

Genus *Linguacycloides* gen. n.

Type species: *Linguacycloides trapes* sp. n.

Derivation of the name: From Latin *lingua* – tongue, due to tongue-shaped cupular zone.

Diagnosis. — Marginals are trapezium-shaped. At the lateral articulation surface there are alveolae and weakly developed teeth (up to three), commonly united into strips.

Remarks. — Contact of neighbouring marginals limited to distal fragments only, presence and shape of tubercles on the cupule, and outline of the marginal plates and the number of cupules (from one to three) indicate, that the genus is a member of the *Apycnodiscus* lineage. Its characteristic features are the narrow crest and the presence of stripes instead of teeth on the lateral surface of marginals (Text-fig. 24D).

Linguacycloides trapes sp. n.
(Pl. 9: 14–17; Text-fig. 24D–H)

Holotype: GIUS 4-562 Mrz./150/1, Text-fig. 24D.

Type horizon: Late Givetian, Early *Mesotaxis falsiovalis* Zone.

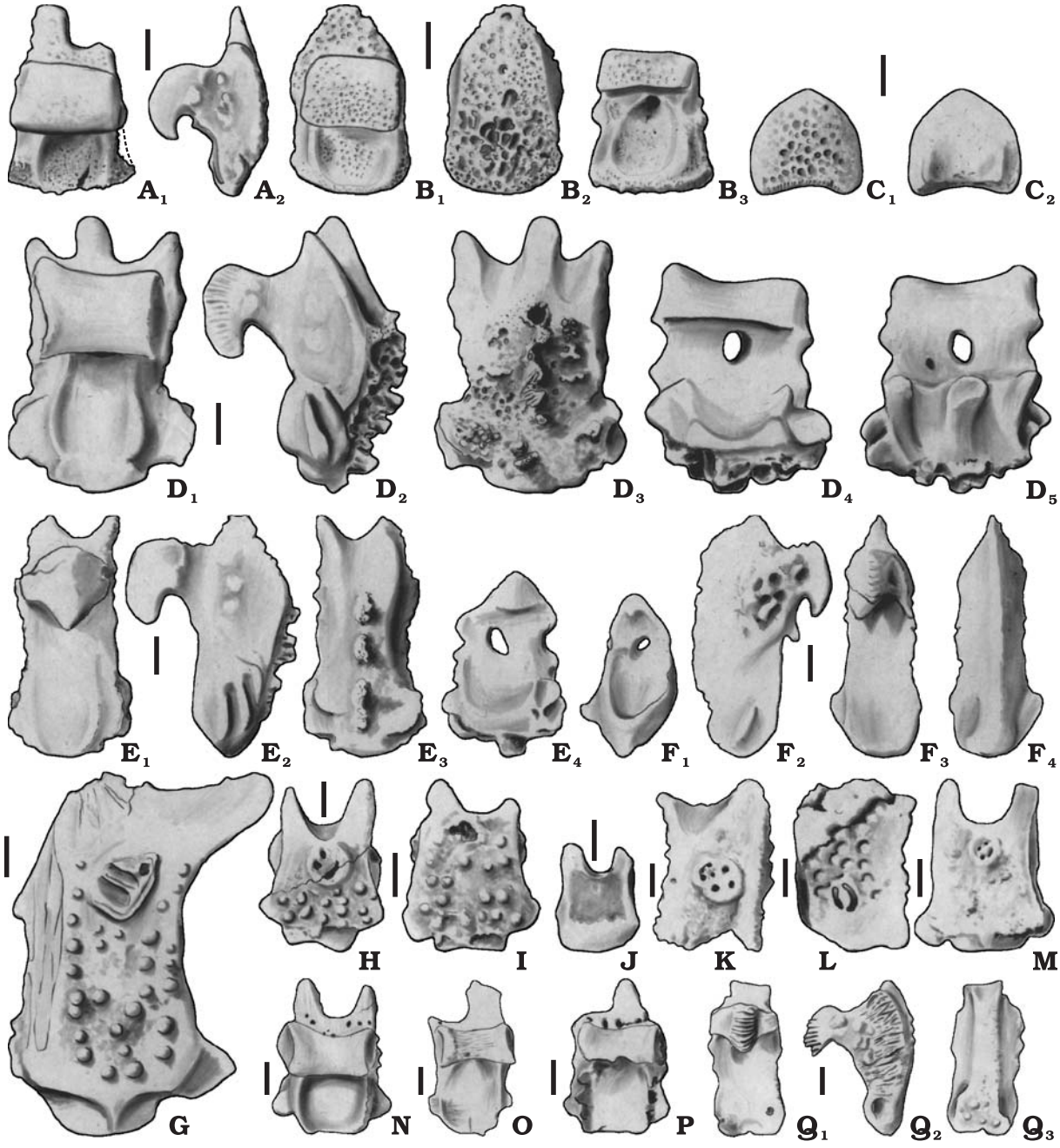

Fig. 22. Skeletal elements of Cyclocystoidea from the Devonian of the Holy Cross Mountains. **A–C**. *Concavocycloides eifeliensis* sp. n. from the Late Eifelian set XVII of Skały. **A**. Marginal ossicle GIUS 4-648 Ska./848/2; A_1 ventral view, A_2 lateral view. **B**. Holotype marginal ossicle GIUS 4-648 Ska./848/1; B_1 ventral view, B_2 dorsal view, B_3 distal face view. **C**. Frontal plate GIUS 4-648 Ska./848/3; C_1 distal face view, C_2 proximal face view. **D–Q**. *Concavocycloides givetiensis* sp. n., marginal ossicles from the Late Givetian of Marzysz and set C of Sowie Górki (H, I, K–Q); samples Marzysz II/W/2 (D), Marzysz II/15 (E, J), and Marzysz II/7 (F, G). **D**. Holotype GIUS 4-564 Mrz./489/1; D_1 ventral view, D_2 lateral view, D_3 dorsal view, D_4 distal face view, D_5 proximal face view. **E**. Narrow form with double radial process, GIUS 4-587 Mrz./481/4; E_1 ventral view, E_2 lateral view, E_3 dorsal view, E_4 distal face view. **F**. Narrow form with single radial process, GIUS 4-578 Mrz./307/1; F_1 distal face view, F_2 lateral view, F_3 ventral view, F_4 dorsal view. **G**. The biggest specimen GIUS 4-578 Mrz./307/2, dorsal view. **H**. Median form GIUS 4-744 Sow./717/2, dorsal view. **I**. Small specimen GIUS 4-744 Sow./717/3, dorsal view . **J**. Juvenile specimen GIUS 4-587 Mrz./481/2, dorsal view. **K**. Irregular form GIUS 4-744 Sow./717/5, dorsal view. **L**. Irregular specimen without radial facet processes, GIUS 4-744 Sow./717/9, dorsal view. **M**. Specimen with regular radial process, GIUS 4-744 Sow./717/11, dorsal view. **N**. Typical specimen with regular radial facet, GIUS 4-744 Sow./717/1, ventral view. **O**. Specimen with one big and another short radial process, GIUS 4-744 Sow./717/7, ventral view. **P**. Specimen with single radial process, GIUS 4-744 Sow./717/8, ventral view. **Q**. Narrow form with abnormal striae on the crest, GIUS 4-744 Sow./717/6; Q_1 ventral view, Q_2 lateral view, Q_3 dorsal view. Scale bar 200 μm.

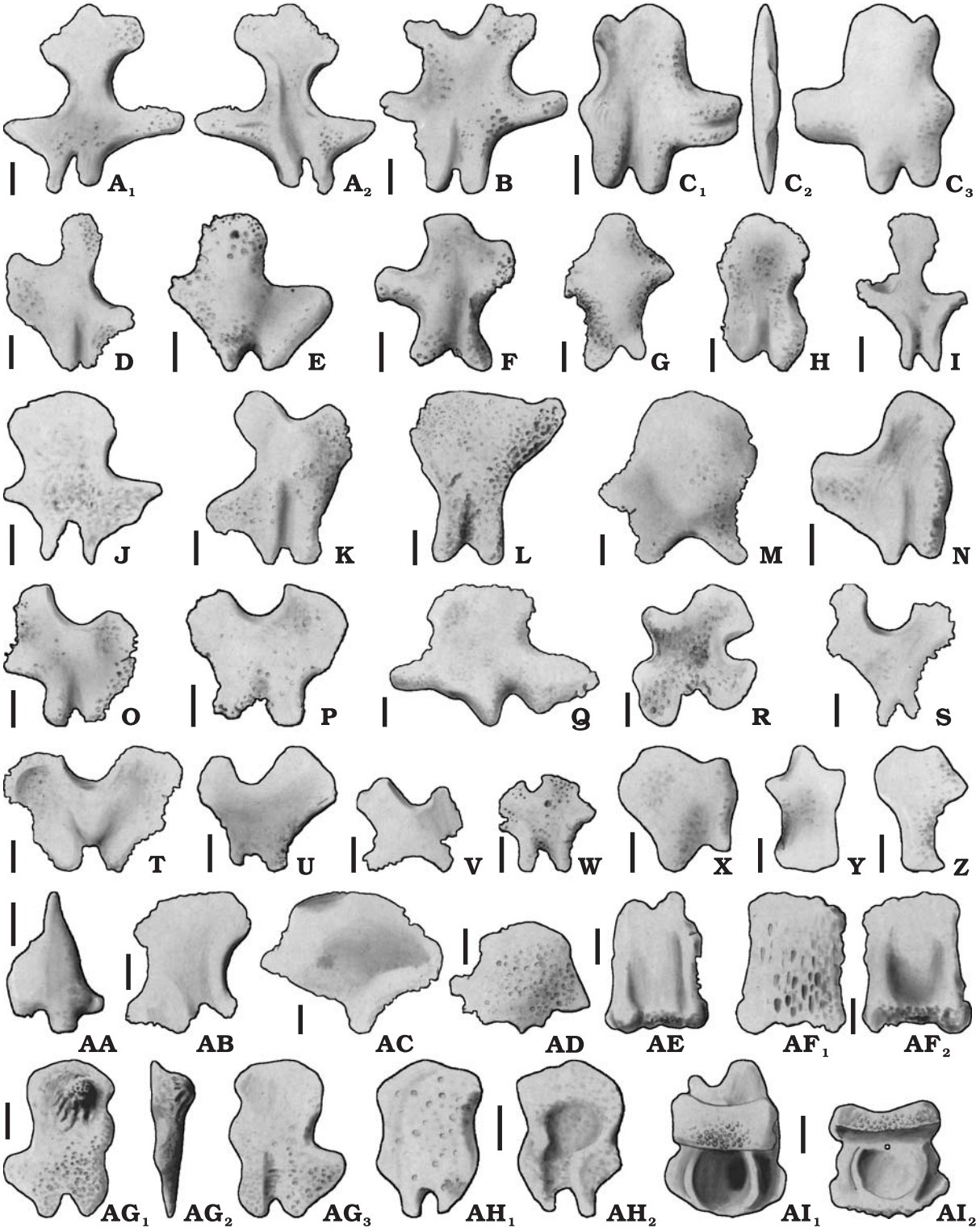

Fig. 23. Skeletal elements of Cyclocystoidea from the Late Givetian of Marzysz and set C of Sowie Górki (J, AE–AF); samples Marzysz II/W/6 (A–B, D, N, S–T), and Marzysz II/13 (C, E–G, O–R, W–AA, AG–AH), Marzysz II/11 (H), Marzysz II/4 (I, V, AI), Marzysz II/7 (K–M, AB–AD), and Marzysz II/15 (U), Holy Cross Mountains. **A**–**AF**. *Concavocycloides givetiensis* sp. n. **A**–**AD**. Ventral disc plates. **A**–**O**. Radial plate GIUS 4-568 Mrz./108/2; A_1 ventral view, A_2 dorsal view. **B**. GIUS 4-568 Mrz./108/6, ventral view. **C**. GIUS 4-584 Mrz./243/3; C_1 ventral view, C_2 lateral view, C_3 dorsal view. **D**. GIUS 4-568 Mrz./108/5, ventral view. **E**. GIUS 4-584 Mrz./243/13, dorsal view. **F**. GIUS 4-584 Mrz./243/15, ventral view. **G**. GIUS 4-584 Mrz./243/14, dorsal view. **H**. GIUS 4-584 Mrz./243/17, ventral view. **I**. GIUS 4-575 Mrz./464/3, ventral view. **J**. GIUS 4-744 Sow./697/1, dorsal view. **K**. GIUS 4-578 Mrz./308/1, ventral view. **L**. GIUS 4-578 Mrz./308/2, ventral view. **M**. GIUS 4-578 Mrz./308/3, ventral view of primary radial plate. **N**. GIUS 4-568 Mrz./108/1, ventral view. **O**. GIUS 4-584 Mrz./243/12, ventral →

Type locality: Trench II, sample 0 at Marzysz, Holy Cross Mountains.

Derivation of the name: From Latin *trapes* – trapezium, from the trapezoidal outline of the marginal plates.

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)			
Number of specimens	Features	Holotype	Minimum	Mean	Maximum
Marginals: 44	Length	880	800	920	1355
	Breadth	915	730	910	1050
	Height	610	610	780	965
	Length of crest	795	290	800	880
	Breadth of crest	320	320	340	475
	Number of cupules	2	1	2	3
	Length of cupule zone	390	390	405	680
	Breadth of cupule zone	900	645	940	1015
Radial plates: 6	Length	–	1030	1500 (?)	1800 (?)
	Breadth	–	990	1010	1270

Diagnosis. — As for the genus.

Description. — Marginals. Mostly with double, rarely with single or triple cupules, each with a large tubercle. The crest is a narrow, undercut cylinder, with a deep groove beneath for the circumferential channel. Besides the articulation teeth there are alveolae and lateral striae on the lateral surface, limited to the crest zone. The radial processes are weakly developed as an irregular strip, rarely also as a triple strips in forms with three cupules (Pl. 9: 16). In forms with a single cupule there is only a tongue-shaped process. The facet canals are clearly visible; in forms with a single cupule there is a single canal, forms with two cupules have two canals, with three cupules up to nine canals (Pl. 9: 14–17; Text-fig. 24D–G). The crescentic facet on the dorsal surface is present in all these morphotypes. Holes for the radial duct are large, circular, equal in number to cupules, and separated from each other by V-shaped ridges distally. On the dorsal surface numerous fine pustules occur.

Radials. Only fragments of radial plates are known. In their proximal part they have two long, narrow processes, passing into a plate, where they surround a distinct radial groove (Text-fig. 24H). The lateral processes are slim, and, in the large specimens curved, towards the ventral side. Other elements could not be identified. Judging from the isolated elements most probably it was a very small organism, approximately 7.5 mm diameter. In a marginal ring there is estimated to have been at least 24 marginals.

Remarks. — The marginals do not resemble those of any known species of cyclocystoids, although the general plan is rather close to those of *Apycnodiscus*.

Occurrence. — Mid Givetian: Set B of Jaźwica. Late Givetian: outcrop I, trench II at Marzysz; Set C of Sowie Górki, Holy Cross Mountains, Poland.

Genus *Neocyclocystoides* gen. n.

Type species: *Neocyclocystoides neocyclocystoides* sp. n.

Derivation of the name: From Latin *neo* – new.

Diagnosis. — Marginals with indistinct radial duct pore; their laterally expanded wings blade-shaped. Crest and dorsal surface covered with pustules.

Remarks. — The carved crest somewhat resembles that of *Sievertsia* (Text-fig. 26), while the narrow crest, lateral surface with slightly elongate wings, and simple cupules without tubercles, are features of *Concavocycloides* gen. n. It is unknown whether the facet canals completely perforate the marginals.

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view. **P**–**AD**. Interradial plate. **P**. GIUS 4-584 Mrz./243/10, ventral view. **Q**. GIUS 4-584 Mrz./243/1, dorsal view. **R**. GIUS 4-584 Mrz./243/16, dorsal view. **S**. GIUS 4-568 Mrz./108/4, ventral view. **T**. GIUS 4-568 Mrz./108/3, ventral view. **U**. GIUS 4-587 Mrz./481/3, dorsal view. **V**. GIUS 4-575 Mrz./464/2, ventral view. **W**. GIUS 4-584 Mrz./243/6, dorsal view. **X**. GIUS 4-584 Mrz./243/2, dorsal view. **Y**. GIUS 4-584 Mrz./243/4, dorsal view. **Z**. GIUS 4-584 Mrz./243/5, dorsal view. **AA**. GIUS 4-584 Mrz./243/7, dorsal view. **AB**. GIUS 4-578 Mrz./308/4, ventral view. **AC**. GIUS 4-578 Mrz./308/5, dorsal view. **AD**. GIUS 4-578 Mrz./308/6, dorsal view. **AE**–**AF**. Frontal plates ossicles. **AE**. GIUS 4-744 Sow./718/1, proximal face. **AF**. GIUS 4-744 Sow./718/2; AF_1 distal face, AF_2 proximal face view. **AG**. ?*Concavocycloides givetiensis* sp. n., radial plate with possible hydropores, (madreporite?) GIUS 4-584 Mrz./243/8; AG_1 ventral view, AG_2 lateral view, AG_3 dorsal surface with the dorsal channel. **AH**. ?*Neocyclocystoides neocyclocystoides* sp. n., radial plate from ventral disc, GIUS 4-584 Mrz./243/9; AH_1 dorsal view, AH_2 ventral view. **AI**. *Neocyclocystoides neocyclocystoides* sp. n., marginal ossicles GIUS 4-575 Mrz./464/1; AI_1 ventral view, AI_2 dorsal view. Scale bar 200 μm.

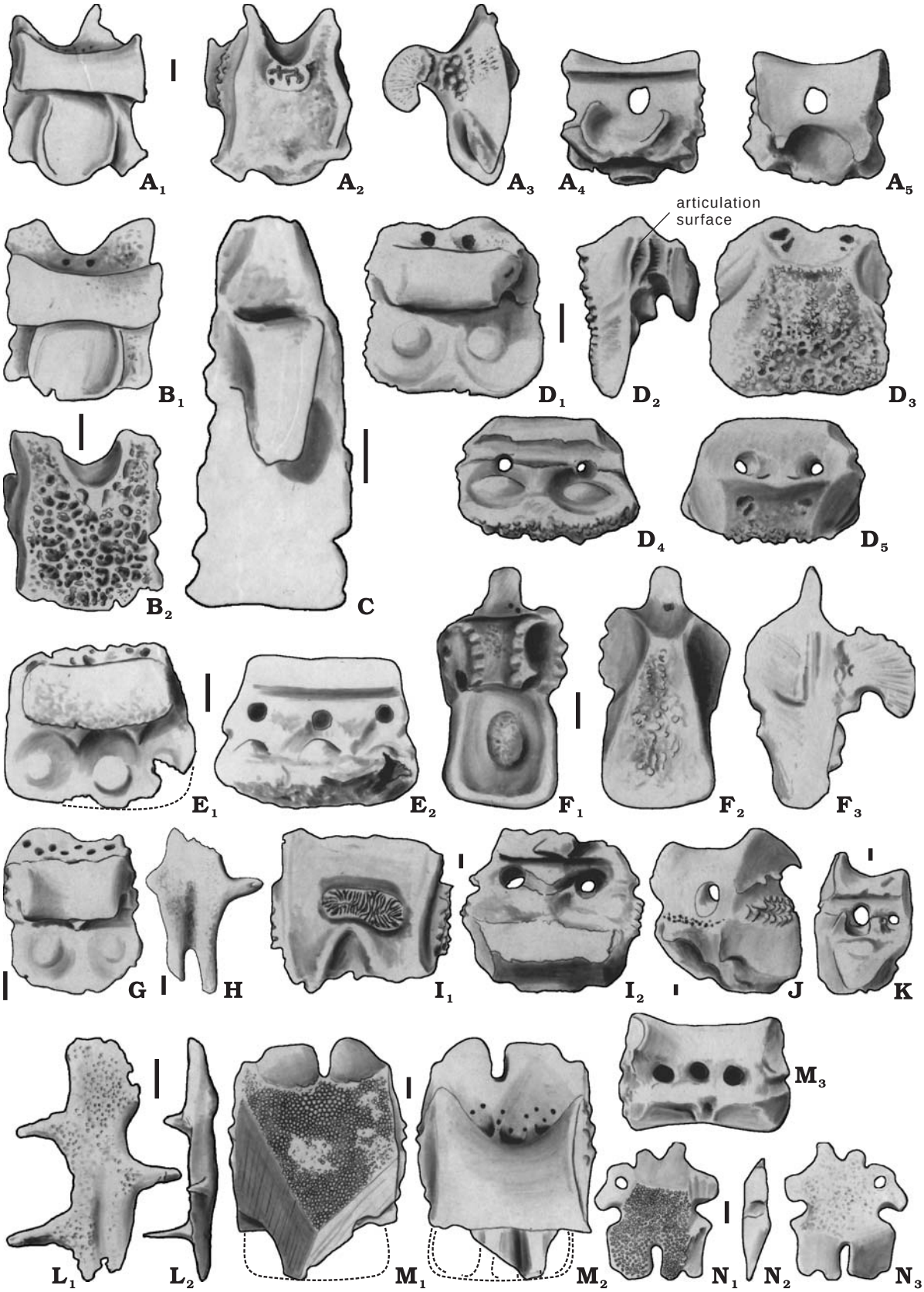

Fig. 24. Skeletal elements of Cyclocystoidea from the Devonian of the Holy Cross Mountains. **A**–**C**. *Concavocycloides frasniensis* sp. n. from the Middle Frasnian of Szczukowskie Górki, sample W6. **A**. Marginal ossicle, the holotype GIUS 4-610 Szg./548/2; A_1 ventral view. A_2 dorsal view, A_3 lateral view, A_4 distal view, A_5 proximal view. **B**. GIUS 4-610 Szg./548/3; B_1 ventral view, B_2 dorsal view. **C**. Narrow specimen, the paratype GIUS 4-610 Szg./548/1. **D**–**H**. *Linguacycloides trapes* sp. n. ➝

Neocyclocystoides neocyclocystoides sp. n.
(Text-fig. 23AF–AI)

Holotype: GIUS 4-575 Mrz./464/1, Text-fig. 23AI.

Type horizon: Late Givetian, Early *Mesotaxis falsiovalis* Zone.

Type locality: Trench II, layer 4 at Marzysz, Holy Cross Mountains.

Derivation of the name: From Latin *neo* – new.

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)			
Number of specimens	Features	Holotype	Minimum	Mean	Maximum
Marginals with:	Length	815	815	818	820
1 cupules: 3	Breadth	645	645	650	655
	Height	560	560	620	650
	Length of crest	575	575	575	575
	Breadth of crest	250	250	250	250
	Length of cupule zone	320	320	325	330
	Breadth of cupule zone	645	645	650	655
Madreporite?: 1	Length	–	830	–	–
	Breadth	–	560	–	–
Radial plates: 2	Length	–	680	690	700
	Breadth	–	475	505	535

Diagnosis. — As for the genus.

Description. — Marginals. Marginal plates are massive, though small; their length is their largest dimension, and their breadth is almost equal to height. Cupule zones, without tubercles, are flanked on both sides by distinct lateral walls; crest undercut; one or two cupules only. On the lateral articulation surface there are four well-developed teeth and alveolae. Lateral striae are numerous along the lateral edge. Two radial processes, of unequal size, are well developed, pierced by two facet canals. The crescentic facet on the dorsal surface is indistinct.

Radialia. Radial plates are massive, and polygonal in outline. Only two parallel proximal processes occur by the radial duct. The latter is broad, curved, expanding distally into a depression. Lateral processes occur only in a rudimentary form, as flattened lateral edges (Text-fig. 23AH). On the dorsal side the plate is perforated. Other elements have not been identified.

Madreporite?. This plate (Text-fig. 23AG) is only tentatively identified as a madreporite, as it has a depression, which is possibly a dorsal channel as in *Sievertsia*. On its ventral side (if orientation of the plate is correct) there is a large perforated tubercle, suggesting this is really the madreporite plate. The diameter of a complete organism is estimated to be ca. six mm, with approximately 26 marginals.

Remarks. — The species is most closely related to C*yclocystoides latus* Smith *et* Paul, 1982, but the presence of the lateral strip and its narrow crest excludes it from that genus. It differs from the species of *Concavocycloides* gen. n. in having a carved crest surface, very small radial duct hole and extended wings. The described radial plate most probably belongs to this species, though such elements are scarce and other species of cyclocystoid were in the same samples. Radials of *Concavocycloides givetiensis* sp. n. are well established and are of the thin-walled type. The massive structure of the marginals readily distinguishes this from all the other species.

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from the Late Givetian. **D**. Holotype marginal ossiclefrom Marzysz II/W/0, GIUS 4-562 Mrz./150/1; D_1 ventral view, D_2 lateral view, D_3 dorsal view, D_4 distal view, D_5 proximal view. **E**. Marginal ossicle with three cupules from set C of Sowie Górki, GIUS 4-744 Sow./686/3; E_1 ventral view, E_2 distal view. **F**. Narrow marginal ossicle from set C of Sowie Górki, GIUS 4-744 Sow./686/2; F_1 ventral view, F_2 dorsal view, F_3 lateral view. **G**. Marginal ossicle from set C of Sowie Górki, GIUS 4-744 Sow./686/14, ventral view. **H**. Radial plate of ventral disc from set C of Sowie Górki, GIUS 4-744 Sow./697/2, ventral view. **I–L**. *Brutocycloides cerebrum* sp. n., marginal ossicles from the Middle Frasnian of Szczukowskie Górki, sample W6. **I**. Holotype GIUS 4-610 Szg./542/1; I_1 dorsal view, I_2 distal view. **J**. Narrow specimen GIUS 4-610 Szg./542/2, distal view. **K**. Incomplete specimen GIUS 4-610 Szg./542/3, oblique view. **L**. Specimen from the Mid Frasnian set D of Wietrznia, GIUS 4-793 Wie./1136/1; L_1 ventral view, L_2 lateral view. **M–N**. *Chimaerocycloides chimaerus* sp. n. from the Mid Frasnian of Szczukowskie Górki, W6. **M**. Holotype marginal ossicle GIUS 4-610 Szg./1133/1; M_1 dorsal view, M_2 ventral view, M_3 distal view. **N**. Radial plate from ventral disc, GIUS 4-610 Szg./595/1; N_1 dorsal view, N_2 lateral view, N_3 ventral view. Scale bar 200 μm.

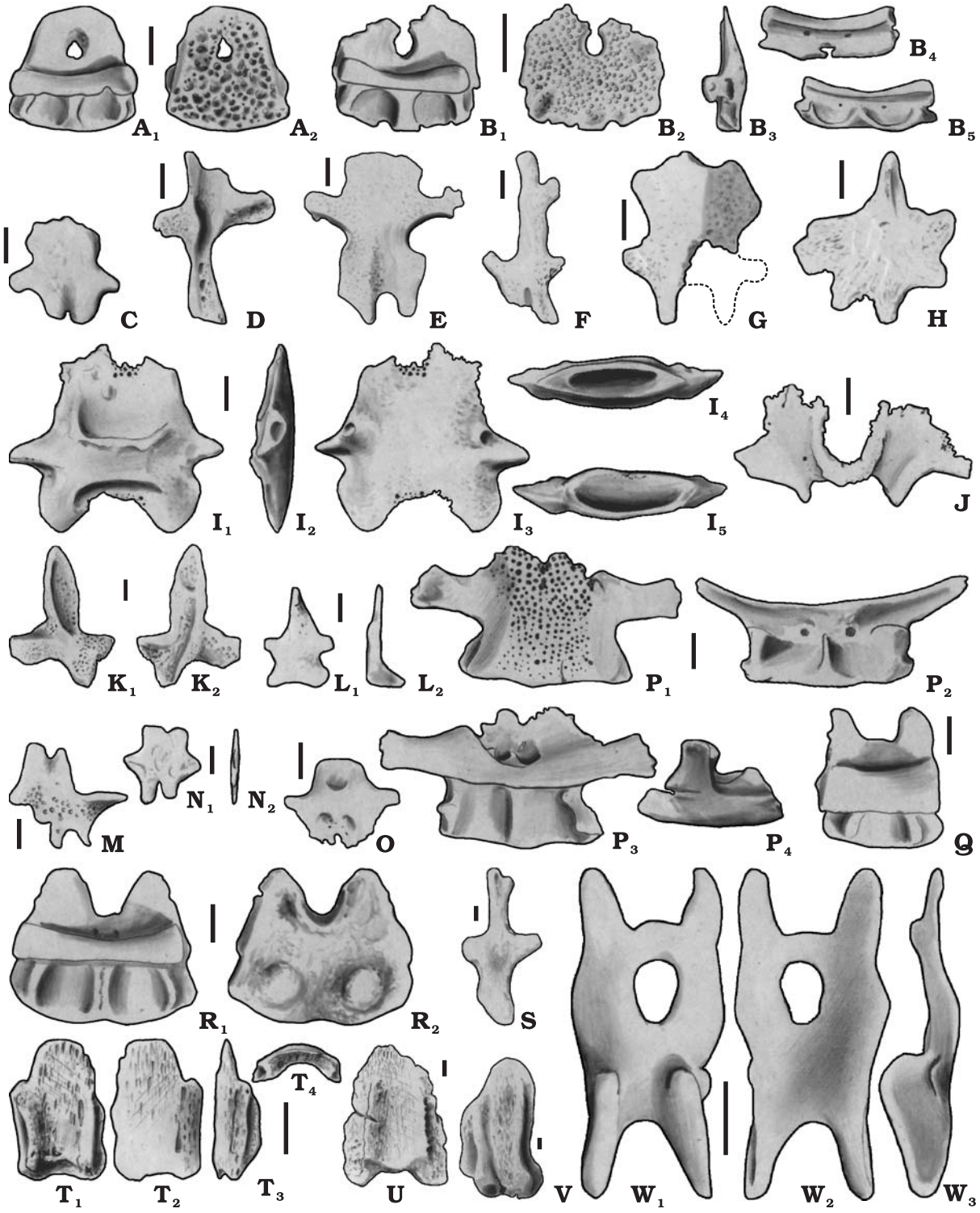

Fig. 25. Skeletal elements of the Cyclocystoidea from the Devonian of the Holy Cross Mountains. **A**–**H**. *Platycycloides foraminis* sp. n. from the Mid Frasnian, set D of Wietrznia II in Kielce. **A**. Holotype marginal ossicle GIUS 4-793 Wie./524/2; A_1 ventral view, A_2 dorsal view. **B**. Marginal ossicle GIUS 4-793 Wie./524/1; B_1 ventral view, B_2 dorsal view, B_3 lateral view, B_4 proximal view, B_5 distal view. **C**–**F**. Radial plates from ventral disc. **C**. GIUS 4-793 Wie./525/4, ventral view. **D**. GIUS 4-793 Wie./525/7, ventral view. **E**. GIUS 4-793 Wie./525/3, ventral view. **F**. GIUS 4-793 Wie./525/6, ventral view. **G**–**H**. Interradial plate from ventral disc. **G**. GIUS 4-793 Wie./525/2, dorsal view. **H**. GIUS 4-793 Wie./525/1, ventral view. **I**–**J**. *Paradoxocycloides planus* sp. n. from the Late Givetian. **I**. Holotype marginal ossicle from Marzysz II/13, GIUS 4-584 Mrz./441/1; I_1 ventral view, I_2 lateral view, I_3 dorsal view, I_4 distal view, I_5 proximal view. **J**. Probable interradial plate from ventral disc from Marzysz II/4, GIUS 4-575 Mrz./1134/1. **K**–**P**. *Apparatocycloides satanus* sp. n. from the Mid Frasnian of Szczukowskie Górki, sample W6. **K**. Plate from ventral disc GIUS 4-610 Szg./541/5; K_1 dorsal view, K_2 ventral view. **L**. Radial plate from ventral disc →