As for the assumed madreporite plate, so far it has never been identified in cyclocystoids and Smith and Paul (1982) suggested the water system might lack specialised skeletal structures. The plate under consideration might belong to *Neocyclocystoides neocyclocystoides* sp. n. rather than to *Concavocycloides givetiensis* sp. n., due to its thickness and similarity of shape with radial plates.

Occurrence. — Only known from the type locality.

Genus *Smithocycloides* gen. n.

Type species: *Smithocycloides paulii* sp. n.

Derivation of the name: From the name of A.B. Smith, one of the authors of the monograph on the cyclocystoids.

Diagnosis. — Marginals with small hole for radial duct, narrow crest, without tubercles on cupules but with tubercles on dorsal side.

Remarks. — Cupules simple, without tubercles; marginal ring flexibility limited by contact with neighbouring marginals along almost the entire lateral surface, but without full contact along the dorsal edge. The wing is long. The presence of one or two cupules only suggests that the genus is derived from *Neocyclocystoides* gen. n. Along with the primary rigidity of the marginal ring, the skeleton became flatter and the crest narrowed into a smooth arch-shaped roll.

Smithocycloides paulii sp. n.
(Pl. 9: 22; Text-fig. 25Q–R)

Holotype: GIUS 4-610 Szg./1135/1, Text-fig. 25R.

Type horizon: Mid Frasnian, Early *Palmatolepis hassi* to Early *Palmatolepis rhenana* Zones.

Type locality: Layer W6 of Szczukowskie Górki, Holy Cross Mountains.

Derivation of the name: From the name of C.R.C. Paul, a co-author of the monograph on cyclocystoids.

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)			
Number of specimens	Features	Holotype	Minimum	Mean	Maximum
Marginals: 9	Length	815	745	790	850
	Breadth	980	660	800	980
	Height	475	425	450	475
	Length of crest	900	625	775	925
	Breadth of crest	185	100	195	275
	Number of cupules	2	1	2	2
	Length of cupule zone	320	185	260	320
	Breadth of cupule zone	980	625	805	980

Diagnosis. — As for the genus.

Description. — Marginals. These plates have single or double cupules without tubercles. The cupules occur only at the lateral walls, if they occur in pairs, each cupule has its own wall and is separated by a groove (Pl. 9: 22; Text-fig. 25Q–R). The crest forms a narrow, smooth roll; seen from the side it is curved distally like a parrot's beak, forming a shallow groove for the circumferential channel. The forms with double cupules have a curved crest. On the lateral articulation surface there are up to five weakly developed teeth and alveolae. Lateral striae near the dorsal edge are weakly developed but are very distinct at the lateral surface of the crest (Pl. 9: 22). Besides the exterior lateral walls there are narrow, horizontal bars, so the contact with neighbouring

GIUS 4-610 Szg./541/2; L_1 dorsal view, L_2 lateral view. **M**. Radial plate from ventral disc, GIUS 4-610 Szg./541/4, ventral view. **N**. Interradial plate from ventral disc, GIUS 4-610 Szg./541/3; N_1 ventral view, N_2 lateral view. **O**. Juvenile form of marginal ossicle, GIUS 4-610 Szg./594/4. **P**. Holotype marginal plate GIUS 4-610 Szg./594/1; P_1 dorsal view, P_2 ventral view, P_3 distal view, P_4 lateral view. **Q–R**. *Smithocycloides paulii* sp. n. from the Mid Frasnian of Szczukowskie Górki, sample W6. **Q**. Marginal ossicle with single cupule zone, GIUS 4-610 Szg./1135/2, ventral view. **R**. Holotype marginal ossicle with double cupule zone, GIUS 4-610 Szg./1135/1; R_1 ventral view, R_2 dorsal view. **S**. Possible plate from ventral disc of *Platycycloides foraminis* sp. n. from the Mid Frasnian of Szczukowskie Górki, W6, GIUS 4-610 Szg./541/1. **T–V**. Frontal plates of a cyclocystoid, possibly *Brutocycloides cerebrum* sp. n., same sample. **T**. GIUS 4-610 Szg./540/2; T_1 proximal view, T_2 distal view, T_3 lateral view, T_4 ventral view. **U**. GIUS 4-610 Szg./540/3, proximal view. **V**. GIUS 4-610 Szg./540/1, proximal view of the biggest form. **W**. Probable cyclocystoid juvenile specimen from the Late Givetian sample Marzysz II/W/6, GIUS 4-568 Mrz./76/1; W_1 ventral view, W_2 dorsal view, W_3 lateral view. Scale bar 200 μm.

marginals along the dorsal side occurs almost along their entire length, except at the dorsal edge. Whatever the number of cupules there are always two radial processes. Two facet canals are very distinct. The crescentic facet of the dorsal surface is narrow and bordered dorsally by a roll. Dorsal tubercles correspond with the cupules on the other side. Other elements could not be recognised. The diameter of the largest specimen, as deduced from the largest isolated elements, is ca. five mm and the marginal ring might contain 18 marginals.

Remarks. — Lack of tubercles at the cupules and the presence of a narrow, smooth crest makes this species somewhat similar to some forms of the genera *Neocyclocystoides* gen. n., *Concavocycloides* gen. n., and *Minicycloides* Haude *et* Thomas, 1994. It is distinguished from species of these genera by presence of dorsal tubercles correspond with the cupules on the other side.

Occurrence. — Only known from the type locality.

Genus *Platycycloides* gen. n.

Type species: *Platycycloides foraminis* sp. n.

Derivation of the name: From Greek *plath* – flat, skeletal membranes contained a very strongly flattened body.

Diagnosis. — Smooth, cylindrical crest concave axially. Two large, flattened lobe-shaped radial processes well developed, either connected proximally to form a large oval foramen, or disconnected and defining a C-shaped slit.

Remarks. — Cupules without tubercles and the saddle-shaped crest of the axial part suggest the genus *Smithocycloides* evolved from *Smithocycloides* gen. n. (Text-fig. 26). The consequent flattening of the body, skeletal lightening and increase in flexibility of the disc, was attained by increasing the contact distance between neighbouring marginals.

Platycycloides foraminis sp. n.
(Text-fig. 25A–H, S?)

Holotype: GIUS 4-793 Wie./524/2, Text-fig. 25A.

Type horizon: Mid Frasnian, Late *Palmatolepis hassi* to *Palmatolepis jamieae* Zones.

Type locality: Set D of Wietrznia II quarry, Holy Cross Mountains.

Derivation of the name: From Latin *foramen* – hole, from the presence of a pore at the proximal part of the marginal plate.

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)			
Number of specimens	Features	Holotype	Minimum	Mean	Maximum
Marginals with	Length	660	430	560	660
2 cupules: 6	Breadth	680	510	600	680
	Height	170	150	160	170
	Length of crest	680	450	445	440
	Breadth of crest	150	50	110	150
	Length of cupule zone	200	150	180	200
	Breadth of cupule zone	680	460	570	680
Radials: 16	Length	–	580	1440	1940
	Breadth	–	580	922	1100
Interradials: 4	Length	–	795	820	900
	Breadth	–	710	750	865

Diagnosis. — As for the genus.

Description. — Marginals. The plates resemble a flat polygon. Their length is equal to, or smaller than, their breadth, and their height is the smallest dimension. Two cupules without tubercles are separated by a radial ridge and by lateral walls (Text-fig. 25A–B). Undercutting for the circumferential channel is shallow and narrow. On the lateral articulation surface only fine wrinkles but no teeth can be seen. Lateral striae, facet canals and crescentic facet are all absent. The radial duct openings are very small. Numerous small pits cover the dorsal surface.

Radials and interradials. Radial plates are thin, elongate or uniformly flat and resemble a cross. The radial groove is deep and clearly distinguishable (Text-fig. 25C–F, S?). The two proximal processes are short, the two to four lateral processes may be longer. Their dorsal side is pitted, as in the marginals. Interradial plates are either flat or bent, with six processes, and with typical pitting dorsally (Text-fig. 25G–H).

Other skeletal elements could not be identified. The diameter of whole the organism is estimated to be ca. 7.5 mm, with 19 marginals.

Remarks. — This cyclocystoid is quite unlike any other species described. Slight morphological similarities do suggest, however, that it could be ancestral to *Apparatocycloides satanus* sp. n.

Occurrence. — Mid Frasnian: Set D of Wietrznia II quarry, Late *Palmatolepis hassi* to *Palmatolepis jamieae* Zones; Szczukowskie Górki quarry, Early *Palmatolepis hassi* to Early *Palmatolepis rhenana* Zones, Holy Cross Mountains, Poland.

Genus *Apparatocycloides* gen. n.

Type species: *Apparatocycloides foraminis* sp. n.

Derivation of the name: From Latin *apparatus* – splendid, excellent.

Diagnosis. — Crest forms a broad lateral expansion, greatly extending the outline of the marginal plate. No undercut channel. Lateral surfaces lack any traces of articulation contact.

Remarks. — Its flat body, lack of tubercles at the cupules and saddle-shaped crest suggest this form evolved from *Platycycloides* gen. n. (Text-fig. 26). The large distance between the marginals, and the narrow, almost point contact, of the laterally expanded crest, indicates a continuation of the main evolutionary trend. This is the oldest species in which such a type of connection is seen. Some similarities can be observed by *Diastocycloides stauromorphus* Smith *et* Paul, 1982 where the point contact of the proximal part of lateral surface can be observed.

Apparatocycloides satanus sp. n.
(Text-fig. 25K–P)

Holotype: GIUS 4-610 Szg./594/1, Text-fig. 25P.

Type horizon: Mid Frasnian, Early *Palmatolepis hassi* to Early *Palmatolepis rhenana* Zones.

Type locality: Layer W6 of Szczukowskie Górki, Holy Cross Mountains.

Derivation of the name: From Latin *satanus*, the distal side of the marginal plate resembles an effigy of Satan's head.

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)			
Number of specimens	Features	Holotype	Minimum	Mean	Maximum
Marginals with 2 cupules: 2	Length	745	475	610	745
	Breadth	900	455	680	900
	Height	455	280	370	455
	Length of crest	1510	630	1070	1510
	Breadth of crest	190	85	135	190
	Length of cupule zone	310	200	255	310
	Breadth of cupule zone	900	455	675	900
Radials: 2	Length	–	690	710	730
	Breadth	–	490	665	845
Interradials: 1	Length	–	555	–	–
	Breadth	–	550	–	–

Diagnosis. — As for the genus.

Description. — Marginals. Marginal plates very much wider than long; their height is ca. half to one-third of their breadth. Two cupules without tubercles are separated by two ridges and are bordered by walls. The smooth, cylindrical crest is concave axially. The flattened ends of the crest of one plate abut the crest of the neighbouring marginalium, and are the only point of contact. Proximally there is a thin lobe of coalesced radial processes (Text-fig. 25P). Facet canals and crescentic facet are both absent. Radial duct perforations on the distal side are small and unequal, but on the proximal side are three times as large and placed in pockets, separated by a vertical blade. The dorsal surface is flat and strongly pitted.

Radials. These plates are thick, elongated and irregular in shape. Radial grooves are deep and well-marked (Text-fig. 25K). Two proximal processes are short, the single lateral one is flat.

Interradials. Interradial plates are flat, and star-shaped, with five or six processes of which one may be rotated through 90° and vertical.

Other elements have not been recognised. The whole organism, is estimated to have had a diameter of ca. seven mm and a marginal ring composed of 16 marginals.

Remarks. — The large distance between the marginals and the unique type of lateral contact between marginals justifies the creation of a new genus for this species. Ventral disc structure indicates strong links to *Platycycloides* gen. n. The structure of isolated skeletal elements suggest that the whole skeleton was very open-in construction.

Occurrence. — Only known from the type locality.

Genus *Paradoxocycloides* gen. n.

Type species: *Paradoxocycloides planus* sp. n.

Derivation of the name: From Latin *paradoxus* – strange, paradoxical, because of the atypical, simplified structure.

Diagnosis. — Very flat marginals of simplified structure. Crest smooth and blade-like.

Remarks. — In spite of the simplified structure, numerous characters indicate relationships with *Apparatocycloides* gen. n. (Text-fig. 26). The main evolutionary trends, apparent already in *Sievertsia*, namely flattening of the body, disappearance of sculpture, increased delicacy of skeleton, decrease of body size and lack of tubercles in cupules, continue in *Paradoxocycloides* gen. n. The other trend, visible in *Diastocycloides stauromorphus* Smith *et* Paul, 1982, is a decrease in the lateral contact of neighbouring marginals, which, in the opinion of Smith and Paul (1982), increased the flexibility of the disc. Point contact of the marginals occurs in *Diastocycloides*, as in *Paradoxocycloides* gen. n. and *Apparatocycloides* gen. n.

Paradoxocycloides planus sp. n.
(Text-fig. 25I–J)

Holotype: GIUS 4-584 Mrz./441/1, Text-fig. 25I.

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 *planus* – flat, due to its having the most flattened thecae of all the known cyclocystoids.

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)			
Number of specimens	Features	Holotype	Minimum	Mean	Maximum
Marginals with 1 cupules: 1	Length	1050	1050	–	–
	Breadth	915	915	–	–
	Height	290	290	–	–
	Length of crest	1220	1220	–	–
	Breadth of crest	255	255	–	–
	Length of cupule zone	525	525	–	–
	Breadth of cupule zone	745	745	–	–
Plates from disc: 4	Length	–	640	–	–
	Breadth	–	1305	–	–

Diagnosis. — As for the genus.

Description. — Marginals. Length equal to breadth; height ca. quarter of length. A single cupule, without tubercle, is present. Undercutting for the circumferential channel is absent as are the radial duct and facet canals. On the lateral articulation surface there are two large, flat processes, with fine dorsal pits at their bases. These processes formed the only point of contact of adjacent marginals. Other marginal cannot be distinguished.

Ventral disc plates. These elements are thin and form ring-like structures (Text-fig. 25J). Other elements were not recognised. It is impossible to evaluate the size of the whole organism.

Remarks. — Were it not for the size of individual elements and the postulated evolutionary trends of the group, one might suppose the material represents the juvenile elements of some cyclocystoid.

Occurrence. — Only known from the type locality.

Genus *Concavocycloides* gen. n.
(Text-fig. 21A–C)

Type species: *Concavocycloides givetiensis* sp. n.

Derivation of the name: From Latin *concavus* – as the genus is possibly evolved from *Sievertsia concava.*

Diagnosis. — All marginals with single cupules lacking tubercles. The crown, with facet canal openings, has irregularly arranged channels at its surface.

Description. — Marginals. The marginal plates are sandal-shaped and longer than broad. Their cupule zone is bordered on both sides by a feeble to strongly developed lateral wall. The crest is cylindrical, curved in the shape of a parrot beak in lateral view with a deep distal groove for the circumferential channel. On the lateral articulation surface are a variable number of teeth, alveolae and lateral striae. Stabilising the connection between the marginals, and also limiting the flexibility of whole the organism are wing-shaped processes (Text-fig. 24A–C). The radial processes are well developed, one to three in number. Up to seven facet canals are usually well marked except in *Concavocycloides eifeliensis* sp. n. On the dorsal surface the canals open into a specialised structure, named herein "crown", with apertures concentrated into a central depression. A dorsal crescentic facet occurs only in specimens with more than two radial processes. The radial duct is commonly well marked. The skeletal sculpture is usually developed, depending on the species.

Remarks. — The lineage stems from *Sievertsia concava*, as this is the first cyclocystoid which has the dorsal apertures of facet canals in the shape of meandering slits on the crescentic facet (*vide* Smith and Paul 1982). In *Concavocycloides* gen. n. there was a gradual shifting of the crown from the proximal edge to the middle part of the dorsal surface, and this differentiates it from other genera; only *Brutocycloides* gen. n. has a similar appearance. Thus it seems probable that *Concavocycloides* gen. n. and *Brutocycloides* gen. n. shared a common ancestor (Text-fig. 26). *Sievertsia gotus* (Prokop, 1980) is, on the other hand, the first species with secondarily simplified cupules without tubercles, as in all species of *Concavocycloides* gen. n. The other important change is a decrease of flexibility of the marginal ring through expansion of the wings, though by *Concavocycloides* the contact is not complete, analogous to the blade in *Smithocycloides* gen. n. This also separates *Concavocycloides* from others. Three species occur in the Eifelian, Givetian, and Frasnian, respectively, forming a single evolutionary lineage and show gradual increasing complexity of the crown and expansion of the wings.

Concavocycloides eifeliensis sp. n.
(Text-fig. 22A–C)

Holotype: GIUS 4-648 Ska./848/1, Text-fig. 22B.

Type horizon: Late Eifelian, Set XVII of the Skały Beds, *Tortodus kockelianus* Zone.

Type locality: Skały, Holy Cross Mountains.

Derivation of the name: From Latin *eifeliensis* – in reference to the age of the species.

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)			
Number of specimens	Features	Holotype	Minimum	Mean	Maximum
Marginals with 1 cupule: 4	Length	795	795	845	915
	Breadth	510	510	550	625
	Height	610	610	625	660
	Length of crest	440	440	500	560
	Breadth of crest	290	290	590	320
	Length of cupule zone	280	280	720	455
	Breadth of cupule zone	525	525	1100	630
Frontal plates: 3	Height	–	520	530	540
	Breadth	–	515	520	525

Diagnosis. — Marginals with weakly marked facet canal openings and with indistinct winglets. Crown not developed; in place of a central depression there is a single, large opening at the centre.

Description. — Marginals. These plates have either rectangular or rounded angles. Their crest is convex axially. On the lateral articulation surface up to four weakly developed teeth and alveolae can be seen; lateral striae are either absent or only weakly marked. The wings occur as flake-shaped bars. Radial processes are well marked, one or two in number. The crescentic facet is weakly marked in specimens with two radial processes, and absent from specimens with a single radial process. The radial duct opening has a very small lumen. The skeleton of marginal plate is composed of a coarse open stereom, especially on the dorsal surface. The remaining elements are typical for the genus.

Frontal plates. They are shaped like the blade of a spade and convex to the exterior. Their outer surface is formed of a loose stereom network and there are fine riblets on the dorsal edge.

Other elements have not been recognised. The total diameter, as inferred from isolated remains, is ca. four mm, the marginal ring consisted of 19 marginals.

Remarks. — This is the oldest species of *Concavocycloides* and still strongly resembles *Sievertsia*. The strong porosity of the skeleton hinders recognition of the facet canals, though in fractured specimens their presence can easily be detected. Absence of a crown is a primitive character. Profile of the marginal plates is typical for this evolutionary lineage. Bar-shaped wings did not allow for such an isolation of neighbouring marginals as can be observed in the younger species. On the smooth ventral side are blade-shaped attachment fields of the adductor muscles.

Occurrence. — Only known from the type locality.

Concavocycloides frasniensis sp. n.
(Pl. 9: 23; Text-fig. 24A–C)

Holotype: GIUS 4-610 Szg./548/2, Text-fig. 24A.

Type horizon: Mid Frasnian, Early *Palmatolepis hassi* to Early *Palmatolepis rhenana* Zones.

Type locality: Layer W6 of Szczukowskie Górki, Holy Cross Mountains.

Derivation of the name: From Latin *frasniensis* – in reference to the age of the species.

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)			
Number of specimens	Features	Holotype	Minimum	Mean	Maximum
Marginals with 1 cupules: 9	Length	1655	1000	1300	1655
	Breadth	1315	575	920	1315
	Height	1255	1010	1120	1255
	Length of crest	1170	880	1020	1170
	Breadth of crest	630	320	540	630
	Length of cupule zone	855	440	680	855
	Breadth of cupule zone	1285	590	845	1285

Diagnosis. — Marginals with large, rectangular wings. Apertures always with two clearly marked facet canals on the ventral side which open into a weakly to strongly marked crown lacking a central depression. Apertures at the centre of the crown are either irregular or in a meandering arrangement.

Description. — Marginals. The marginals are either rectangular or square in outline, and usually longer than broad, but occasionally as broad as long. Breadth is approximately equal to height. The specimens with a single radial process are narrow and elongated. The crest is concave in its axial part. Cupule zones are bordered by lateral walls. On the lateral articulation surface there are from five to seven teeth and alveolae. Lateral striae are best developed proximally. Radial processes are well marked, one or two in number. A crescentic facet is well developed only in specimens with two radial processes (Pl. 9: 23). The radial duct is almost circular and has a large lumen. On the dorsal surface varied sculpture can be seen; it may be porous and the crown not very distinct (Text-fig. 24B) or its surface may be covered with fine granules and the crown very well marked. Marginals with a single radial process lack crescentic facets, and elements of the lateral surface, including the wings, are weakly developed. Other features are typical of the genus. Other elements have not been recognised. The whole organisms might attain ca. 17 mm in diameter, their marginal ring might contain about 60 marginals.

Remarks. — This species is the most advanced in its lineage with the largest wings. The diversified sculpture of its dorsal surface is characteristic and unique.

Occurrence. — Only known from the type locality.

Concavocycloides givetiensis sp. n.
(Pl. 9: 18–21; Text-figs 22D–Q, 23A–AF)

Holotype: GIUS 4-564 Mrz./489/1, Text-fig. 22D.

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 *givetiensis* – in reference to the age of the species.

Material. — Number of specimens and dimensions:

Material		Dimensions (µm)			
Number of specimens	Features	Holotype	Minimum	Mean	Maximum
Marginals with 1 cupule: 77	Length	1305	510	950	1760
	Breadth	745	410	560	1425
	Height	970	810	950	1010
	Length of crest	560	270	595	850
	Breadth of crest	355	200	340	355
	Length of cupule zone	660	290	340	1050
	Breadth of cupule zone	900	150	745	1190
Radials: 115	Length	–	865	880	1050
	Breadth	–	525	745	1085
Interradials: 64	Length	–	525	845	930
	Breadth	–	540	760	1390
Frontal plates: 12	Height	–	745	750	760
	Breadth	–	575	590	610

Diagnosis. — Marginals with large, sharply terminated wings. Apertures of facet canals on the ventral side are well marked and open into a distinct central depression of the crown with few pores.

Description. — Marginals. Specimens with a single radial process are narrow and highly elongated. The smooth, spool-shaped crest is concave axially (Text-fig. 22N–Q). The cupule zone has well-marked lateral walls. The lateral articulation surface has from three to seven distinct teeth and alveolae. Lateral striae are numerous at the lateral edge, and, occasionally, at the lateral face of the crest (Text-fig. 22D). One lateral face usually has two winglets, the other just one, the latter penetrating between the two neighbouring winglets. Radial processes are well developed, one to three in number, and pierced by three to seven facet canals. The crescentic facet of the dorsal surface is well marked only in specimens with two radial processes. The radial duct is either oval or irregular and its lumen large. The dorsal surface is covered by pustules of various shape, if they are high then they are pillar-shaped. This species has a very characteristic and well marked crown, surrounding the central depression. Within the latter are isolated or grouped pores, in irregular, meandering or rosette-shaped arrangement (Pl. 9: 20–21; Text-figs 21A, B, C; 22D, G–M). Marginals with a single radial process have a low lateral wall and the wings are very well marked. Lateral striae of the crest are very deep and connect with each other on the ventral side. They lack the crown, thus sculpture of the dorsal surface, if present, is in the form of tubercles only (Text-fig. 22E). Other features are typical of the genus.

Radials. The plates are flat, usually with six processes, occasionally with five or fewer (Pl. 9: 18; Text-fig. 23A, B). The two lateral processes by the radial duct, commonly the narrowest of all and almost parallel to each other. The radial duct is narrow and straight, shallowing distally. Lateral processes thin laterally and are arranged perpendicularly to the plate. They can also be narrow and wing-shaped. The distal part is expanded, with occasionally an additional pair of processes. In the latter case the four outgrowths border the semicircular incision, which played the role of a sutural pore. The radial duct was covered in life by a cover plate. On the dorsal side the plates are smooth. Plates close to the peristome have a broader distal part and asymmetrical processes (Text-fig. 23C–O).

Interradials. These plates are flat and usually X-shaped. Flat and usually butterfly-shaped processes flank the fragments of the sutural pores, which are usually semicircular in shape (Pl. 9: 19; Text-fig. 23P–AD).

Frontal plates. These elements are rectangular, their outer surface porous, the internal one has a groove, flanked by two ridges, probably acting as muscle attachment sites (Text-fig. 23AE–AF). On the dorsal edge the ridges are expanded, for articular connection with the marginal plate. These plates always co-occur with the other elements described here.

Other elements were not recognised. The size of isolated elements suggests a total diameter for a complete specimen of about 12 mm; the marginal ring may be contained 36 marginals.

Remarks. — This is the most common species of *Concavocycloides* gen. n. found in residues. It differs from the other species by the sculpture of its dorsal surface, its sharply terminated wings, the presence of strong lateral striae on the crest and its spool-shaped crest. It differs from *Neocyclocystoides neocyclocystoides* in the shape of its marginal plates and the lack of sculpture on its crest.

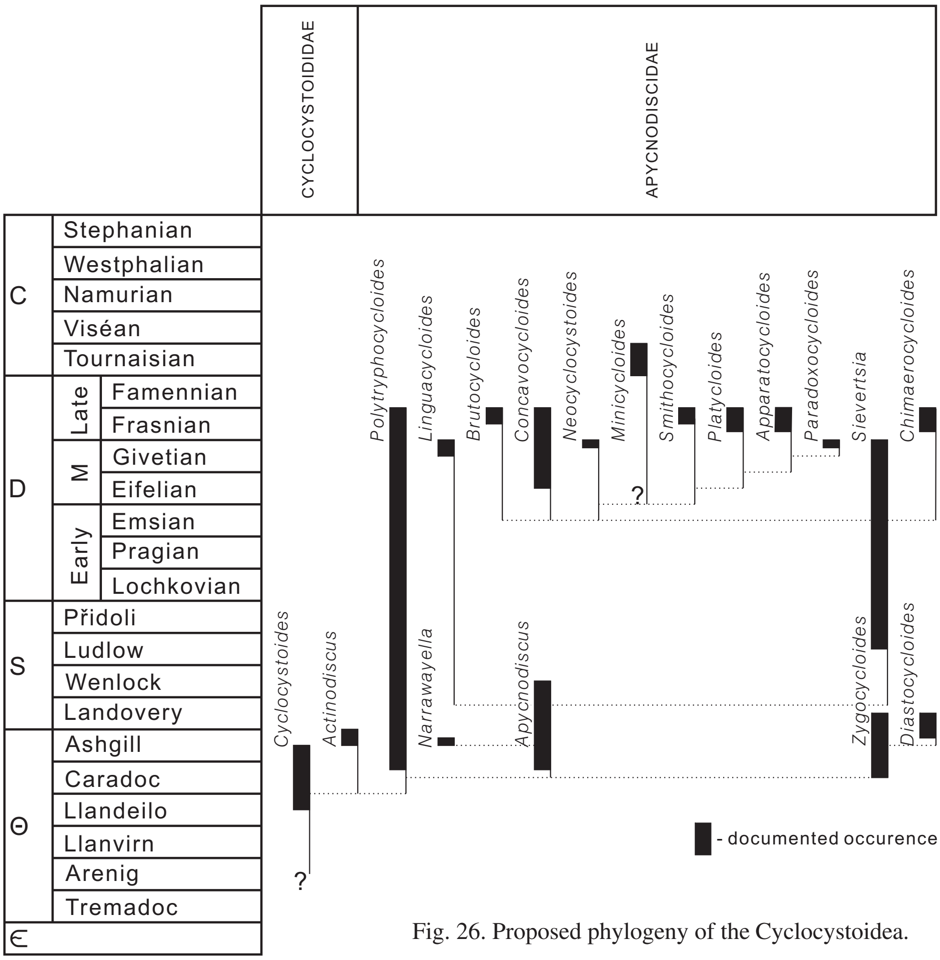


Fig. 26. Proposed phylogeny of the Cyclocystoidea.

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 *Brutocycloides* gen. n.

Type species: *Brutocycloides cerebrum* sp. n.

Derivation of the name: From Latin *brutus* – heavy, due to massive structure of its skeletal elements.

Diagnosis. — Large, massive marginals with one or two cupules, excavated at their centre, with weakly developed tubercles. Extremely numerous (up to 20) facet canals are well marked on the ventral side and open into a crown. Kidney-shaped elevated crown with complicated, meandering system of apertures.

Remarks. — The genus probably comes from the *Sievertsia concava* lineage, and is another genus in which apertures of the facet canals are displaced towards the central part of the plate and meandering in structure (Text-fig. 26). *Brutocycloides* shares a common ancestry with *Concavocycloides* as both have tubercles at the cupules. The dominating trend in *Brutocycloides* is a transformation of the internal architecture of the marginal plates.

Brutocycloides cerebrum sp. n.
(Text-fig. 24I–L)

Holotype: GIUS 4-610 Szg./542/1, Text-fig. 24I.

Type horizon: Mid Frasnian, Early *Palmatolepis hassi* to Early *Palmatolepis rhenana* Zones.

Type locality: Layer W6 of Szczukowskie Górki, Holy Cross Mountains.

Derivation of the name: From Latin *cerebrum*, – brain, as the crown surface is folded like a brain.

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)			
Number of specimens	Features	Holotype	Minimum	Mean	Maximum
Marginals: 5	Length	2350	1800	2075	2350
	Breadth	2850	1600	2280	2850
	Height	2550	2300	2570	2750
	Length of crest	2150	1500	1875	2150
	Breadth of crest	1000	900	970	1000
	Number of cupules	2	1	2	2
	Length of cupule zone	750	600	690	750
	Breadth of cupule zone	2550	1100	1850	2550
Radials: 14	Length	–	?	?	1220
	Breadth	–	?	?	900
Frontal plates: 8	Height	–	1230	1270	1310
	Breadth	–	800	1090	1340

Diagnosis. — As for the genus.

Description. — Marginals. Marginal plates are square in outline, when observed from the dorsal side. The crest is in the shape of a smooth, narrow, undercut cylinder, concave axially with a deep groove for the circumferential channel. On the lateral articulation surface there are numerous (up to 18) well developed teeth and alveolae. Lateral striae are absent. One or two of radial processes are usually only weakly developed. The dorsal crescentic facet is well marked and flanked by a V-shaped ridge (Text-fig. 24I–K). Very large, circular holes for the radial ducts do not correspond in number with the cupules, as in some specimens there is one cupule and two holes (Text-fig. 24J). From the distal side a V-shaped furrow connects the holes.

Radials. Radial plates are known only from fragments (Text-fig. 24L). In their proximal part they lack processes, and the radial groove is poorly marked. On the other hand the plates have three or four prominent lateral processes, arranged alternately, with hook-like curvature towards sthe exterior.

Frontal plates. Some boat-shaped plates (Text-fig. 25T–V) possibly belong to this species. Their outer surface is smooth or slightly porous; the more porous inner surface has a groove, flanked by two ridges, possibly muscle attachment structure sites. On the dorsal edge the ridges expand as an articulation surface to the marginal plates.

Other elements were not recognised. From the size of isolated elements the total diameter of whole the specimen is estimated as ca. 36 mm, and the marginal ring consisted of at least 45 elements.

Remarks. — The preservation of the material, at least of some surfaces, is very poor. Cyclocystoids whose marginals have almost parallel lateral surfaces must have contained very numerous marginalia and attained a relatively large size. The ossicles described here are quite unlike any species recognised so far. The specimens from Wietrznia are slightly smaller, and might suggest that the species attained a larger size in reefal environments, i.e. at Szczukowskie Górki. Difficulty with recognising the frontal plates (see above) is caused by the high species diversity of the Szczukowskie Górki assemblage. However, from their massive structure and large size, they most probably the plates belong to *Brutocycloides cerebrum* sp. n.

Occurrence. — Mid Frasnian: layer W6 of Szczukowskie Górki; Set D of Wietrznia II, Holy Cross Mountains, Poland.

Genus *Chimaerocycloides* gen. n.

Type species: *Chimaerocycloides chimaerus* sp. n.

Derivation of the name: From Greek *cimaira* – chimaera, horrific, due to atypical, strange shape.

Diagnosis. — Flat marginals of rectangular outline. Crest smooth, concave in its axial part, forming two hood-like overlaps laterally, oriented towards the proximal side.

Remarks. — The present form is possibly derived from *Sievertsia gotus*. Extreme flattening of the body, the secondary disappearance of tubercles from cupules, disappearance of sculpture from the ventral surface of the crest and the saddle-shaped form of the latter, are all new features in a history of the Devonian cyclocystoids (Text-fig. 26).

Chimaerocycloides chimaerus sp. n.
(Text-fig. 24L–M)

Holotype: GIUS 4-610 Szg./1133/1, Text-fig. 24L.

Type horizon: Mid Frasnian, Early *Palmatolepis hassi* to Early *Palmatolepis rhenana* Zones.
Type locality: Layer W6 of Szczukowskie Górki, Holy Cross Mountains.
Derivation of the name: From Greek *cimaira* – chimaera, horrific.

Material. — Number of specimens and dimensions:

Material		Dimensions (µm)			
Number of specimens	Features	Holotype	Minimum	Mean	Maximum
Marginals with 3 cupules: 1	Length	2255	2255	–	–
	Breadth	1630	1630	–	–
	Height	1085	1085	–	–
	Length of crest	1430	1430	–	–
	Breadth of crest	1260	1260	–	–
	Length of cupule zone	515	515	–	–
	Breadth of cupule zone	1370	1370	–	–
Radial plates: 1	Length	1285	1285	–	–
	Breadth	1170	1170	–	–

Diagnosis. — As for the genus.

Description. — Marginals. Plate longer than wide and wider than tall. Three cupules without tubercles are separated by two radial ridges. On the distal side the crest is strongly undercut by the groove for the circumferential channel (Text-fig. 24L). The lateral articulation surface has seven weakly marked teeth and alveolae, also present around the crest. Lateral striae are absent. Two broad, lobe-shaped radial processes are well marked, between which there occurs a U-shaped slit. Facet canals are fine and numerous (15); their apertures cannot be seen on the dorsal side. The crescentic facet is double and well marked. The radial ducts are large and circular, underlined on the proximal side by a groove. The dorsal surface is covered by numerous granules.

Radials. Radial plates are thick, uniformly flat, and with six processes. The two proximal processes are short and obliquely truncated dorsally (Text-fig. 24M), the two additional processes have the same truncation dorsally, and project laterally. The distal two processes are truncated ventrally and are separated by a U-shaped slit, as the marginalium. Such a pattern of truncation indicates ventral disc plates were imbricated. No radial duct could be detected. The sculpture on the dorsal side is granular and identical to that of the marginals, thus the absence of the annular plate seems quite probable.

Other elements were not recognised. The total diameter is estimated to have been close to *Sievertsia* (ca. 20 mm), but with more numerous plates in the marginal ring – about 40 marginals.

Remarks. — The species is somewhat similar to *Sievertsia gotus*, but differs in its lack of sculpture ventrally, development of sculpture dorsally and decrease in the number of cupules to three. Moreover, *Sievertsia* had brittle annular plates, possibly wholly absent in *Chimaerocycloides* gen. n., as indicated by the observation that sculpture over its dorsal surface of disc plates is identical to that of the marginals. Loss of the additional membrane was connected with the general flattening of body, compensated by thickening of plates of the ventral disc and tight juxtaposition of the latter, in an imbricating pattern. This must have led to a partial decrease in flexibility. Large, truncated radial processes of marginal plates were covered in tesselate pattern of radial plates. Such contact of two kinds of plates was already noted by Regnéll (1945) in *Polytryphocycloides lindstroemi* (Regnéll, 1945).

Occurrence. — Only known from the type locality.

Cyclocystoidea *incertae sedis*

Juvenile marginal plates
(Text-fig. 25W)

Material. — Number of specimens and dimensions:

Material		Dimensions (µm)		
Number of specimens	Features	Minimum	Mean	Maximum
Marginals with 1 cupules: 2	Length	750	825	895
	Breadth	380	400	420
	Height	215	220	225

Description. — Sledge-shaped element, with its flat region corresponding with the cupule zone, the latter with a central pore. Two distal processes correspond with the articulation area of the frontal plate. From the proximal side there are two, slightly larger processes, possibly initial radial processes; the walls diverging from the latter structure are an initial crest.

Remarks. — The plates may represent the juvenile marginals of *Concavocycloides givetiensis* sp. n.

Occurrence. — Late Givetian Early *Mesotaxis falsiovalis* Zone: trench II, layer W/6 at Marzysz, Holy Cross Mountains, Poland.

Subphylum **ECHINOZOA** Haeckel *in* Zittel, 1895
Class **OPHIOCISTIOIDEA** Sollas, 1899

In 1899 W.J. Sollas distinguished the ophiocistioids as a separate group of echinoderms and assigned them to the class Ophiuroidea. Later in 1912 W.J. Sollas jointly with I.B.J. Sollas elevated them to the rank of an independent class. At that time only three species were known, all from the Ludlow of Great Britain, each now types of the monotypic genera *Eucladia*, *Euthemon*, and *Sollasina* (Fedotov 1926; Sollas 1899; Woodward 1869). In 1930 Richter described the genus *Rhenosquama*, based on fragments of tube-feet, from the Late Eifelian Selscheid Beds of the Rhenish Slate Mountains.

The earliest ophiocistioids, *Volchovia* come from the Early Ordovician of St. Petersburg area (Gekker [Hecker] 1938, 1940) and Norway (Regnéll 1948) and from the Late Ordovician of Ohio (Ubaghs 1966). *Volchovia* is so peculiar in structure that for years it was considered to represent the eocrinoid *Rhipidocystis* (Ubaghs 1966; Jaekel 1901, 1918). Schuchert (1915) described a Devonian ophiocistioid based on enigmatic and poorly preserved remains, altered also during preparation (Haude and Langenstrassen 1976b) and unsuitable for identification (Ubaghs 1953, 1966). Quite commonly the dispersed fragments of ophiocistioids were identified as holothurian sclerites (Croneis and McCormack 1932) or even as echinoids (Spandel 1898; *vide* Boczarowski 1997b). Examples of these misassignments include *Microantyx* from the Permian of Kansas (Kornicker and Imbrie 1958), Devonian of Germany (Beckmann 1965), and Namurian of Slovakia (Kozur *et al.*, 1976), or *Protocaudina* (described as *Microantyx* by Boczarowski 1997b) from the Carboniferous of Poland (Alexandrowicz 1971), Indiana, Montana, Missouri (Gutschick 1959; Gutschick *et al.* 1967), and China (Ding 1985; Zhang 1987). The two studies of Haude and Langenstrassen (1976a, b) marked a turning point. They not only reviewed all the taxa known but also described complete specimens of *Rotasaccus* from the Early Devonian of Germany and *Anguloserra thomasi* Haude *et* Langenstrassen, 1976 from the Early Carboniferous of Germany (Haude and Thomas 1994; *vide* Boczarowski 1997b). Langer (1991) described the genus *Linguaserra* from the Early Givetian of Rhenish Slate Mountains, as well as sclerites and goniodonts of the other ophiocistioids, some of the latter classified as holothurian sclerites. Another important contribution concerns the complete specimens of *Gillocystis* from the Early Devonian of Humevale Formation, Australia (Jell 1983). Ebner and Fenninger (1980) illustrated specimens from clasts of Devonian limestones found in the Carboniferous molasse (Westphalian D) of Falcovec, Bulgaria. Although in general ophiocistioids are considered to be uncommon (Ubaghs 1953, 1966), in my material their remains are ubiquitous in the open-marine Devonian, and not only in the Holy Cross Mountains. Taxonomic revision of wheel-shaped sclerites of Ophiocistioidea and Holothuroidea has been published earlier (Boczarowski 1997b).

Family **Sollasinidae** Fedotov, 1926

Remarks. — Ophiocistioids in this family display an evolutionary increase in the number of tube-feet within a single ambulacrum, from four to six in *Euthemon*, six to eighth in *Sollasina*, and up to 15 in *Gillocystis* (Cuénot 1948; Jell 1983). Moreover, *Gillocystis* has the largest perradial plates. The only representative of the Eucladiidae, *Eucladia*, also has a large number of tube-feet per ambulacrum (12–14 according to various authors: Cuénot 1948; Ubaghs 1953, 1966). Most probably *Eucladia*, like *Gillocystis*, derived from *Sollasina*. Eucladiidae differ from Sollasinidae also in the number of plates surrounding the peristome, 20 in Eucladiidae, 15 or 16 in Sollasinidae. A general trend can also be observed in the entire group towards a greater number of plates composing the test, allowing for more flexibility of the body. On the other hand, in contrast to Rotasacciidae, their body wall incorporated multiangular plates, unconnected by sutures, like primitive echinoids. Rotasacciidae, have sclerites instead of plates, like Holothuroidea. Generally the whole group is in the intermediate position between echinoids and holothurians, justifying their classification into a common systematic unit (Haude and Langenstrassen 1976a, b). Most probably the three groups shared a common ancestor.

Genus *Sollasina* Fedotov, 1926

Type species: *Sollasina woodwardi* (Sollas, 1899).

Sollasina minima (Romanek, 1984)
(Pl. 9: 1; Text-fig. 27C)

1980. Goniodonten; Ebner and Fenninger, p. 7, Taf. 4: 5, 6.
1984. *Cardioserra minima* gen. n., sp. n.; Romanek, pp. 550–551 (partim), Tab. I: 2, 4, 5 (non 1, 3).

Holotype: Romanek 1984: Tab. I: 5.
Type horizon: Early Eifelian, Set VIII of the Grzegorzowice Beds.
Type locality: Grzegorzowice, Holy Cross Mountains.

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)			
Number of specimens	Features	Battery	Minimum	Mean	Maximum
Goniodonts: 88	Length of tooth	1710	?	?	?
	Breadth of tooth	1965	?	?	?
Battery: 1	Height of tooth lamina	980	870	910	930
	Length of tooth flank	1745	?	?	?
	Height of main denticle	155	100	150	170
	Breadth of main denticle	110	100	110	115
	Max. height of side denticles	145	65	140	150
	Distance between denticles of two subsequent goniodonts	180	?	?	?

Emended diagnosis. — Both distal and proximal margins of goniodonts almost straight V-shaped. The main denticle larger and broader than in remaining denticles. Lateral denticles numerous (26–44), becoming smaller and smaller. The tooth lamina slightly vaulted. The impressions of earlier generation teeth distinct.

Remarks. — The ophiocistioid remains described by A. Romanek (1984) unequivocally belong to two taxa. The holotype of *Cardioserra minima* is incomplete, so diagnosis of *Cardioserra* must be based on the paratype of Romanek (1984: p. 550, tab. I, fig. 1). This differs from the holotype of *S. minima* both in outline of goniodonts and development of teeth. In the type horizon and type locality the relatively large and brittle goniodonts of *C. minima* occur as fragments of various size, from which the reconstruction is based. *C. minima* occurs also in the underlying topmost Emsian at the type locality, where not only numerous tooth fragments, but also complete tooth batteries (Pl. 9: 1) were found. The goniodonts from both levels are of the same species. These elements of the ophiocistioid sclerotome have not been collected either above the Eifelian or from the roughly coeval strata of the Kielce and Zbrza Devonian, though this may be due to poor sampling. On the other hand *Erisserra romaneki* also occurs in the *Polygnathus partitus* Zone (*Chimaerothyris dombrowiensis* Zone, the earliest Eifelian) of the Ogrodzieniec IG 2 borehole (Upper Silesian Massif) and in Zbrza.

Occurrence. — Devonian: clasts of limestones in the Carboniferous molasse (Westphalian D) at Falcovec, Bulgaria. Late Emsian: Set V of the Grzegorzowice Beds at Grzegorzowice. Early Eifelian: *Polygnathus partitus* Zone, Set VIII of the Skały beds at Grzegorzowice; brachiopod *Polygnathus partitus* Zone at Zbrza, Holy Cross Mountains, Poland.

Sollasina westfalica (Richter, 1930)
(Text-fig. 30M–O)

1930. *Rhenosquama westfalica* n. sp.; Richter, pp. 286–295, text-figs 2–4, 7.
1966. *Rhenosquama westfalica* Richter; Ubaghs, p. U187, text-fig 139.
1976b. (?) *Sollasina westfalica* (Richter); Haude and Langenstrassen, p. 147, text-fig 13B.

Holotype: Richter 1930: text-figs 2–3.
Type horizon: Early Eifelian, Selscheid Beds.
Type locality: Ebbelinghausen, Rhenish Slate Mountains, Germany.

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)		
Number of specimens	Features	Minimum	Mean	Maximum
Scale plates: 210	Length	390	550	660
	Width	590	690	845

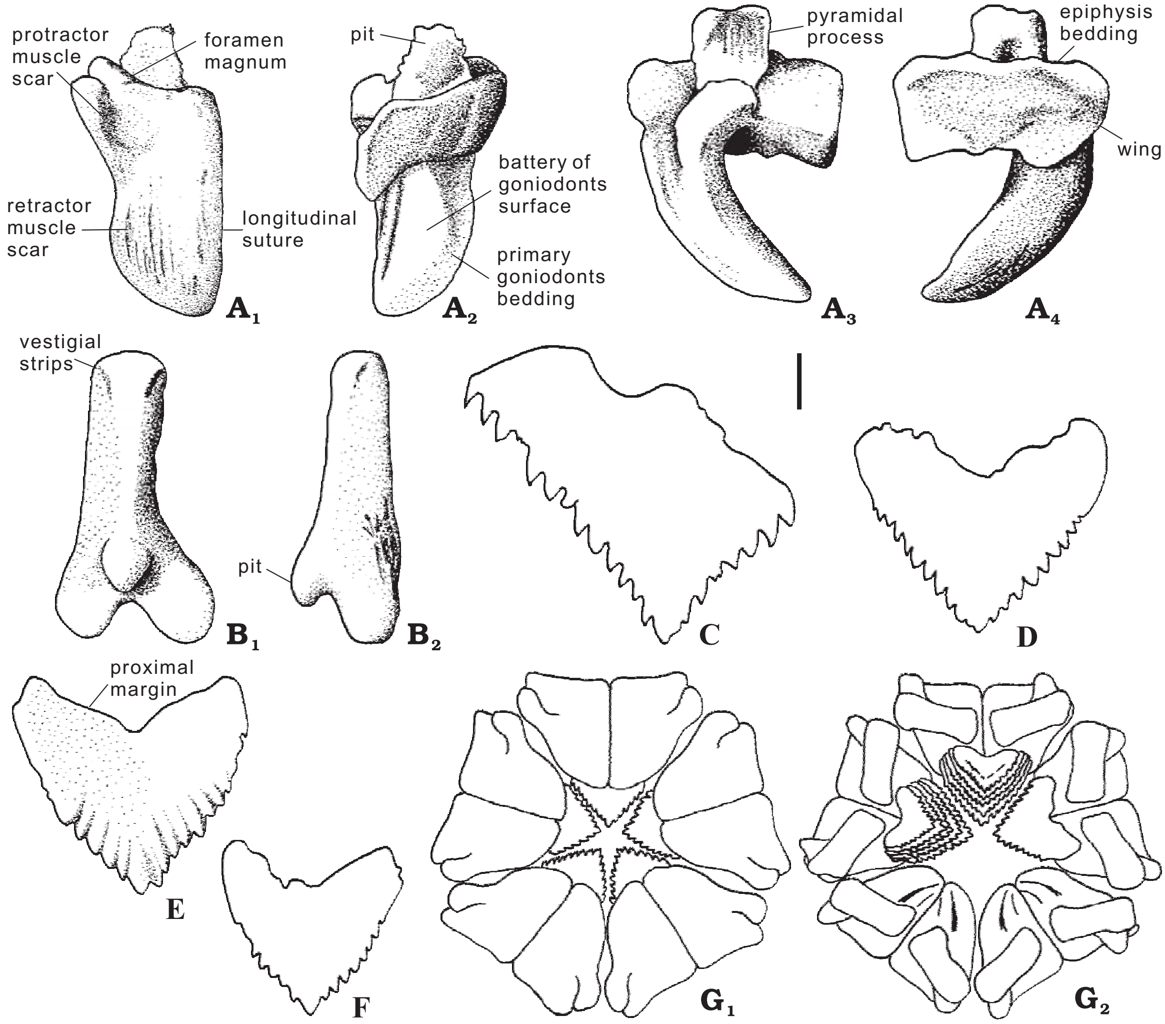


Fig. 27. Ophiocistioid skeletal elements from the earliest Eifelian *Chimaerothyris dombrowiensis* horizon, set VIII, sample P4/1 from roof of J. Malec pit at Grzegorzowice, Holy Cross Mountains. **A**, **B**, **D**–**G**. *Erisserra romaneki* sp. n. **A**. Demipyramid GIUS 4-618 Grz./429/1; A_1 external face, A_2 inner face, A_3 internal face, A_4 interpyramidal face. **B**. Rotula GIUS 4-618 Grz./396/1; B_1 oral surface, B_2 lateral side. Adaxial end is on the bottom of the figure. **D**–**F**. Goniodonts. **D**. GIUS 4-618 Grz./378/2, outer view. **E**. GIUS 4-618 Grz./378/3, inner view. **F**. Juvenile specimen GIUS 4-618 Grz./378/4, outer view. **G**. Reconstruction of the pyramid with teeth; G_1 oral view, G_2 apical view (not to scale). **C**. *Sollasina minima* (Romanek, 1984), goniodont GIUS 4-618 Grz./378/1, outer view. Scale bar 200 μm.

Remarks. — In addition to scales from tube-feet, fragments of goniodonts have been found presumably belonging to the same species. Very numerous and well preserved flat scales from the tube-feet, collected in the clay-rich carbonate deposits at Skały, do not differ significantly from the material described from elsewhere (see Haude and Langenstrassen 1976b; Richter 1930; Ubaghs 1966). In section they thicken distally. They are terminated by a single short and flattened spine or sometimes two spines (Text-fig. 30M–O). The scales of the tube-feet are somewhat broader, larger and more strongly flattened when compared to the type material of *Sollasina* (Haude and Langenstrassen 1976b).

Occurrence. — Early Eifelian: Selscheid Beds at Ebbelinghausen, Rhenish Slate Mountains, Germany. Late Eifelian: Sets XVI, XVII, XVIII of the Skały Beds at Skały, Holy Cross Mountains, Poland.

Family **Rotasacciidae** Haude *et* Langenstrassen, 1976

Remarks. — These ophiocistioids somewhat resemble echinoids in their body shape, orientation, geometry and above all, presence of an Aristotle's lantern. The sclerites from the body wall are wheel-shaped, similar to those of some holothuroids (e.g. Chiridotidae). On the other hand the skeletal bodies from tube-feet are similar to perforate plates – elements typical also of the Holothuroidea. These similarities were the reason of frequent confusion of the scleritomes of Holothuroidea and Ophiocistioidea.

Genera included. — *Rotasaccus* Haude *et* Langenstrassen, 1976; *Microantyx* Kornicker *et* Imbrie, 1958 emend. Boczarowski, 1997; *Pararotasaccus* Kozur *et* Mostler, 1989; *Protocaudina* Croneis, 1932 emend. Boczarowski, 1997.

Genus *Microantyx* Kornicker *et* Imbrie, 1958 emend. Boczarowski, 1997

Type species: *Microantyx permiana* Kornicker *et* Imbrie, 1958.

Microantyx praedulcis sp. n.
(Pl. 9: 6–7; Text-fig. 30P–Q)

Holotype: GIUS 4-671 Ska./791/2, Pl. 9: 6.

Type horizon: Late Eifelian, Set XVIII of the Skały Beds, *Tortodus kockelianus* Zone.

Type locality: Skały, Holy Cross Mountains.

Derivation of the name: From Latin *prae* – before, *dulcis* – sweet, nice.

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)			
Number of specimens	Features	Holotype	Minimum	Mean	Maximum
Rotulae: 3	Length	–	880	945	1000
	Width	–	270	320	440
Wheels: 27	Diameter	395	340	380	395
	Width of button	285	230	275	285
Sieve plates: 49	Length	–	220	485	655
	Width	–	190	325	415
Madreporites: 1	Diameter	–	560	–	–
	Height	–	335	–	–

Diagnosis. — Sclerites from the body wall have alternating pores centrally; along their longer axis are two large oval pores, with two smaller and drop-shaped pores along their shorter axis.

Description. — Aristotle's lantern. Rotulae are Y-shaped, their adaxial end is split into two lobes, separated by a groove; on the oral surface there are shallow depressions of paired inner fossa, this part being relatively flattened compared to the rest of the element. The lateral sides of the adaxial part has shallow depressions (sites of attachment for the interior rotular muscles) and more delicate, elongated furrows (for the exterior rotular muscles; Text-fig. 30P). The element is narrowest, midlength and here becomes triangular in section.

Madreporites. The outer side of this plate is mushroom-shaped, surrounded by a collar, and ornamented by ribs and furrows. Externally there are eleven pores while only five on the inner side; also four furrows and two wrinkles, joined axially. The plate is strongly perforated (Text-fig. 30Q).

Sclerites. The sieve plates from the tube-feet are in the form of a straight or bifurcated blade with simple perforations. The marginal zone of the plate is broad. Pores are of unequal size, the largest being at the margins. (Pl. 9: 7).

Plates from the body wall are circular or oval. In the marginal zone there are ten oval pores. The hub is oval in outline and flat. The arches of the central cross are not perpendicular but form an angle 65–70°. Bars of the arches are flat, becoming thickened at their intersection. Flat spokes separate marginal zone pores. The pores are of similar diameter to the larger pores of the central zone. The marginal ring is broad, duplicated towards the bottom and thinning towards the centre. The ventral button is cone-shaped, with weak concentric rings (Pl. 9: 6).

Remarks. — The general similarity of this madreporite to the ones discovered in complete specimens of ophiocistioids (cf. Haude and Langenstrassen 1976b) allows its placement into family Rotasacciidae. This is the only species of the family found in at Skały (sets XVII, XVIII). Rotulae, when compared with those from *Rotasaccus*, do not have the central groove at the oral surface, although the general outline is typical of the genus. Plates from the tube-feet have the broadest marginal zone of the species (*Ornatoserra* gen. n., *Rotasaccus*), where the structure could be observed. Moreover, the ratio of branched vs. straight forms is the highest. This species differs from *Protocaudina dulcis* in the structure of its wheels; pores at the centre of a sclerite are oppo-

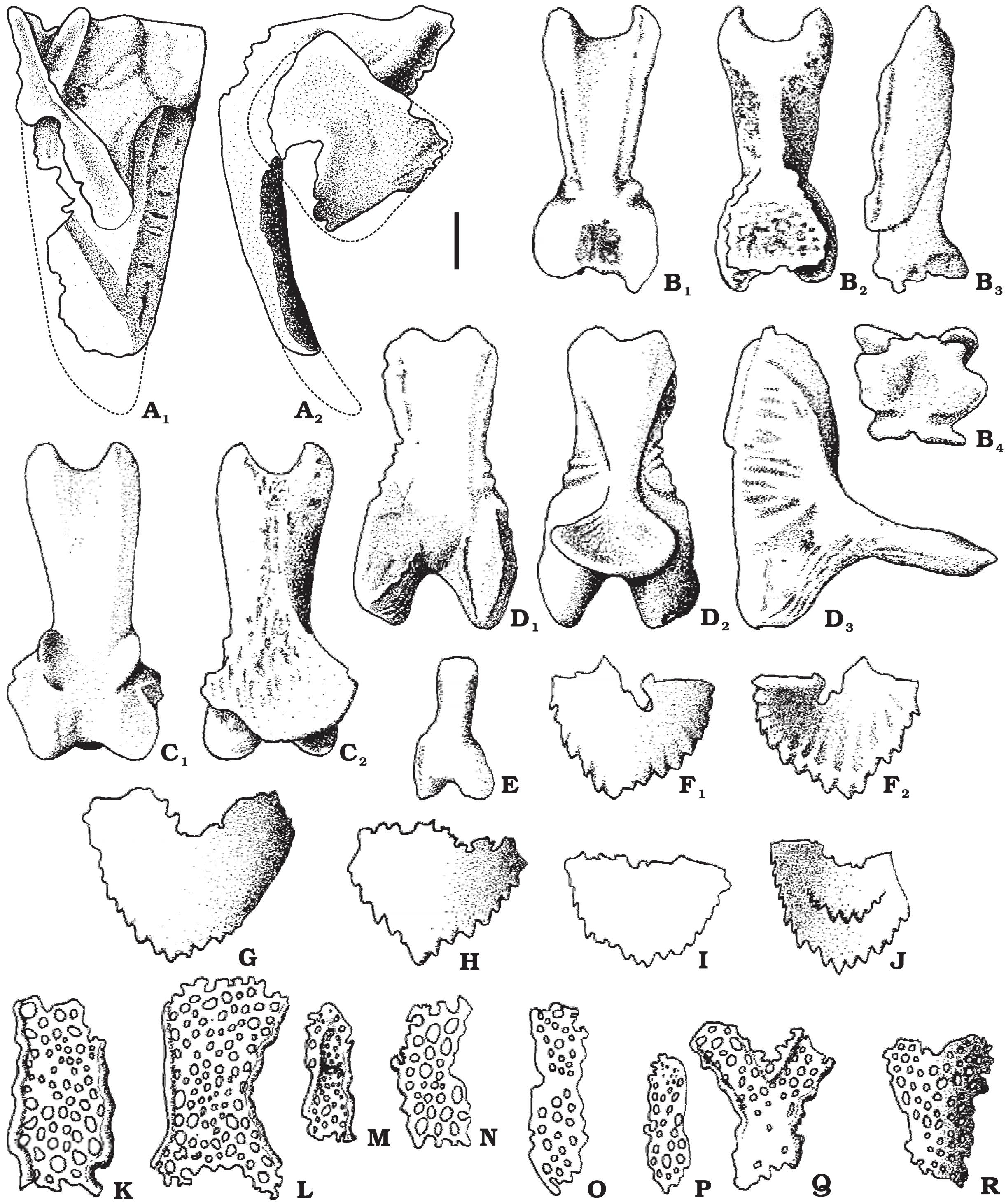


Fig. 28. *Ornatoserra ovalis* sp. n. from the Late Givetian, set C of Sowie Górki, Holy Cross Mountains. **A**. Demipyramid GIUS 4-744 Sow./693/1; A_1 inner face, A_2 interpyramidal face, apical view. **B**. Rotula GIUS 4-746 Sow./680/1; B_1 apical view, B_2 oral view, B_3 lateral side view, B_4 adaxial view. **C**. Rotula GIUS 4-746 Sow./680/2; C_1 apical view, C_2 oral view. **D**. Rotula GIUS 4-747 Sow./716/1; D_1 apical view, D_2 oral view, D_3 lateral side view. **E**. Rotula GIUS 4-746 Sow./680/3, apical view. **F**–**J**. Goniodonts. **F**. The holotype GIUS 4-747 Sow./698/1; F_1 outer view, F_2 the same, inner view. **G**. GIUS 4-747 Sow./698/2, outer view. **H**. GIUS 4-747 Sow./698/3, outer view. **I**. GIUS 4-747 Sow./698/4, outer view. **J**. GIUS 4-747 Sow./698/5, inner view of goniodont battery. **K**–**R**. Sieve plate from tube foot. **K**. Simple form with marginal callosity, GIUS 4-746 Sow./705/1. **L**. Simple form with bifurcate end and marginal callosity, GIUS 4-746 Sow./705/2. **M**. Simple form with rounded end and marginal callosity, GIUS 4-746 Sow./705/4. **N**. Simple form without marginal callosity, GIUS 4-747 Sow./699/1. **O**. Similar form GIUS 4-747 Sow./699/2. **P**. Specimen GIUS 4-747 Sow./699/3. **Q**. Form with Y-shaped end and marginal callosity, GIUS 4-746 Sow./705/3. **R**. Form with Y-shaped end and without marginal callosity, GIUS 4-747 Sow./699/4. Scale bar 200 μm.

site, spokes are wider, and the ring is broader. Moreover, they have ten and not eight marginal pores. *Rotasaccus* differs from *M. praedulcis* in having four pores at the hub of its wheels.

Species included. — *Microantyx permiana* Kornicker *et* Imbrie, 1958 (non: Beckmann 1965, Mostler 1971d, Kozur *et al.* 1976, Langer 1991; see Boczarowski 1997b); *Microantyx praedulcis* sp. n.

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

Genus *Protocaudina* Croneis, 1932 emend. Boczarowski, 1997

Type species: *Cheirodota*(?) *traquairii* Etheridge, 1881.

Remarks. — Croneis designated *Cheirodota*(?) *traquairii* Etheridge, 1881 as the type of his genus *Protocaudina* (Croneis in Croneis and Mc Cormack 1932) and subsequently various authors have described more species of *Protocaudina*. However, as demonstrated by Gilliland (1993) only the type species of *Protocaudina* is based on ophiocistioid sclerites. In the original illustration of Etheridge (1881) only one side of the type specimen is presented. On the opposite side, however, there is a characteristic, and diagnostic ventral button (cf. Gilliland 1993; Boczarowski 1997b). *Protocaudina* is very similar to *Microantyx* Kornicker *et* Imbrie, 1958 (see Text-fig. 31; Boczarowski 1997b), differing from the latter in the number of its marginal pores and the development of its central zone. The specimen from the Early Carboniferous of Utah, illustrated by Sandberg and Gutschick (1984), and assigned to holothurian species *Rota campbelli*, is also a sclerite of *Protocaudina*.

Species included. — *Protocaudina traquairii* (Etheridge, 1881), *Protocaudina botoni* (Gutschick, 1959) of Ding (1985), Gutschick (1959), Gutschick, Canis and Brill (1967), Frizzell and Exline (1966), but not of Alexandrowicz (1971) and Mostler (1971d), *Protocaudina sosioensis* (Kozur *et* Mostler, 1989), *Protocaudina tarazi* (Mostler *et* Rahimi-Yazd, 1976); *Protocaudina dulcis* sp. n. (see Boczarowski 1997b).

Protocaudina dulcis sp. n.
(Pl. 9: 10–12; Text-fig. 29A–J)

Holotype: GIUS 4-584 Mrz./244/3, Text-fig. 29E.

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 *dulcis* – sweet, nice.

Material. — Number of specimens and dimensions:

Material		Dimensions (µm)			
Number of specimens	Features	Holotype	Minimum	Mean	Maximum
Goniodonts: 270	Length of tooth	845	490	770	1320
	Breadth of tooth	985	455	840	1730
	Height of tooth lamina	475	320	460	540
	Length of tooth flank	730	475	705	1355
	Height of main denticle	50	35	45	85
	Breadth of main denticle	50	35	45	100
	Max. height of side denticles	70	15	60	100
	Distance between denticles of two subsequent goniodonts	170	70	155	220
Pyramids: 6	Height of demipyramid	–	980	1190	1220
	Width of demipyramid	–	360	530	540
Wheels: > 1000	Diameter	–	160	190	220
	Width of button	–	45	50	60
Sieve plates: 98	Length	–	220	390	680
	Width	–	290	295	305

Diagnosis. — Heart-shaped goniodonts with strongly incised distal margin, margins straight; narrowed, rounded corners. Hubs in shape of a star, narrow, thin and flat. The arches of the central cross thin, oval in section and intersect perpendicularly, to forming a short common bar separating the four central pores where they intersect. There are eight pores of more or less triangular outline (occasionally fully oval), separated by flat spokes in the marginal zone. These pores are significantly larger than those of the central zone.

Description. — Aristotle's lantern. Goniodont tooth lamina is flat, side denticles (from 20 to 40 and more), diminish in size towards the axis.

Demipyramid of the Aristotle's lantern spade-shaped and narrow adorally. Retractor muscle scars are visible as fine longitudinal furrows on the outer surface, but the protractor muscle scar is shallow, almost indistinct, with transverse wrinkles. Foramen magnum shallow, arch-shaped, small and weakly marked and is displaced towards centre. Longitudinal suture between demipyramids very long and straight. Epiphyses attachment short and straight. Wing normal, rectangular, covered with fine ribs. This area is flat with two distinct fields in larger specimens. The crest pit is triangular in outline and shallow. Pyramidal process thick and perpendicular. Goniodonts battery surface without sulcus dentalis. On the ventral side, at the axis of the longitudinal suture between demipyramids, there occur two grooves and two rims for each demipyramid, radially arranged from the oral point. On the outer edges there occur indistinct arches of the primary (the oldest) goniodonts attachment in the battery (Text-fig. 27A).

Sclerites. Sieve plates from the tube-feet form blades; they are straight, delicate, non-branched and simply perforated. Marginal zone of the plates narrow; the plates are known only from broken fragments.

The wheels are circular or oval. Pores of the central zone alternate with two small pores, along the long axis and two larger ones along the minor axis; all of them are triangular in shape. In some specimens the pores may be oval (Text-fig. 29H). The marginal ring is narrow, bar-shaped, with slight duplication at the bottom. Ventral button of typical conical shape, covered by well marked concentric rings. Other elements could not be identified.

Remarks. — This species is possibly derived from *Microantyx praedulcis* sp. n. (Text-fig. 31). This is indicated by the structure of wheels from the body wall. One can observe a decrease in pore number in the marginal zone, from ten (*Microantyx praedulcis* sp. n.) to eight (*Protocaudina dulcis* sp. n.). While this reduction was taking place the *Rotasaccus* lineage split from *Microantyx*, with nine marginal pores in both small and large wheels (cf. Haude and Langenstrassen 1976b). Moreover, in *Rotasaccus* the three central pores are separated by three arches. *Protocaudina dulcis* sp. n. differs from *Microantyx praedulcis* in the development of central pores – central pores are centred opposite to marginal pore centres, whereas in *Microantyx praedulcis* central pore centres are placed opposite to spokes.

Romanek (1984) mentioned Marzysz as a locality where his *Cardioserra minima* had been collected, but this was probably based on goniodonts of other ophiocistioids. In ontogenetic series of goniodonts of *Protocaudina dulcis* sp. n. (Text-fig. 29C–F) the juvenile forms are very similar to those of *Erisserra romaneki* sp. n., as they are heart-shaped. The adult specimens do not display this shape.

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

Genus *Rotasaccus* Haude *et* Langenstrassen, 1976

Type secies: *Rotasaccus dentifer* Haude *et* Langenstrassen, 1976.

Species included. — *Rotasaccus dentifer* Haude *et* Langenstrassen, 1976 (Haude 1983; Haude and Langenstrassen 1976, 1991; Langer 1991); *Rotasaccus praedentifer* sp. n., *Rotasaccus haudei* sp. n.

Rotasaccus praedentifer sp. n.
(Pl. 9: 8)

Holotype: GIUS 4-708 Ska./741/1, Pl. 9: 8.

Type horizon: Early Givetian, Set XXV of the Skały beds, Early *Polygnathus varcus* Zone.

Type locality: Skały, Holy Cross Mountains.

Derivation of the name: From Latin *prae* – before, precedes the species *dentifer*, *dentifer* – teeth-bearing.

Material. — Number of specimens and dimensions:

Material		Dimensions (µm)			
Number of specimens	Features	Holotype	Minimum	Mean	Maximum
Wheels: 16	Diameter	195	180	195	205
	Width of button	80	75	80	85

Diagnosis. — Circular wheels with broad, flat stellate hub. In the marginal zone there are nine oval, or, more commonly, triangular pores.

Description. — Sclerites. Three flat bars, join at the centre of the wheel and separate three oval pores, crowning the void space of a ventral button. The flat spokes taper towards the marginal ring. The marginal pores are significantly larger than those of the central zone. The marginal ring is narrow, circular in section,

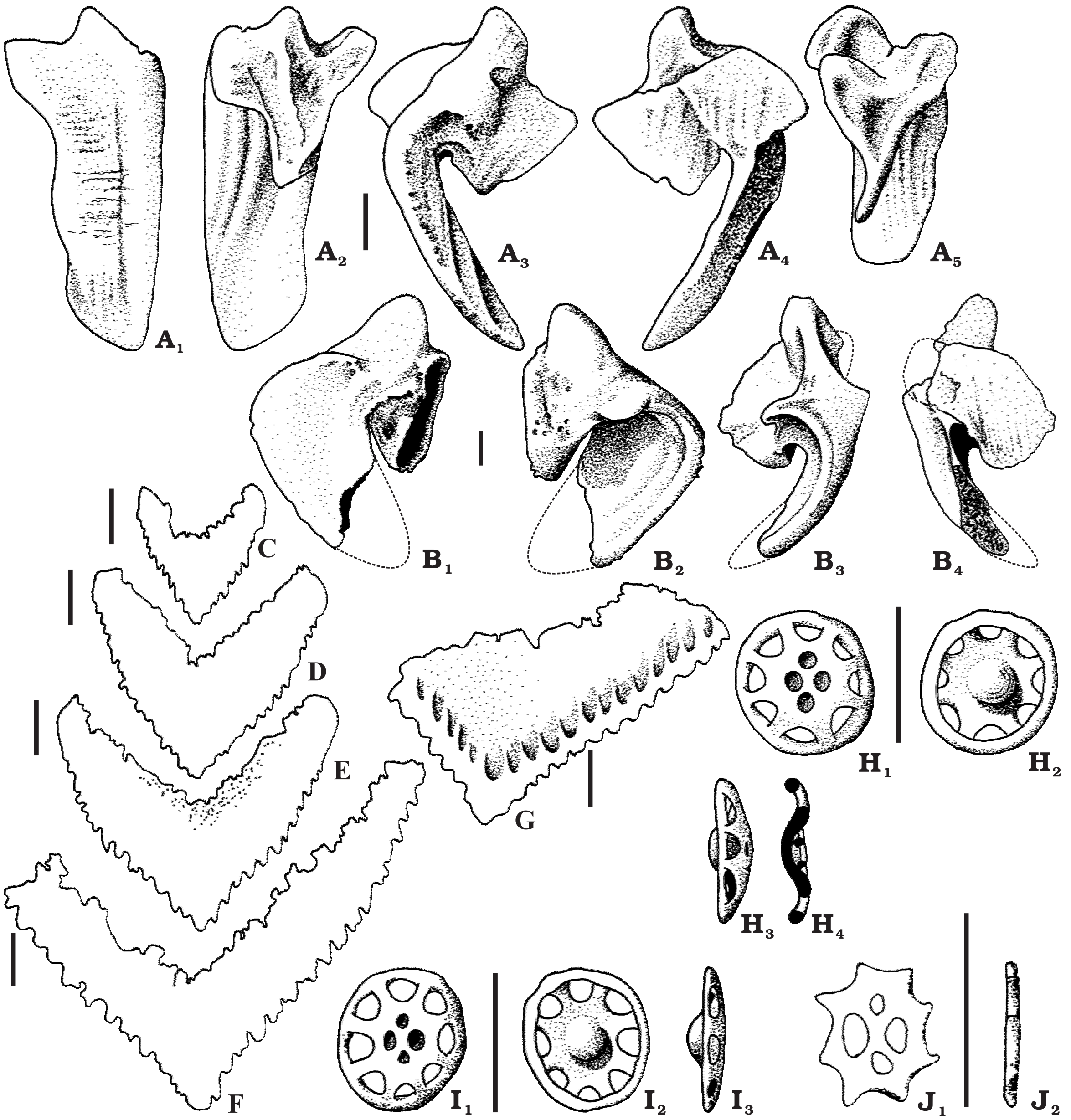


Fig. 29. *Protocaudina dulcis* sp. n. from the Late Givetian of Marzysz, Holy Cross Mountains; samples Marzysz II/13 (A, C–F, H–I), Marzysz II/W/0 (B), and Marzysz II/W/6 (G, J). **A**. Demipyramid, GIUS 4-584 Mrz./687/7; A_1 external face, A_2 inner face, A_3 internal face, A_4 interpyramidal face, A_5 apical view. **B**. Demipyramid GIUS 4-562 Mrz./147/1, oblique view. **C**–**G**. Goniodonts. **C**. GIUS 4-584 Mrz./244/1, outer view. **D**. GIUS 4-584 Mrz./244/2, outer view. **E**. GIUS 4-584 Mrz./244/3, outer view of the holotype. **F**. GIUS 4-584 Mrz./244/4, outer view. **G**. GIUS 4-568 Mrz./96/1, inner view. **H**–**J**. Wheels from body wall. **H**. GIUS 4-584 Mrz./245/1; H_1 central porous side, H_2 button side, H_3 lateral side, H_4 section. **I**. GIUS 4-584 Mrz./245/2; I_1 central porous side, I_2 button side, I_3 lateral side. **J**. Juvenile specimen GIUS 4-577 Mrz./97/1; J_1 central porous side, J_2 lateral side. Scale bar 200 μm.

without duplicature. The ventral button is typically cone-shaped (Pl. 9: 8). Other elements could not be identified.

Remarks. — This species differs from *Rotasaccus dentifer* in very narrow spokes and *Rotasaccus haudei* sp. n. in strongly elongated marginal pores.

Occurrence. — Only known from the type locality.

Rotasaccus haudei sp. n.
(Pl. 9: 9)

Holotype: GIUS 4-708 Ska./745/1, Pl. 9: 9.

Type horizon: Early Givetian, Set XXV of the Skały Beds, Early *Polygnathus varcus* Zone.

Type locality: Skały, Holy Cross Mountains.

Derivation of the name: In honour of R. Haude, the German student who, with F. Langenstrassen, described the complete specimens of the genus.

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)			
Number of specimens	Features	Holotype	Minimum	Mean	Maximum
Wheels: 42	Diameter	165	160	165	170
	Width of button	60	55	60	75

Diagnosis. — Wheels with a flat and broad, but rather small circular hub. In the marginal zone there are nine elliptical pores, significantly larger than the pores of the central zone.

Description. — Sclerites. Wheels most probably had three flat bars meeting centrally, separating three small, oval pores. In the material studied the lack of bars may be caused by their brittleness. Flat spokes expanding towards periphery separate the pores of the marginal zone. The marginal ring is as broad as the spokes and is duplicated on the underside. The ventral button is typically conical (Pl. 9: 9). Other elements could not be identified.

Remarks. — This species differs from all others by the extremely dense arrangement of pores in the central zone and also by the strongly elongated, elliptical pores of the marginal zone.

Occurrence. — Only known from the type locality.

Genus *Erisserra* gen. n.

Type species: *Erisserra romaneki* sp. n.

Derivation of the name: From Latin *eris* – breast, due to peculiar contour.

Diagnosis. — Small goniodonts with parabolic contour at the distal margin and only weakly incised, and wavy proximal margin. The teeth corners tapering and rounded. Goniodonts length exceeds width.

Remarks. — Judging from the similarity of structure of demipyramids and goniodonts the genus possibly shares a common ancestor with *Rotasaccus*. Although the latter is geologically younger, *Erisserra* gen. n. is the more primitive of the two.

Erisserra romaneki sp. n.
(Pl. 9: 2–5; Text-fig. 27A–B, D–G)

1984. *Cardioserra minima* gen. n., sp. n.; Romanek, pp. 550–551 (partim), Tab. I: 1, 3 (non 2, 4, 5).
non 1991. *Cardioserra minima* Romanek; Langer, p. 43, Taf. 3: 5.

Holotype: GIUS 4-618 Grz./378/10, Pl. 9: 2.

Type horizon: Early Eifelian, Set VIII of the Grzegorzowice Beds, *Polygnathus partitus* Zone.

Type locality: Grzegorzowice, sample P4/1 from the top of J. Malec trench, Holy Cross Mountains.

Derivation of the name: In honour of A. Romanek, a student of Devonian ophiocistioids, who was the first to illustrate these forms.

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)			
Number of specimens	Features	Holotype	Minimum	Mean	Maximum
Goniodonts: 298	Length of tooth	540	520	680	850
	Breadth of tooth	540	520	680	865
	Height of tooth lamina	445	430	540	610
	Length of tooth flank	400	380	420	460
	Height of main denticle	75	70	75	85
	Breadth of main denticle	60	55	60	85
	Max. height of side denticles	45	40	45	65
	Distance between denticles of two subsequent goniodonts	110	100	105	115
Pyramids: 15	Height of demipyramid	–	1000	1100	1220
	Width of demipyramid	–	545	550	595
Rotulae: 2	Length	–	980	1040	1100
	Width	–	510	550	595

Diagnosis. — As for the genus.

Description. — Aristotle's lantern. The main goniodont denticle is of similar height to the primary lateral denticles, or only slightly higher, but markedly broader. All the denticles are slightly elongated. Lateral denticles are not numerous (12–18); their size decreases abaxially. Tooth lamina slightly vaulted. On the inner side are furrows, beginning at the periphery at incisions between the lateral denticles (Pl. 9: 2–3; Text-fig. 27D–F).

Demipyramids are rounded and broad adorally. Retractor muscle scars are developed as elongated grooves on the outer surface; the protractor muscle scar is well-marked, oval and close to the abaxial margin. The foramen magnum is shallow and arch-shaped, the longitudinal suture long and straight. The epiphyses attachment area is also long, but wavy. The narrow, rectangular wing lacks fine ribbing but its surface is wavy. The crest pit is irregular and shallow. Pyramidal processes are thin and square-shaped. The goniodont battery surface does not form a sulcus dentalis. On the ventral side, parallel to the axis of longitudinal suture there are two grooves within each demipyramid, converging adorally. On the outer edges are the typical recurvate primary goniodont attachment surfaces (Pl. 9: 5a; Text-fig. $27A_2$). Text-fig. 27G presents an attempt to reconstruct the Aristotle's lantern of this ophiocistioid.

Rotulae are Y-shaped, with short, vestigial strips on the oral surface. The rotula is triangular in transverse section. On the adaxial end, which is split into two lobes, there is an oral process. The latter is ornamented only on its aboral side. Other elements could not be identified.

Remarks. — This species differs from the others by the small, parabolic outline of goniodont with weakly incised distal margin, and not numerous (12–18) denticles. The specimen of Langer (1991) unequivocally represents the same genus, but differs from *Erisserra romaneki* sp. n. in lacking tapering corners, having a shallower incision on the distal margin, and being shorter than wide. The main denticle in the only specimen he illustrated is as in *E. romaneki* similar in length to the lateral denticles, also it is broader than the latter and of triangular outline. Generally the main denticle in the specimens of Langer is broader and shorter than in the corresponding goniodonts of *E. romaneki.* The specimen under consideration somewhat resembles the goniodonts of *Ornatoserra ovalis* gen. et sp. n. Its shape is intermediate between the two species. The Langer's material came from the Early Givetian of Germany (Daasberg near Gerolstein, Rhenish Slate Mountains.).

Occurrence. — Early Eifelian *Polygnathus partitus* Zone: Set VIII of the Grzegorzowice Beds at Grzegorzowice, Zbrza; borehole Ogrodzieniec IG 2, depth: 1269.4 m, 1119.7 m, Cracow Upland, Poland. Late Eifelian: Set XIV of the Skały Beds at Skały, Holy Cross Mountains, Poland.

Genus *Longiserra* gen. n.

Type species: *Longiserra longa* sp. n.

Derivation of the name: From Latin *longus* – long, *serra* – saw.

Diagnosis. — Large, V-shaped goniodonts with elongated wings. Distal margin strongly incised; the rounded corners narrow towards terminations.

Remarks. — Similarity of goniodonts indicates that *Protocaudina dulcis* sp. n. may be ancestral to the genus. Though the juvenile goniodonts are heart-shaped, unlike those of *Erisserra*, they have a similar very deep distal incision. The other novelty is the thickening of single tooth laminae in *Longiserra* sp. n., which resulted in overall strengthening of its tooth. This might have been necessitated by thinning of the wings along whole the tooth, which presumably increased the risk of its breaking along its axial line. Although no complete teeth batteries have been found, the narrowing observed presumably led to an increase in the number of goniodonts in the oral apparatus.

Longiserra longa sp. n.
(Text-fig. 30H–L)

Holotype: GIUS 4-790 Tud./506/2, Text-fig. 30I.

Type horizon: Mid–Late Frasnian, Early *Palmatolepis hassi* to Early (Late?) *Palmatolepis rhenana* Zones.

Type locality: Tudorów, Holy Cross Mountains.

Derivation of the name: From Latin *longus* – long.

Material. — Number of specimens and dimensions:

Material		Dimensions (µm)			
Number of specimens	Features	Holotype	Minimum	Mean	Maximum
Goniodonts: 39	Length of tooth	1085	800	1010	1315
	Breadth of tooth	1400	540	1380	1685
	Height of tooth lamina	655	255	650	830
	Length of tooth flank	855	370	610	855
	Height of main denticle	85	40	80	85
	Breadth of main denticle	65	35	60	70
	Max. height of side denticles	60	20	60	80
	Distance between denticles of two following goniodonts	340	115	200	350

Diagnosis. — As for the genus.

Description. — Aristotle's lantern. The main denticle is larger than the side denticles (20–34 in number) which decrease in size abaxially. Tooth laminae are slightly vaulted. On the inner side is a furrow marking the proximal margin of the next gonionodont's lamella. Dental slat margins are subparallel along almost its entire length. Other elements have not be recognised.

Remarks. — These goniodonts differ from others by having the longest wings, parallel proximal and distal margins. They also grow to a larger size than any other. Their juvenile elements (Text-fig. 30H) display some similarity of shape with the *Protocaudina–Erisserra* lineage.

Occurrence. — Only known from the type locality.

Genus *Ornatoserra* gen. n.

Type species: *Ornatoserra ovalis* sp. n.

Derivation of the name: From Latin *ornatus* – ornamented, *serra* – saw.

Diagnosis. — Goniodonts triangular and distal margin only weakly incised or not at all.

Remarks. — Similarity of goniodonts indicates the genus is derived from *Erisserra*. Both have a similarly weakly incised distal margin; juvenile stages are heart-shaped. Whole goniodonts are not V-shaped (*Winkelzahn* of the German authors) but are compact in the shape of arched platelets. The other shared character is the presence of a tongue-shaped process on the oral side of their rotula.

Ornatoserra ovalis sp. n.
(Text-fig. 28A–C, F–R)

Holotype: GIUS 4-747 Sow./698/1, Text-fig. 28F.

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

Type locality: Set C of Sowie Górki, Holy Cross Mountains.

Derivation of the name: From Latin *ovalis* – oval.

Material. — Number of specimens and dimensions:

Material		Dimensions (µm)			
Number of specimens	Features	Holotype	Minimum	Mean	Maximum
Goniodonts: 49	Length of tooth	560	510	530	645
	Breadth of tooth	645	490	640	760
	Height of tooth lamina	475	370	460	490
	Length of tooth flank	430	405	445	525
	Height of main denticle	50	30	50	70
	Breadth of main denticle	65	35	60	85
	Max. height of side denticles	60	15	50	90
	Distance between denticles of two subsequent goniodonts	120	120	145	190
Pyramids: 1	Height of demipyramid	–	1490	–	–
	Width of demipyramid	–	695	–	–
Rotulae: 4	Length	–	980	1105	1205
	Width	–	445	510	575
Sieve plates: 330	Length	–	495	610	810
	Width	–	150	220	525

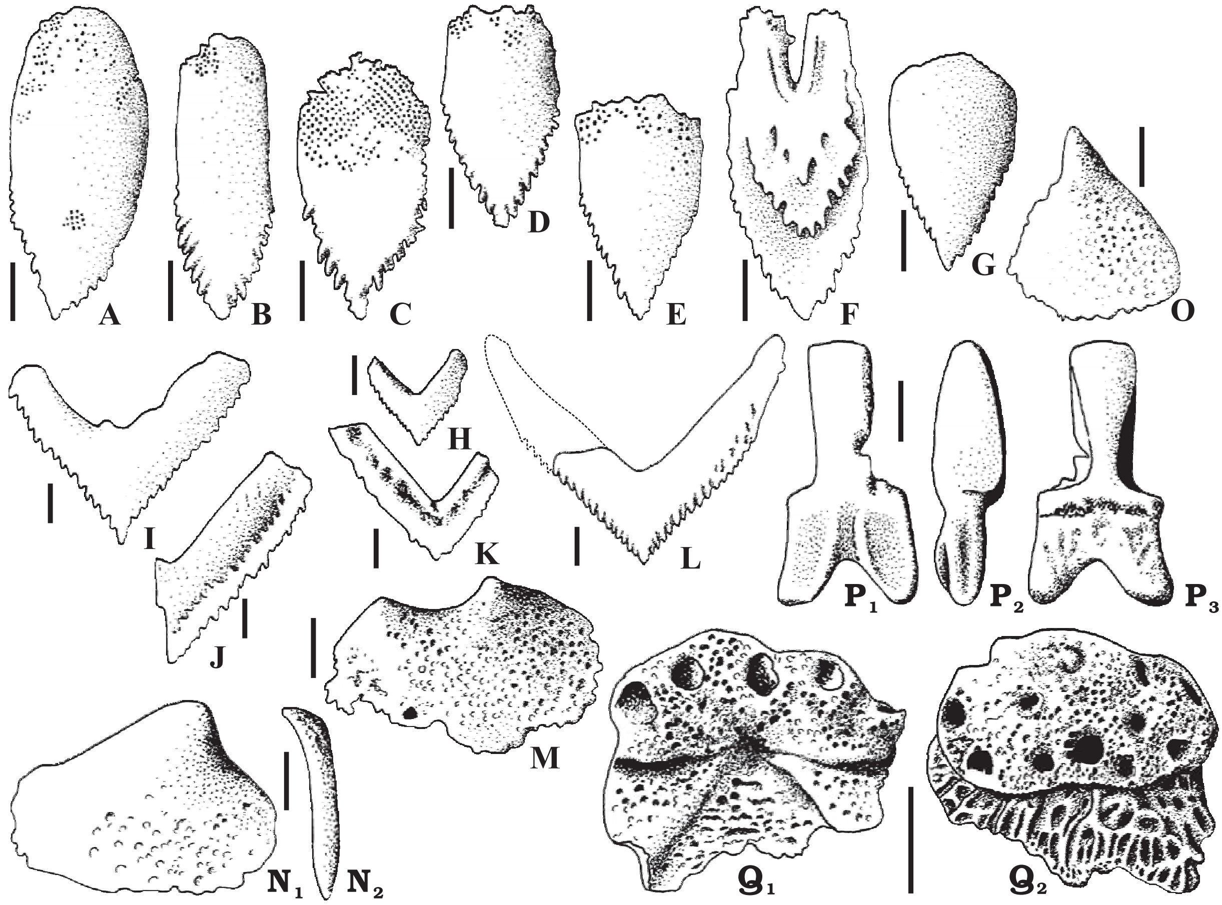


Fig. 30. Ophiocistioid skeletal elements from the Devonian of the Holy Cross Mountains. **A**–**G**. *Linguaserra ligula* Langer, 1991 goniodonts from the Late Givetian, sample Marzysz II/13 (A–F) and set C of Sowie Górki (G). **A**. GIUS 4-584 Mrz./222/1, outer view. **B**. GIUS 4-584 Mrz./222/2, outer view. **C**. GIUS 4-584 Mrz./222/3, outer view. **D**. GIUS 4-584 Mrz./222/4, outer view. **E**. GIUS 4-584 Mrz./222/5, outer view. **F**. Goniodont battery GIUS 4-584 Mrz./222/6, inner view. **G**. GIUS 4-744 Mrz./621/1, outer view. **H**–**L**. *Longiserra longa* gen. et sp. n. goniodonts from the Mid (Late?) Frasnian, Tudorów. **H**. Small specimens GIUS 4-790 Tud./506/1, outer view. **I**. Holotype GIUS 4-790 Tud./506/2, outer view. **J**. Fragmentary specimen GIUS 4-790 Tud./506/3, inner view. **K**. Fragmentary specimen GIUS 4-791 Tud./500/1, inner view. **L**. Fragmentary specimen GIUS 4-791 Tud./500/2, outer view. **M**–**O**. *Sollasina westfalica* (Richter, 1930), scale plates of tube feet from the Late Eifelian set XVII of the Skały Beds at Skały. **M**. GIUS 4-648 Ska./846/2, outer view. **N**. GIUS 4-648 Ska./846/3; N_1 outer view, N_2, lateral view. **O**. GIUS 4-648 Ska./846/4, outer view. **P**–**R**. *Microantyx praedulcis* sp. n. from same horizon. **P**. Rotula GIUS 4-648 Ska./847/5; P_1 oral view, P_2 lateral view, P_3 apical view. **Q**. Madreporite GIUS 4-648 Ska./847/4; Q_1 inner view, Q_2 outer view. Scale bar 200 μm.

Diagnosis. — As for the genus.

Description. — Aristotle's lantern. Main denticle only rarely differs in size from the primary lateral denticles. The lateral denticles are not numerous (12–20) and are of subequal size along the whole length, except for the most distal which can be smaller. The tooth lamina is vaulted (Text-fig. 28A–C, F–R).

Demipyramids are rounded and broad proximally. The protractor and retractor muscle scars are not very distinct and the foramen magnum is absent. The longitudinal suture is straight and long, as is the site of epiphyse attachment. The wing is large and rectangular, without fine ribbing, and with a slightly wavy surface. The crest pit is irregular and shallow. Pyramidal processes are weakly marked. On the ventral side of the goniodont battery, along the longitudinal axis, there is a wide groove along its entire length. From this groove slightly narrower grooves diverge obliquely to the right and left, bordering the field of attachment of primary goniodonts (Text-fig. $28A_1$).

Rotulae are X-shaped, similar to those of echinoids, but with long polycrystalline vestigial strips (term of Märkel 1979). A flat or hemispherical process ends each elliptical, convex or flat condylus. At the adaxial end there is a flat and tongue-shaped rotular process, which is split into two lobes.

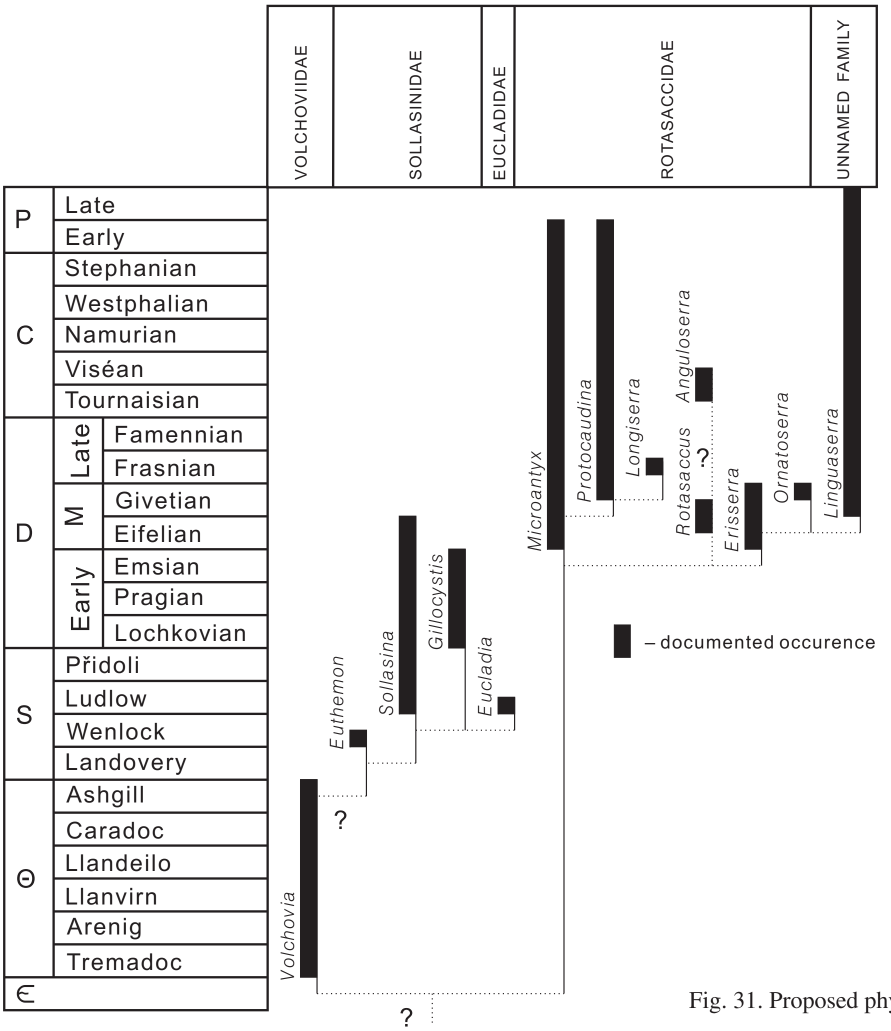


Fig. 31. Proposed phylogeny of the Ophiocistioidea.

S c l e r i t e s. Sieve plates from the tube-feet form straight, delicate, bifurcated, or rarely non-bifurcated, simply perforated blades. The marginal zone of the plate is narrow, occasionally absent. Some fragments of sclerites are imperforated. Other elements could not be identified.

Remarks. — Rotulae and goniodonts are somewhat similar to *Erisserra*. On the other hand sclerites from the tube-feet suggest links to Rotasacciidae.

Occurrence. — Only known from the type locality.

Unnamed ophiocistioid family
Genus *Linguaserra* Langer, 1991

Type species: *Linguaserra ligula* Langer, 1991.

Remarks. — These were ophiocistioids with small, tongue- or tear-shaped goniodonts. Distal margins of goniodonts are very short and narrow, or totally absent; thus the lamella is a relatively compact plate lacking wings. Batteries have a low number of teeth (up to three), the younger generations not forming independent blades but intergrown with the active blade and rudimentary. The main denticle is typically the largest, whereas the side denticles are fine, decreasing in size abaxially, 12–20 in number. Tooth lamellae are thin, so their abaxial part is translucent and is densely perforated with fine pores. Such a peculiar structure of goniodonts implies that *Linguaserra* deserves to be separated into a new family. The oldest note and illustrations of these very characteristic specimens were given by Spandel (1898), who classified them as echinoid pedicellaria of *Archaeocidaris keyserlingi* (Geinitz, 1848). His specimens were from the Zechstein of Ranis (Thuringia). Croneis and Mc Cormack (1932), who interpreted them as holothurian remains, used the same illustrations.

The compact structure of these goniodonts indicates that ancestors of the family are to be found within *Ornatoserra* gen. n. The reduction in number of goniodonts to three (Text-fig. 30F) is significant because this reduction caused acceleration of growth of new teeth generations, so the latter can be observed fused to the active tooth. The growth and exchange of goniodonts must have been quick, since enormous quantities of these goniodonts are found in samples. Besides the teeth no other corresponding elements could be found.

Linguaserra ligula Langer, 1991
(Pl. 9: 13; Text-fig. 30A–G)

1991. *Linguaserra ligula* n. g., n. sp.; Langer, pp. 43–44, Taf. 4: 6, 10.

Holotype: Langer 1991: Taf. 4: 6.

Type horizon: Early Givetian, Loogh Formation, Barley-Hustley Member.

Type locality: Daasberg near Gerolstein, Rhenish Slate Mountains.

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)		
Number of specimens	Features	Minimum	Mean	Maximum
Goniodonts: > 25000	Length of tooth	710	1000	1050
	Breadth of tooth	290	430	460
	Height of tooth lamina	760	?	?
	Length of tooth flank	240	390	540
	Height of main denticle	50	85	120
	Breadth of main denticle	20	85	90
	Max. height of side denticles	15	35	65
	Distance between denticles of two subsequent teeth	290	?	?

Remarks. — The specimens from the Early Givetian of the Rhenish Slate Mountains described by Langer (1991) differ from the Polish material in fine details only (result of intraspecific variability). In specimens from Germany the angle between working edges is on average 50° and in Polish specimens is 55°; number of lateral denticles is 16–24 and 12–20, respectively. Specimens from Poland have deflection of active edge where disappear lateral denticles. In almost all specimens (99.99%) the tooth lamella has a semicircular termination. If, however, teeth of ophiocistioids grew as in echinoids (cf. Jensen 1980, 1981; Märkel 1970a, b; Märkel *et al.* 1977; Märkel and Titschack 1969) then their denticle must have been only weakly calcified. The arched and vaulted large and thin lamellae of goniodonts might have been broken eventually.

Occurrence. — Early Givetian at the typic locality. Mid Givetian: Set B of Jaźwica. Late Givetian: outcrop I, trench II at Marzysz; Set B of Posłowice, Holy Cross Mountains, Poland.

Class **ECHINOIDEA** Leske, 1778

Studies of the Devonian echinoids are relatively few, although it is the period when important evolutionary diversification of the group took place. The most important investigations of this group have been on the order Echinocystitoida (Bindemann 1938; Dehm 1952, 1961; Haffer and Jentsch 1962, Stearn 1956). Echinoids from the Holy Cross Mountains have been only partially dealt (Jesionek-Szymańska 1979, 1982).

The oldest pedicellariae described so far come from Silurian echinoids (Ludlow of Herefordshire, Great Britain), and were found associated with *Echinocystites pomum* and *Palaeodiscus ferox* (Blake 1968). Other Palaeozoic pedicellariae have been described by Geis (1936), Philip (1963), and Mostler (1971d). Pedicellariae are present in almost all the rocks abounding in echinoid remains. A review of pedicellariae and their systematics has been given by A.C. Campbell (1983).

Subclass **PERISCHOECHINOIDEA** M'Coy, 1849
Order **Echinocystitoida** Jackson, 1912
Family **Lepidesthidae** Jackson, 1896
Genus *Meekechinus* Jackson, 1912

Type species: *Meekechinus elegans* Jackson, 1912.

Meekechinus sp. A
(Pls 10: 5–9, 11; 12: 10, 11; Text-figs 32M, 33A–D, F–H, K)

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)		
Number of specimens	Features	Minimum	Mean	Maximum
Ambulacral plates: > 500	Length	915	1935	4920
	Width	845	1115	1200
Interambulacral plates: > 1000	Diameter	2080	3200	4650
	Diameter of tubercles	120	205	240
Spines: > 1000	Length	1955	?	3700 (?)
	Diameter of base	145	275	300

Description. — Ambulacrals. These plates are thick, most commonly triangular or irregular in outline, with straight or wavy borders and parallel margins, of cidaroid type. Surface of the plates sculpted with wavy wrinkles. Margins are strongly bevelled (Pl. 10: 5–8; Text-fig. 33A–D) so the plates were imbricating. Pores are oval and one is more elongate than the other. Neuropore very distinct. Inner surface with strong internal process (Text-fig. 33A–D). The interporiferous zone may contain a single tubercle probably only on plates near the peristome; in the poriferous zone all plates have a prominent tubercle. Plates from the oral side of the test are the thickest and largest (Text-fig. 32M) with large, flat auricles (cf. Termier and Termier 1953).

Interambulacrals. These plates are oval or, more commonly, polygonal, with strongly truncated beveled edges, as a result of original imbrication. The primary tubercles (comp. Melville and Durham 1966) cannot easily be distinguished, as all the tubercles are usually of subequal size and are either chaotically or uniformly distributed over the whole surface (Pl. 10: 9; Text-fig. 33F–H, K). The tubercles have no foramen, but have an undercut neck. Occasionally they are totally absent (Pl. 10: 11) or are only weakly protruding (Text-fig. 33K). The interambulacral plates are of very simple structure, without scrobicula.

Spines. The primary spines differ from the secondary ones only by their larger size and more densely spaced ribs. These elements are straight and end in a mace-shaped thickening. The shaft is covered by irregular ribs connected by trabeculae and bifurcating distally. Base with narrow annulus, the neck and collar are absent. Acetabulum small and central.

Remarks. — The plates regularly occur in assemblages, often as the only constituent (e.g. Marzysz, sample Ic/5/12). Characteristic both for the family and genus is the occurrence of numerous rows of imbricating ambulacral plates (Jackson 1912; Kier 1966). The peculiar shape and oblique truncations of the margins of the ambulacral plates indicate they formed numerous belts in each ambulacrum. Another important feature is the presence of internal processes on ambulacrals. Many interambulacral plates totally lack tubercles, as is typical of Echinocystitoida, where plates without tubercles form an inner interambulacral belt, as in the family Lepidocentridae e.g. *Eupholidocidaris belli* Kier, 1957 (Late Carboniferous of Texas; Kier 1957). *Meekechinus* sp. A differs from *M. elegans* Jackson, 1912 from the Late Permian and *M.*? *herbornensis* Bindemann, 1938 from the Early Carboniferous in the strongly bevelled, commonly triangular ambulacral plates (cf. Bindemann 1938; Jackson 1912). The some ambulacral plates of *Meekechinus* sp. A (oral ambulacrals – if interpretated) are very massive, but lack primary tubercles. Other features are typical of the genus. This Devonian species is more primitive in structure than subsequent forms.

Occurrence. — Late Givetian: outcrop I, trench II at Marzysz; set A of Wietrznia II, Holy Cross Mountains, Poland.

Family **Lepidocentridae** Lovén, 1874
Genus *Albertechinus* Stearn, 1956

Type species: *Albertechinus montanus* Stearn, 1956.

Albertechinus devonicus sp. n.
(Pls 10: 1–4, 12–13, 16; 11: 1–13, 15–16, 12: 5–7, 12–13;
Text-figs 32A, D–E, G–L, 33E, I, L–O, 34A–F, 35E–M)

1979. Serrate tooth; Jesionek-Szymańska, p. 284, pl. 24.

Holotype: GIUS 4-568 Mrz./980/1, Text-fig. 32I.

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

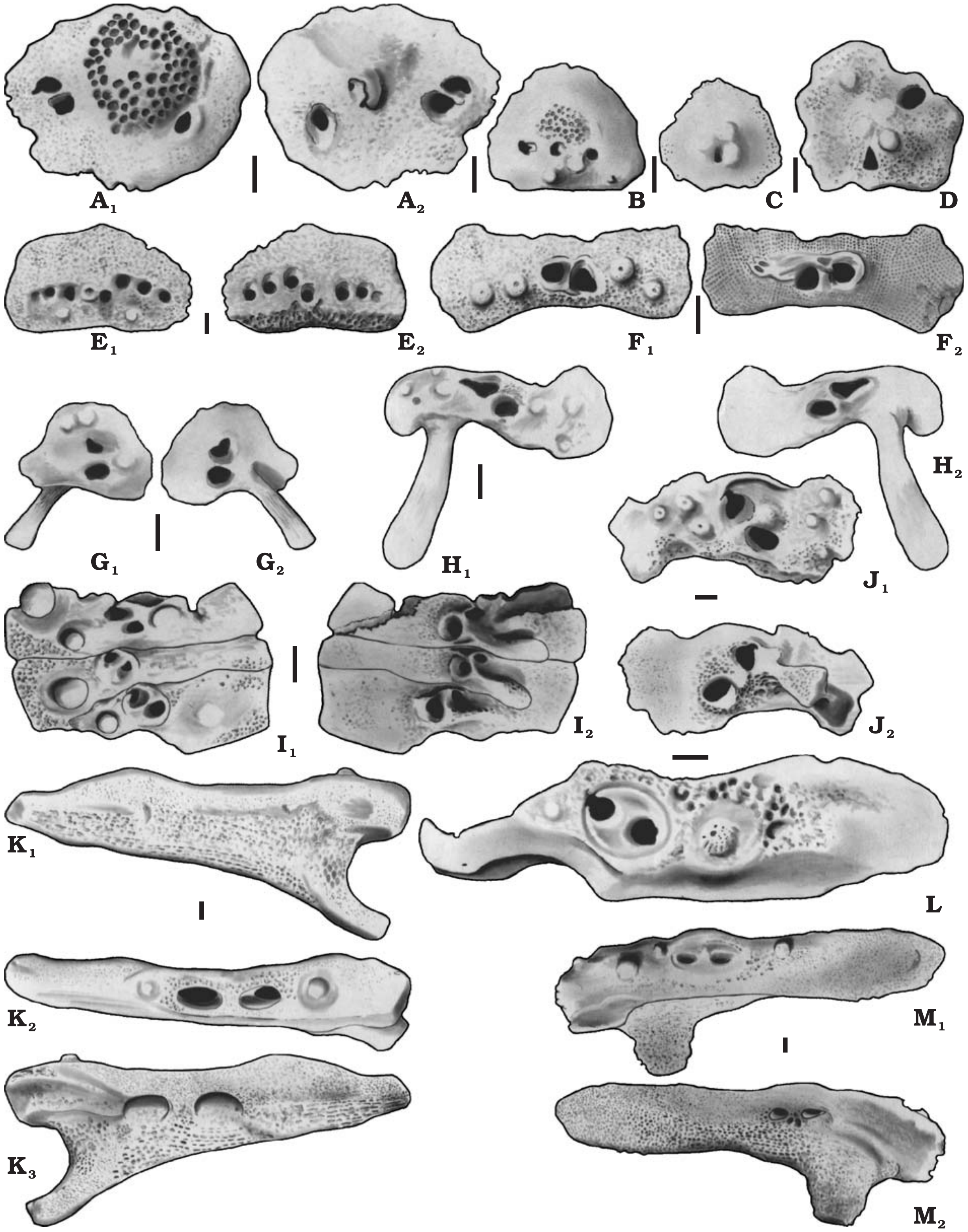


Fig. 32. Elements of echinoid tests from the Late Givetian of Marzysz, Holy Cross Mountains, samples Marzysz II/15 (A, J, M), Marzysz II/13 (B–D, K), Marzysz II/W/6 (E–I), and Marzysz II/W/2 (L). **A**. Madreporite plate of *Albertechinus devonicus* sp. n., GIUS 4-587 Mrz./987/1; A_1 outer view, A_2 inner view. **B**. Madreporite plate of *Lepidechinoides* sp. A, GIUS 4-584 Mrz./991c/11, outer view. **C**. The ocular plate of *Lepidechinoides* sp. A, GIUS 4-584 Mrz./991c/12, outer view. **D**. The ocular plate of *Albertechinus devonicus* sp. n., GIUS 4-584 Mrz./991a/10, outer view. **E**. Genital plate of *Albertechinus devonicus* sp. n., GIUS 4-568 Mrz./49/1; E_1 outer view, E_2 inner view. **F**. Plate from apical part of *Lepidechinoides* sp. A test, GIUS 4-568 Mrz./50/1; F_1 outer view, F_2 inner view. **G–L**. Ambulacral plates of *Albertechinus devonicus* sp. n. **G**. Ambulacral plate of the apical part of test, GIUS 4-568 Mrz./51/1; G_1 outer view, G_2 inner view. **H**. Plate from the middle part of test, GIUS 4-568 ➛

Type locality: Trench II, layer W/6 at Marzysz, Holy Cross Mountains.
Derivation of the name: From Latin *devonicus* – Devonian.

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)			
Number of specimens	Features	Holotype	Minimum	Mean	Maximum
Madreporites: > 500	Diameter	–	985	1280	1320
	Diameter of sieve	–	600	625	645
Genital plates: > 500	Diameter	–	1250	1650	1745
Ocular plates: > 500	Diameter	–	720	970	1385
Ambulacral plates: > 1000	Length	1405	660	1320	5160
	Width	390	300	725	1040
Interambulacral plates:>1000	Diameter	–	420	?	7585 (?)
	Diameter of tubercles	–	80	340	600
Demipyramids: 220	Height	–	1570	2150	2600
	Width	–	800	1005	1170
Rotules: 85	Length	–	1115	1930	2820
	Width	–	390	420	525
Epiphyses: 110	Length	–	1020	1955	2670
	Width	–	335	770	1170
Compasses: 17	Length	–	1005	1220	1405
	Width	–	405	510	590
Teeth: > 500	Length	–	1100	2440	2950
	Width	–	525	620	740
Spines: > 1000	Length	–	1350	?	3975 (?)
	Width of base	–	115	?	285 (?)
Ophicephalous pedicellariae: > 500	Length	–	1950	1100	1195
	Valve width	–	245	315	355
Tridentate pedicellariae:>500	Length	–	495	2105	4230
	Valve width	–	220	530	830

Diagnosis. — Inner side of ambulacral plates with long, lingulate process.

Description. — Apical skeleton. Madreporites are oval, with two or three pores, symmetrically disposed on both sides of a sieve (Pl. 10: 1; Text-fig. 32A). On the inner side the stone canal opening is C-shaped. Ocular plates are either irregularly shaped or triangular, with a single triangular opening or with an accompanying oval pore (Pl. 10: 4; Text-fig. 32D). In their centre is a boss with three to five tubercles. The genital plates are triangular or elliptical, with numerous (five to eight) pores, the central part has a tubercle, sometimes with two additional ones placed symmetrically (Pl. 10: 2–3; Text-fig. 32E).

Ambulacrals. They are formed of simple, triangular plates, with parallel borders, of cidaroid type. The suture between plates is not straight. The pores are in oval depressions, separated by a convex well, and are nonconjugate. Neuropore very distinct. Pore pairs irregularly offset in column (Text-fig. 32I). In the interporiferous zone there are irregularly placed tubercles (one to three), of the same number as in the pore zone. One kind of the test plate (probably from the apical part – in compare with other articulated species; see Kier 1966) is triangular in outline; a second more elongate (probably located closer to the peristome Pl. 10: 13; Text-fig. 32G–K). The thickest, largest and longest plates have oblique bevelled margins (probably from the oral zone Text-fig. 32L). The largest of all have prominent auriculae (Text-fig. 32K), and differ from other ambulacrals in having two tubercles on either side of the ambulacral pores. Their contact, as in the extant echinoids, formed a suture on one side, but imbricating contact on the other (cf. Märkel 1976a).

Interambulacrals. They are oval, or more commonly irregular, large plates with thinned beveled edges. A very large primary tubercle is usually present and offset, and has an undercut neck, elliptical and

Mrz./51/2; H_1 inner view, H_2 outer view. **I**. Fragment of articulated ambulacral zone from the middle part of test, holotype GIUS 4-568 Mrz./980/1; I_1 lateral view, I_2 outer view. **J**. Ambulacral plate from the middle part of test, GIUS 4-587 Mrz./986/1; J_1 outer view, J_2 lateral view. **K**. Ambulacral plates of echinoid from the oral part of test with the auricle, GIUS 4-584 Mrz./238/1; K_1 lateral view, K_2 outer view, K_3 inner view. **L**. Ambulacral plate from the oral part of test with the auricle, GIUS 4-564 Mrz./998/4, outer view. **M**. Ambulacral plate from oral part of *Meekechinus* sp. A test with the auricle, GIUS 4-587 Mrz./982/1; M_1 outer view, M_2 inner view. Scale bar 200 μm.

shallow foramen and shallow, oval scrobicula of simple structure. The primary tubercle is surrounded by up to five secondary tubercles with similar structure, but commonly significantly smaller.

Aristotle's lantern. Demipyramid rather broad, as are the arches of the oval foramen magnum. Retractor muscle scar deep and the protractor muscle scar shallow but very distinct. Longitudinal suture between the demipyramids long, contact surface in oral part is four times as broad. Epiphyses seating long and slightly wavy. Wing in shape of an equilateral triangle with broad ribs on the interpyramidal muscle platform. The pit is wide, amphora-shaped (Text-fig. 34A_6), the process prominent and rounded. Dental slide (*sulcus dentalis*) broad and shallow; tooth clamp weakly distinguished. Flat and weakly outlined styloid process is located high.

Teeth belong to the serrate type. There is a median groove flanked by two shallower grooves, with two additional outer grooves in the largest specimens. Prisms cover the central groove, the axial face is smooth. The tooth consists of two halves that separate readily. The chewing tip has only a single central tooth and two to four smaller lateral ones. The shaft of the tooth is short, the plumula bifurcate, with a U-shaped slit in its middle. At this end multilamellar structure can be seen clearly (Pl. 11: 10).

Epiphyses have a structure typical of the Aristotle's lantern of the Palaeozoic echinoids. The element is long, blade-shaped, with a little, triangular wing. Both inner and middle tubercles are lacking, in their place there occur two flat and triangular processes (Text-fig. 34D). Interior rotular muscle area is large and flat, not separated from the attachment surface of interpyramidal muscle; exterior rotular muscle surface is also flat and gradually passes into the glenoid cavity. Connected fields of attachment of the above mentioned muscles and of glenoid cavity are separated by crista, which follow significantly different routes than in modern echinoids, being closer to the interradial axis (cf. Märkel 1976b, 1979, Text-fig. 5). The protractor muscle of the inner oral surface had a displaced attachment area, almost parallel to the interradial axis. On the other hand the area leaning on the process of the demipyramid is bordered by a distinct crista contacting with the rotula. Two epiphyses bordered the deep groove for the rotula, they are oriented not parallel but obliquely in respect to the pyramid.

The rotula is narrow and elongate, with a narrow condylus and long narrow epicondylus. Polycrystalline vestigial strips (cf. Märkel 1979) on the oral surface are long and distinct. They commence at the margins, separating the condylus, and come into contact at the so-called growth centre (cf. Märkel 1979). The surfaces of the attachment of interior and exterior muscles of the rotula are well developed, large, with ribbed surface. Inner fossa absent, middle fossa small, shallow and narrow.

Adaxial parts (Gabel of Märkel 1976b) of compass are broad and flat, so the compass depressor muscle had a wide attachment area. Its middle part is flattened and more strongly expanded, forming an attachment area for the elevator muscles. Only fragments of the distal part of compasses were identified, their flat proximal tip indicating that a proximal hook had been present.

Spines. The primary spines are straight, truncate and long. Numerous straight ribs cover the shaft; at the base of the spine they unite in pairs, gradually disappearing. The base has a simple structure; annulus, neck and collar are absent. The acetabulum is large and centrally located in larger specimens, but excentric and small in the smaller ones. The secondary spines differ only in having the middle part of their shaft contracted.

Ophicephalous pedicellariae (morphotype I). Exclusively trivalved pedicellariae, with truncate blade (at a half of their height), with narrow ribs on the inner side, provided with minute, proximally bent hooks; number of the hooks increases adaxially. Ribs are narrow on the inner side but on the outer and adaxially they become more and more broad and cover the whole valve as well as the blade. A short keel separates two elliptical depressions, possibly locations of adductor muscle attachment. The lateral and central cog-teeth first appear in the broadest part of a valve and toward the proximal side they unite into homogenous transverse ribs. The handle, with U-shaped depression, is unperforate and the opening angle of the valves is 90–120°.

Tridentate pedicellariae (morphotype I). Exclusively trivalved form of simple structure similar to that of spines. Truncate long blades, forming half of height in small specimens to four-fifths of height in larger ones, are covered on all sides by ribs, as is the valve on its outer side. Depressions between the ribs expand proximally. Keel bifurcates at the base of the blade and distally it is provided with a furrow, in this way two ribs form the pedicellarial blade proper, with minute teeth (Text-fig. 35I–K). Valve, of triangular shape, with two deep triangular depressions internally for attachment of the adductor muscles. The lateral and central cog-teeth appear at the broadest part, i.e. the proximal valve edge, where they are connected into uniform transverse ribs.

Remarks. — Most material has been collected loose, although always numerous and commonly also mass-occurring (Marzysz, Posłowice). In some samples full sets of the elements from the Aristotle's lantern are the only echinoid remains (Jaźwica, set B). Characteristic both for the family and for the genus is the oc-

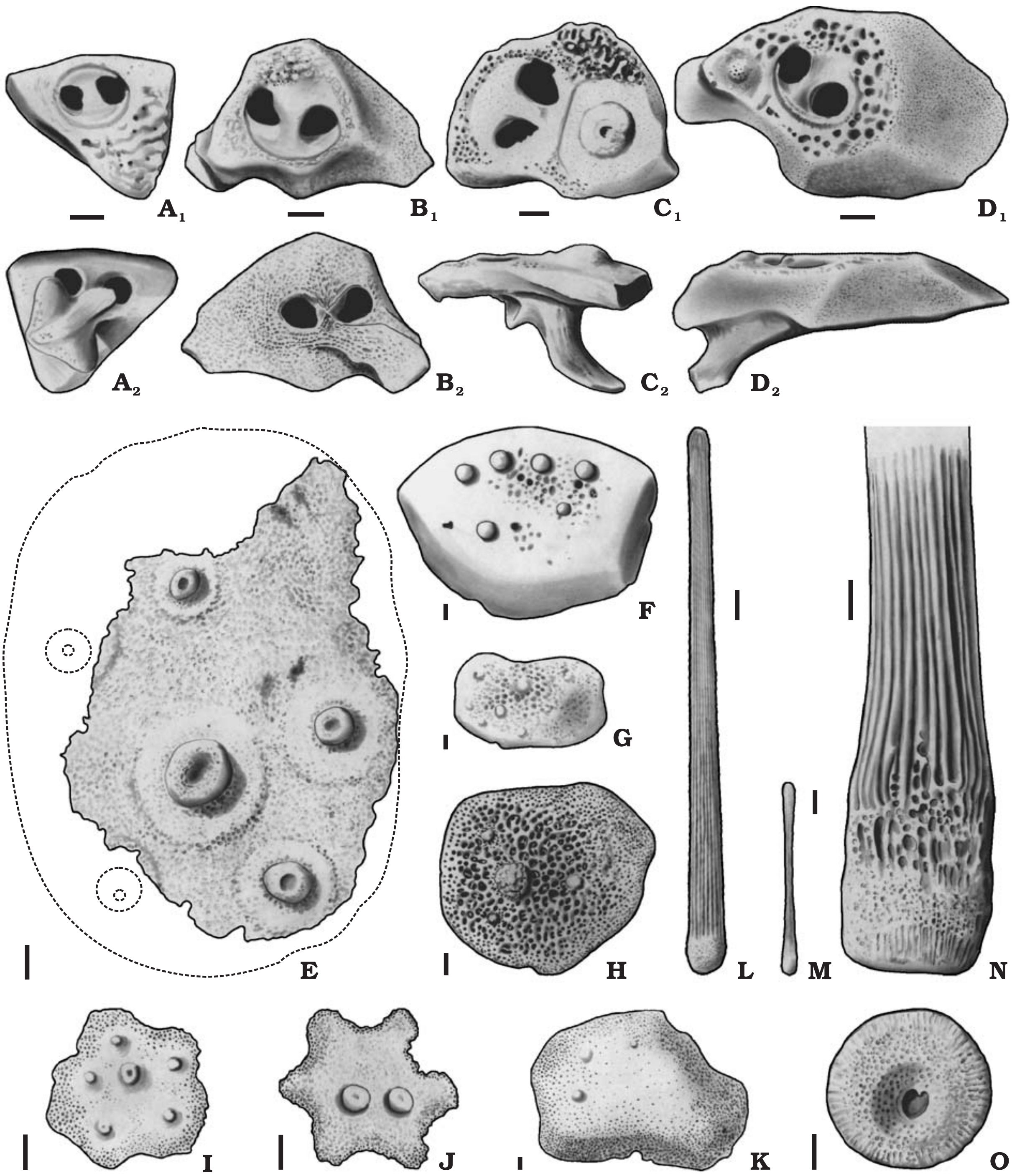


Fig. 33. Elements of echinoid tests from the Late Givetian of Marzysz, Holy Cross Mountains, samples Marzysz II/W/2 (A, C–D), Marzysz II/15 (B, E–H, K), and Marzysz II/13 (I–J, L–O). **A**–**D**. Ambulacral plates of *Meekechinus* sp. A from the aboral part of test, GIUS 4-564 Mrz./998/3; A_1 outer view, A_2 inner view. **B**. GIUS 4-587 Mrz./986/2; B_1 outer view, B_2 inner view. **C**. GIUS 4-564 Mrz./998/1; C_1 outer view, C_2 lateral view. **D**. GIUS 4-564 Mrz./998/2; D_1 outer view, D_2 lateral view. **E**. Large interambulacral plate of *Albertechinus devonicus* sp. n. from the middle part of test, GIUS 4-587 Mrz./981/1, partially reconstructed. **F**–**H**, **K**. Interambulacral plates of *Meekechinus* sp. A from the middle part of test. **F**. GIUS 4-587 Mrz./983/1. **G**. GIUS 4-587 Mrz./983/2. **H**. GIUS 4-587 Mrz./983/3. **K**. GIUS 4-587 Mrz./983/4. **I**. Juvenile or aboral interambulacral plate of *Albertechinus devonicus* sp. n., GIUS 4-584 Mrz./992/1. **J**. Juvenile or aboral interambulacral plates of *Lepidechinoides* sp. A, GIUS 4-584 Mrz./992/2. **L**–**O**. Spines of *Albertechinus devonicus* sp. n. **L**. Primary spine GIUS 4-584 Mrz./239/1. **M**. Secondary spine GIUS 4-584 Mrz./239/2. **N**. Base of primary spine GIUS 4-584 Mrz./239/4, lateral view. **O**. Acetabulum of primary spine GIUS 4-584 Mrz./239/3, proximal view. Scale bar 200 µm.

currence of irregular plates in two columns within each ambulacrum (Kier 1966). Other diagnostic features are the presence of the inner processes on the ambulacrum, ambulacral plates with uniserial pore pairs, arranged in two columns of in each ambulacrum, irregular interambulacral plates with big main tubercle surrounding by secondary tubercles. *Albertechinus devonicus* sp. n. differs from *A. montanus* Stearn, 1956 from the Late Devonian of Fairholme Formation (Alberta) in having longer inner processes, and narrower ambulacral plates. Prominent auriculae most resemble the type characteristic of the order Pedinoida (e.g. *Caenopedina* A. Agassiz, 1869, Pedinidae; cf. Termier and Termier 1953). Interambulacral plate sculpture in *A. montanus* is more pronounced and there are more secondary tubercles (in *Albertechinus devonicus* sp. n. main tubercle is common surrounding by five secondary tubercles). The largest ambulacral plates (probably oral) of *A. devonicus* sp. n. are very massive and the other ambulacrals are of similar shape to *Archaeocidaris* McCoy, 1844 (cf. Kier 1958) but the latter lack processes. Pyramids of a very similar structure have been described by Hoare and Sturgeon (1976, Text-fig. 5, population A) from the Late Carboniferous of North America and ascribed to an unknown cidaroid. According to Smith (1981) it is an archaeocidaroid lantern. Among the lepidocentrid echinoids only the Late Carboniferous *Pholidechinus brauni*, has a similar type of pyramid, while so does the archaeocidarid – *Archaeocidaris rossica* (Regnéll 1956; Jackson 1912). The long longitudinal suture between the demipyramids and the shallow foramen magnum is typical of early echinoids (Jensen 1980). Spines have a very simple, primitive structure. Towards the exterior there occurs some layer forming ribs, closer to axis the radiating layer is built of septa, connected by trabeculae (Pl. 12: 14); the central core consists of an irregular calcareous meshwork. Frequency analysis, presence of spines in original position on some specimens (Pl. 10: 16), details of microstructure and the fact that in the fossil material studied only the tubercles of *Albertechinus devonicus* sp. n. are large enough to fit the acetabulum under consideration determine their systematic position. Ophicephalous pedicellariae commonly occur from the Eifelian to Frasnian and it is impossible to differentiate species among them, as no differences can be observed among them. Morphologically they are simple, with termination and sculpture as in the spines (Text-fig. 35E–F). Complete specimens are quite common. The tridentate pedicellariae described above always occur in company with ophicephalous pedicellariae. Their simple structure also shows some resemblance to spines. They display great morphological variability within a single sample, with clear distinction of juvenile (Text-fig. 35K–L), slightly older (Text-fig. 35I) and mature forms (Text-fig. 35G–H, M). The larger specimens have ventral ribs of their blade more and more similar to the other blade ribs; the blade in section grows from laterally flattened, through oval to circular in adult specimens. Also the cog-teeth are better and better developed in larger specimens. Only selected growth stages are illustrated (Text-fig. 35G–M) but it is quite easy to find all the transitional forms in a large sample. Such ontogenetic variability of shape is quite common in pedicellariae of echinoids. Also complete specimens are not rare. Great similarity of these elements with the spines of *Albertechinus devonicus* sp. n. speaks for their classification into the species. Additional arguments are enormously high frequency in numerous samples and association with remains of this particular species.

Occurrence. — Late Eifelian: sets XVII, XVIII, XIX of Skały. Early Givetian: sets XX, XXI, XXIII, XXIV, XXV of Skały. Mid Givetian: set: XXVII, XXVIII of Skały; set B of Laskowa; set A of Szydłówek; set B of Jaźwica. Mid–Late Givetian: set A of Górno. Late Givetian: set B of Czarnów; Wola Jachowa; set A of Wietrznia Ia; set A of Wietrznia II; outcrop I, trench II at Marzysz; set B of Posłowice; sets C, G of Sowie Górki; sets B, C of Stokówka; set B of Zbrza; set A of Góra Zamkowa, Chęciny. Early Frasnian: set B of Wietrznia Ic; set C of Wietrznia Id, Ie; set B of Góra Cmentarna; set D of Stokówka; Kowala I; set F of Góra Zamkowa, Chęciny. Early-Mid Frasnian: sets B, C of the railroad cutting, Kowala. Mid Frasnian: sets C, D of Górno; Radlin; sets C, D of Wietrznia II; set A of Kadzielnia; Szczukowskie Górki; set D of the railroad cutting, Kowala. Mid–Late Frasnian: Sobiekurów, Holy Cross Mountains, Poland.

Genus *Kongielechinus* Jesionek-Szymańska, 1979

Type species: *Kongielechinus magnituberculatus* Jesionek-Szymańska, 1979.

Kongielechinus magnituberculatus Jesionek-Szymańska, 1979

1979. *Kongielechinus magnituberculatus* gen. n. sp. n.; Jesionek-Szymańska, pp. 286–290, text-figs 1C, 2A–E, 3, 4A, 5, 6; pls 17–23.

Holotype: ZPAL ED 31, Jesionek-Szymańska 1979: text-fig. 1D.

Type horizon: Late Eifelian, Skały Beds.

Type locality: Błonie Valley, Świętomarz, Holy Cross Mountains.

Diagnosis. — Ambulacral plates with up to two primary tubercles situated close to perradially located peripodium. The interambulacral plates with up to four large, primary tubercles, situated excentrically in large areoles. Half-pyramids erect, foramen magnum shallow; teeth flat, oligolamellar; rotulae thick, rectangular.

Remarks. — Plates of the test with obliquely truncate margins.

Occurrence. — Late Eifelian: sets XIV–XIX of Skały; Świętomarz, Holy Cross Mountains, Poland. Although Jesionek-Szymańska (1979) suggested Givetian age of these deposits they belong to the Late Eifelian (Malec 1984, also personal communication).

Genus *Lepidocentrus* Müller, 1857

Type species: *Lepidocentrus eifelianus* Müller, 1857.

Emended diagnosis. — The ambulacral plates with uniserial pore pairs, all in contact with interambulacrum, adoral plates similar to adapical; interambulacrum wide, with many regular columns and small, perforate primary tubercles.

Lepidocentrus rhenanus (Beyrich, 1857)

1857. *Palaechinus rhenanus* n. sp.; Beyrich, p. 4.
1857. *Palaechinus rhenanus* Beyrich; Müller, p. 264, Pl. 4: 4–6.
1874. *Lepidocentrus rhenanus* (Beyrich); Lovén, p. 40.
1912. *Lepidocentrus rhenanus* (Beyrich); Jackson, p. 288, Pl. 20: 7.
1962. *Lepidocentrus rhenanus* (Beyrich); Haffer and Jentsch, p. 80, Text-fig. 1, Pl. 8: 12–13.

Holotype: Beyrich 1857: Pl. 4: 4–6.
Type horizon: Late Eifelian, Ohler slates.
Type locality: Windhausen, Sauerland, Germany.

Description. — Ambulacrals. Thin and straight, pentagonal or bar-like plates with arched margins, of cidaroid type with oval pores and with nonconjugate pore pairs. Neuropore only weakly distinguishable. On either side there occur two tubercles, of equal size. Bevels of the plates are thin and translucent. On the inner side are characteristic processes with flanges that enclosed the radial water vessel. In associated plates these processes do not contact completely, leaving a lumen between them for an ampulla. Reconstruction of ambulacrals of such a type was given by Kier (1968) for the genus *Nortonechinus*, a close relative of *Lepidocentrus*.

Interambulacrals. The plates are hexagonal or, more rarely, pentagonal, thin and with thinned bevels. The tubercles, if present, are irregularly distributed (two to five) and have incised necks. Pentagonal plates occurred immediately by the ambulacrals (Haffer and Jentsch 1962; Kier 1968), the hexagonal ones formed the remainder of the interambulacrum (maximally six columns). Interambulacral plates, typically for numerous representatives of the order Echinocystitoida have irregularly distributed, simple tubercles.

Spines. These elements are very fine and delicately ribbed, similar to the spines of *Albertechinus*.

Remarks. — The skeleton was built of very thin and, delicate plates and, possibly represents material of juvenile specimens. Differences between the particular elements are large, though in the assemblages containing the remains of this species only (Skały) no larger skeletal elements were found. The present material differs from *Lepidocentrus rhenanus* by the more delicate structure of its interambulacral plates. However the specimens of Beyrich were small, the test was 36 mm diameter and only 15 mm in height (Beyrich 1857) and, according to Haffer and Jentsch (1962), who discovered much larger remains, represented juvenile specimens.

Occurrence. — Late Eifelian: Ohler slates, Windhausen, Sauerland, Germany; sets XVII, XVIII, XIX of Skały, Holy Cross Mountains, Poland.

Genus *Lepidechinoides* Olsson, 1912

Type species: *Lepidechinoides ithacensis* Olsson, 1912.

Emended diagnosis. — Ambulacral plates have internal spinose processes on adoral side; internally ambulacral plates opposite horizontal ambulacral sutures expanded laterally, fan shaped; interambulacral plates without primary tubercles arranged in many columns.

Lepidechinoides sp. A
(Pl. 10: 10, 14–15; Text-figs 32B–C, F, 33J)

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)		
Number of specimens	Features	Minimum	Mean	Maximum
Madreporites: 17	Diameter	575	695	880
	Diameter of sieve	105	220	270
Genital plates: 25	Diameter	490	775	935
Ocular plates: 29	Diameter	335	450	695
Ambulacral plates: 118	Length	920	480	595
	Width	450	480	595
Interambulacral plates: 250	Diameter	880	1015	2090
	Diameter of tubercle	110	220	290

Description. — Apical skeleton. Madreporites are triangular, with rounded angles, perforated by two or three openings in linear arrangement (Text-fig. 32B). The sieve is small and flat. Below the pores there may occur two or three tubercles. Ocular plates are oval or triangular, with a single triangular pore, compressed by three surrounding tubercles (Text-fig. 32C). Genital plates are of the same shape as the madreporites.

Ambulacrals. These plates are thin, bar-shaped, with curved bevels, cidaroid in type. Their adradial bevels are more strongly expanded while the central part is narrow and convex. Nonconjugate pore pairs are oval in shape, and the neuropore is not very distinct (Text-fig. 32F). On both its sides there occur two tubercles, of equal size. The remaining bevels of the plates are thin and translucent.

Interambulacrals. Irregular, hexagonal, hexalobate, rarely pentagonal, thin plates (Pl. 10: 10, 15; Text-fig. 33J) with thinned bevelled edges. Over their external surfaces there occur irregularly distributed tubercles (two to five) with undercut necks. The foramen is only delicately outlined or is lacking altogether, as are the primary tubercles and the other morphological structures of the plates. Also quite smooth plates can be observed.

Remarks. — These echinoids either have a very delicate test or they are remains of young specimens. Their characteristic feature is the irregular form of their interambulacral plating. The interambulacral plates, typically for the order Echinocystitoida have irregularly distributed, simple tubercles. The species differs from *L. ithacensis* by the more delicate structure of its plates. So far the genus has been recorded from the Devonian of North America (New York; *vide* Kier 1966).

Occurrence. — Late Eifelian: sets XVII, XVIII, XIX of Skały. Early Givetian: sets XX, XXI, XXIII, XXIV, XXV of Skały. Mid Givetian: sets XXVII, XXVIII of Skały; set B of Laskowa; set A of Szydłówek. Mid–Late Givetian: set A of Górno. Late Givetian: set A of Wietrznia Ia; set A of Wietrznia II; outcrop I, trench II at Marzysz; set B of Posłowice; sets C, G of Sowie Górki; set A of Góra Zamkowa, Chęciny. Early Frasnian: set B of Wietrznia Ic; set C of Wietrznia Id, Ie; set D of Stokówka; Kowala I; set F of Góra Zamkowa, Chęciny. Mid Frasnian: sets C, D of Górno; Radlin; sets C, D of Wietrznia II; set A of Kadzielnia; Szczukowskie Górki; set D of the railroad cutting, Kowala. Mid–Late Frasnian: Tudorów; Sobiekurów, Holy Cross Mountains, Poland.

Order **Cidaroida** Claus, 1880

Family **Archaeocidaridae** M'Coy, 1844

Genus *Archaeocidaris* M'Coy, 1884

Archaeocidaris? sp.
(Pl. 12: 15–16)

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)		
Number of specimens	Features	Minimum	Mean	Maximum
Spines: > 500	Length	1330	1700	2450
	Diameter	105	125	210

Description. — The spines are sharply truncated and have irregular riblets along the entire length of their shafts ending as with short spikes. These riblets interconnected by a dense network of trabeculae. The base has a simple structure; it is expanded and without annulus, necks or collar. The acetabulum is small, elliptical and excentrically situated.

Remarks. — The microstructure of these spines differs from that of other herein described species in having a cortex. These elements generally resemble the spines of *Archaeocidaris*? *diadematoides* Haude *et* Thomas, 1994 from the Late Carboniferous of Germany (Haude and Thomas 1994) but that species has smaller thorns on lateral surfaces of the spines than in the present species.

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

Echinoidea *incertae sedis*

Pyramid – type II

(Text-fig. 34G, I)

Material. — Number of specimens and dimensions:

Material		Dimensions (µm)		
Number of specimens	Features	Minimum	Mean	Maximum
Rotules: 1	Length	2400	–	–
	Width	1230	–	–
Compasses: 1	Length	1645	–	–
	Width	610	–	–

Description. — Rotulae are of proportions typical for the echinoids; i.e. the condylus is narrow and long and the epicondylus short and narrow. Vestigial strips on the oral surface are long and distinct. They occur from the margins, separating the condylus, and fuse at the so called growth centre (cf. Märkel 1979). Inner muscle attachment surfaces are small but well developed, whereas outer muscle attachment surfaces are large and adaxial. Inner and middle fossa are small and shallow and lie close to each other.

Adaxial parts of the compass are narrow, bar-shaped, without bifurcation, so that the depressor muscles had a very narrow field of attachment. The middle part of the compass is flattened and more strongly expanded, and is ornamented by riblets on the oral side. The proximal flat tip of the compass suggests a hook was originally present.

Remarks. — The rotula is more similar to that of modern cidaroids or Euechinoida than to the rotula of *Albertechinus devonicus* sp. n. The compass is distinguishable by its lack of a distal crotch.

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

Pyramid – type III

(Text-fig. 34H)

Material. — Number of specimens and dimensions:

Material		Dimensions (µm)		
Number of specimens	Features	Minimum	Mean	Maximum
Rotules: 1	Length	1235	–	–
	Width	1035	–	–

Description. — Rotula dumpy, short, with anlarged condylus and epicondylus. Polycrystalline vestigial strips are absent. Interior muscle attachment surfaces of rotula are very large (Text-fig. $34H_2$) and well developed, whereas exterior muscle attachment surfaces are smaller. Inner and middle fossa are large but weakly outlined. At the centre of the apical surface is a large boss (Text-fig. $34H_3$).

Remarks. — Proportions indicate that the rotula might belong to an echinoid with a broad but rather low Aristotle's lantern, possibly *Meekechinus* sp. A.

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

Oligolamellar tooth

(Text-fig. 34M)

Material. — Number of specimens and dimensions:

Material		Dimensions (µm)		
Number of specimens	Features	Minimum	Mean	Maximum
Teeth: 2	Length	1100 (?)	?	2675 (?)
	Width	280	290	305

Description. — The teeth are in two halves, connected along the suture, and only a fragment of a single half of a tooth has been found. The abaxial face is flat and was covered by a homogenous calcitic layer, now strongly weathered. The tooth had over 25 lamellae. Its adaxial face had a central groove.

Remarks. — Similar teeth from the Late Eifelian of the Holy Cross Mountains (Skały, set XVI, XVII) were described by Jesionek-Szymańska (1982). These teeth are also built of lamellae arranged obliquely in respect to the chewing margin. The strongest similarities are with Jesionek-Szymańska's "more advanced" type, which have a ridge instead of groove in its central part. Oligolamellar teeth, typical of lepidocentrid echinoids (Jesionek-Szymańska 1982), occur in great quantities in the Devonian of the Holy Cross Mountains.

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

Lamellae of oligolamellar tooth
(Text-fig. 34K–L)

Material. — Number of specimens and dimensions:

Material		Dimensions (µm)		
Number of specimens	Features	Minimum	Mean	Maximum
Teeth lamellae: 18	Length Width	1285 305	1600 (?) 235	2000 (?) 525

Description. — Thin calcareous plates, with sharp, triangular terminations on both ends. Internal surfaces of the lamella with shallow depression in the meshwork zone, expanding as a groove over the whole surface of the element. Furrow at the adaxial edge of adjoining lamella is elongate and bordered by two ridges. This edge is straight or curved, whereas the abaxial edge is denticulate with minute teeth up to 100 mm long. Adoral spaghetti-type apex (= apice in Jesionek-Szymańska 1982) is abaxially curved and up to 500 mm wide. The overlapping region is weakly outlined. On the external surface the lateral area is developed as a broad cylindrical rim, the depression contacting with the neighbouring tooth lamella shallows in the adoral direction.

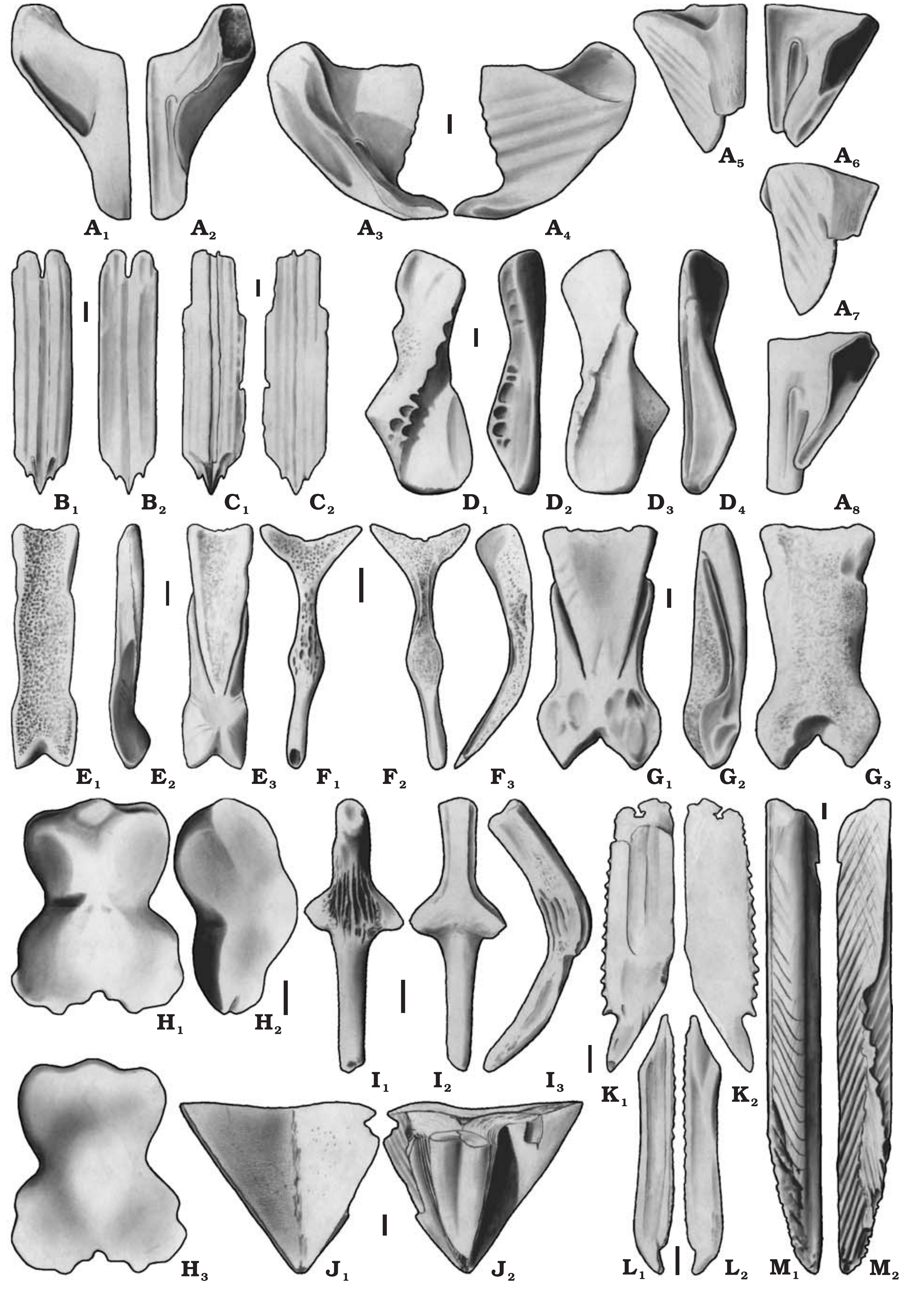
Remarks. — Lamellae of this type belong to the oligolamellar teeth of lepidocentrid echinoids (Jesionek-Szymańska 1982). Due to large size of the tooth lamellae the Aristotle's lantern must have been high, the teeth large and flat, the remaining elements of the Aristotle's lantern correspondingly massive but not so massive as in case of the type III lantern. In material from Poland there is some similarity of size and proportions with the fragments of II type lanterns. It is difficult to say if the lamellae belong to larger specimens with oligolamellar teeth of the type described above. These lamellae might represent *Lepidechinoides* sp. A.

Occurrence. — Late Eifelian: sets XVII, XVIII, XIX, XX, XXI of Skały. Late Givetian: trench II at Marzysz, Holy Cross Mountains, Poland.

Multilamellar tooth
(Pl. 11: 14; Text-fig. 34J)

Material. — Number of specimens and dimensions:

Fig. 34. Elements of Aristotle's lanterns from the Late Givetian of Marzysz, Holy Cross Mountains, samples Marzysz Ic/5 (A), Marzysz II/W/0 (B, D–E, I), Marzysz II/15 (C, H, M), Marzysz II/13 (F), Marzysz II/W/2 (G, J), and Marzysz II/7 (K–L). **A**–**F**. Elements of *Albertechinus devonicus* sp. n. **A**. Demipyramid GIUS 4-561 Mrz./852/1; A_1 external face, interambulacral side, A_2 inner face, A_3 internal face, view from the pyramidal suture, A_4 interpyramidal face, view from the interpyramidal muscles area (radial surface), A_5 oral view in closed position, A_6 apical view in closed position, A_7 oral view in open position, A_8 apical view in open position. **B**–**C**. Serrate teeth. **B**. GIUS 4-562 Mrz./141/1; B_1 abaxial view (outer), B_2 adaxial view (inner). **C**. GIUS 4-587 Mrz./984/1; C_1 abaxial view (outer), C_2 adaxial view (inner). **D**. Right epiphysis GIUS 4-562 Mrz./144/1; D_1 oral view (inside), D_2 right lateral view, D_3 apical view (outside), D_4 left lateral view, adaxial end is at the top of the figures. **E**. Rotula GIUS 4-562 Mrz./990/1; E_1 apical surface, E_2 side, E_3 oral surface, adaxial end is at the bottom of the figures. **F**. Compass, adaxial end is at the bottom of the figures, GIUS 4-584 Mrz./241/1; F_1 oral surface, F_2 apical surface, F_3 side. **G**. Rotula of type II pyramid GIUS 4-564 Mrz./1000/1; G_1 oral surface, G_2 side, G_3 apical surface, adaxial end is at the bottom of the figures. **H**. Rotula of type III pyramid GIUS 4-587 Mrz./1001/1; H_1 oral surface, H_2 side, H_3 apical surface, adaxial end is at the bottom of the figures. **I**. Compass of type II pyramid GIUS 4-562 Mrz./989/1; I_1 oral surface, I_2 apical surface, I_3 side, adaxial end is at the bottom of the figures. **J**. Multilamellar teeth GIUS 4-564 Mrz./490/1; J_1 adaxial face view, J_2 abaxial face view, showing S-like bending of lamellae, ridge is not a carina. **K**–**L**. Lamellae with a denticulate edge. **K**. Specimen GIUS 4-578 Mrz./289/1; K_1 internal surface view, K_2 external surface view (fragment). **L**. Specimen GIUS 4-578 Mrz./289/2; L_1 internal surface view, L_2 external surface view. **M**. Oligolamellar tooth GIUS 4-587 Mrz./979/1; M_1 adaxial view, M_2 abaxial view. Scale bar 200 µm.


A1
A2
A3
A4
A5
A6
A7
A8
B1
B2
C1
C2
D1
D2
D3
D4
E1
E2
E3
F1
F2
F3
G1
G2
G3
H1
H2
H3
I1
I2
I3
J1
J2
K1
K2
L1
L2
M1
M2

Material		Dimensions (μm)		
Number of specimens	Features	Minimum	Mean	Maximum
Teeth: 2	Length	1685	?	3500 (?)
	Width	2285	2740	3200

Description. — Large, multilamellar teeth, with complicated internal microstructure. Only the chewing tip and fragment of the shaft are known. Teeth of two halves, connected along the suture. Their adaxial face is flat and covered by uniform central and lateral fibro-lamellar prisms, and is marked by parallel grooves converging towards the tooth axis. Internal parts of the tooth are S-curved tooth plates (= lamellae). The abaxial face has a median ridge. This is not a carina as it occurs only at the adaxial face (Jensen 1981; Märkel 1970b, c; Märkel *et al.* 1977). A flat and narrow median flank covers the central groove. The lateral cylinder has a sharp edge.

Remarks. — This tooth is a little similar to keeled teeth of modern echinoids (*sensu* Jensen 1981). A similar internal structure occurs in the Echinothurioidea (of Märkel 1970a), and also more primitive representatives of Cidaroidea (Märkel and Titschack 1969). According to the classification of Jensen (1981) the tooth resembles the grooved teeth. This may represent the ancestral type for aulodont teeth (*sensu* Jackson 1912) or early "pedinoid" (*sensu* Smith 1981) e.g. *Diademopsis*, although they are more similar to the later diadematoid teeth (*sensu* Smith 1981; e.g. *Centrostephanus*). The described remains fit the type III Aristotle's lantern and they might belong to an echinoid such as *Meekechinus* sp. A.

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

Pedicellariae

Pedicellariae – morphotype IIa
(Pl. 12: 8)

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)		
Number of specimens	Features	Minimum	Mean	Maximum
Tridentate pedicellariae: 8	Length	505	575	600
	Valve width	220	290	330

Description. — Tridentate pedicellariae. Trivalved, thick-walled pedicellariae with guitar-shaped valves and rod-like blade. Distal edge of valve developed as a transverse bar, forming the base for the blade. Teeth on the gripping area are only weakly developed. Central and lateral cog-teeth are lacking, but at ca. one-third of the valve height there are two symmetrical processes, connecting the individual valves to each other. The keel is weakly developed in the proximal part of a valve. The handle (see Campbell 1983; Lawrence 1987) is semicircular, weakly developed and without an eye. The outer surface of the valve is concave. Stereom is typical for ophicephalous pedicellariae.

Remarks. — This form of pedicellaria is quite unlike any other known. It differs from morphotype IIb by its simplified structure, weakly developed end tooth (grasp) and lack of an outer process.

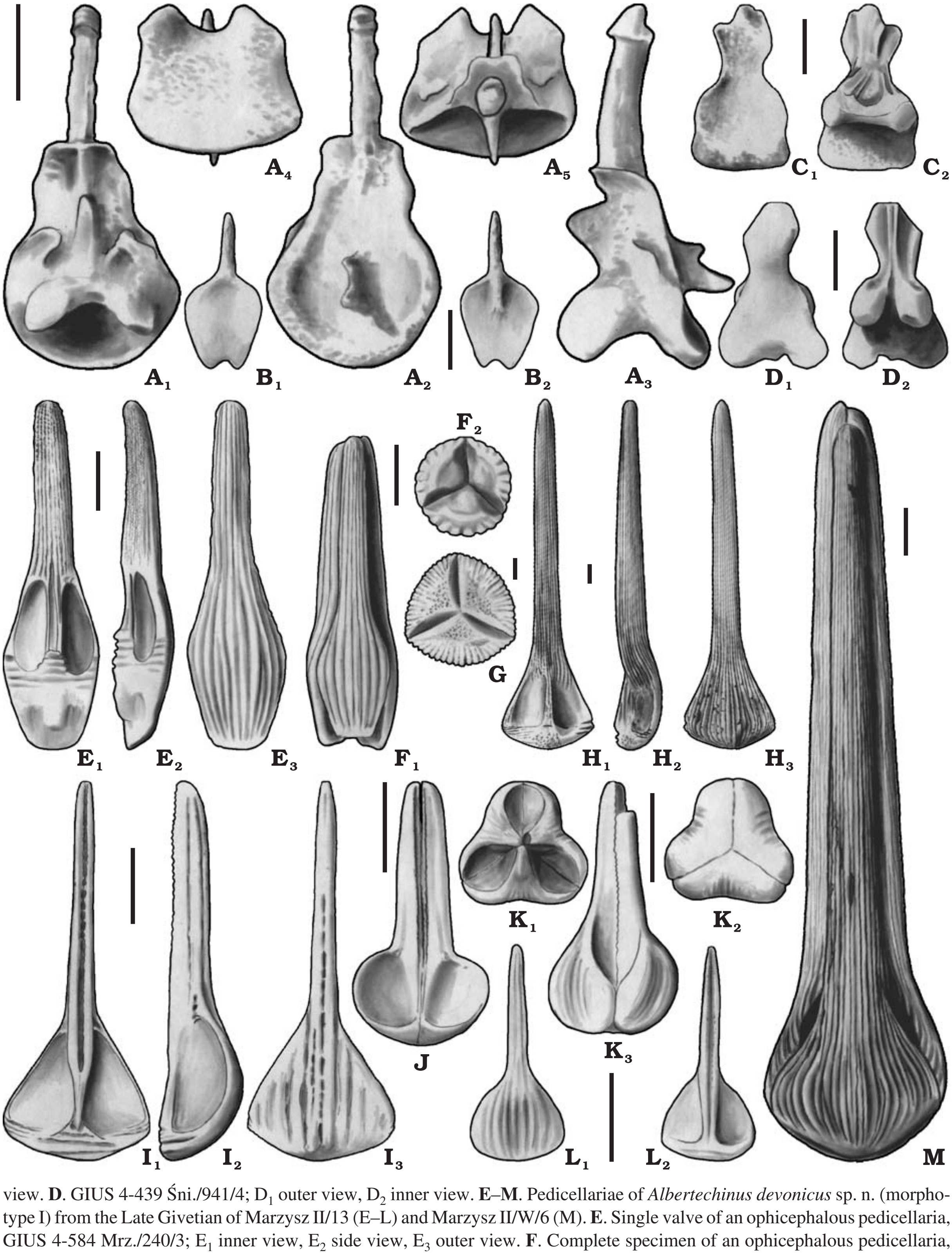
Occurrence. — Late Eifelian: sets XVII, XVIII of Skały, Holy Cross Mountains, Poland.

Pedicellariae – morphotype IIb
(Text-fig. 35A–D)

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)		
Number of specimens	Features	Minimum	Mean	Maximum
Tridentate pedicellariae: 14	Length	530	690	825
	Valve width	265	330	400
Ophicephalous pedicellariae: 4	Length	550	580	610
	Valve width	360	370	375

Fig. 35. Echinoid pedicellariae from the Givetian of the Holy Cross Mountains. **A–B**. Single valves of a tridentate pedicellaria, (morphotype IIb), Early Givetian of outcrop III at Śniadka. **A**. GIUS 4-439 Śni./941b/2; A_1 inner view, A_2 outer view, A_3 side view, A_4 proximal view, A_5 distal view. **B**. Juvenile form GIUS 4-439 Śni./941a/3; B_1 outer view, B_2 inner view. **C–D**. Single valves of ophicephalous pedicellariae (morphotype IIb) from same sample. **C**. GIUS 4-439 Śni./941c/5; C_1 outer view, C_2 inner →



view. **D**. GIUS 4-439 Śni./941/4; D_1 outer view, D_2 inner view. **E**–**M**. Pedicellariae of *Albertechinus devonicus* sp. n. (morphotype I) from the Late Givetian of Marzysz II/13 (E–L) and Marzysz II/W/6 (M). **E**. Single valve of an ophicephalous pedicellaria, GIUS 4-584 Mrz./240/3; E_1 inner view, E_2 side view, E_3 outer view. **F**. Complete specimen of an ophicephalous pedicellaria, GIUS 4-584 Mrz./240/4; F_1 lateral view, F_2 proximal view. **G**. Proximal projection of the complete, tridentate pedicellaria, GIUS 4-584 Mrz./237/2. **H**. Single valve of tridentate pedicellaria, GIUS 4-584 Mrz./237/1; H_1 inner view, H_2 side view, H_3 outer view. **I**. Single valve of tridentate pedicellaria, GIUS 4-584 Mrz./975/4; I_1 inner view, I_2 side view, I_3 outer view. **J**. Tridentate pedicellaria, two valves in natural position, GIUS 4-584 Mrz./975/2, specimen has been prepared. **K**. Tridentate pedicellaria, complete specimen GIUS 4-584 Mrz./975/3; K_1 distal view, K_2 proximal view, K_3 lateral view. **L**. Tridentate pedicellaria GIUS 4-584 Mrz./975/5; L_1 inner view, L_2 outer view. **M**. Complete, tridentate pedicellaria GIUS 4-568 Mrz./53/1, lateral view. Scale bar 200 μm.

Description. — Tridentate pedicellariae. Trivalved pedicellariae with external morphology as in the morphotype IIa (Text-fig. 35A). The valve's blade is well developed, and an outer process is present. There is a very short keel in the proximal part of the valve. The part corresponding to a handle is semicircular, well developed, and without an eye. The outer surface is concave, and surrounded by marginal swelling. At its centre, there is a blade-like process terminated by two spikes, the shorter one distal to the proximal one. Juvenile forms of tridentate pedicellaria (Text-fig. 35B) are also thin walled but differ in being spade-shaped. Its blade is straight and rodlike, with a length ca. half the height of a valve; on the inner side it enters the plate of the valve. The lower part of the valve in the shape of a thin plate, with the curved incision from the proximal side.

Ophicephalous pedicellariae. Trivalved, thick walled, and bottle-shaped in outline (Text-fig. 35C–D). They lack a blade and end tooth. The keel, if present, is up to half of the height of a valve. Central and lateral cog-teeth are also lacking and the central joint processes, which take the place of teeth, are very large and convex. The part representing a handle is variably blade shaped, well developed, and without an eye. The outer surface of the valve may be either concave or convex.

Remarks. — These tridentate pedicellariae differ from others of this type in having a well developed blade, and by the structure of terminal teeth and presence of an outer process. Among the Echinoidea slight similarities can be observed in pedicellariae from the Late Carboniferous of Graham Formation, Texas (Geis 1936: pl. 59: 28–34), *Collyrites* (*Cardiopelta*) *bicordata* (Leske) var. *baltica* Beurlen, 1934 from the Oxfordian of Switzerland (cf. Hess 1971), some pedicellariae of fossil irregular echinoids from the Maastrichtian of Rügen, Germany (Nestler 1966: pl. IV: 2–3), *Acanthotrema* (Recent, Baker, and Rowe 1990), and *Clypeaster* (Recent; Cherbonnier 1959). Similar pedicellariae occur mainly among irregular echinoids, a group which was absent in the Palaeozoic. Some juvenile tridentate pedicellariae are very similar to spines and resemble the oldest evolutionary tridentate types. Their structure is remarkably simple. They always co-occur with the pedicellariae of the morphotypes IIa and IIb.

The ophicephalous form differs from the type IIa in the outline of its valve, lack of blade and end tooth, and long keel. These elements show very strong morphological variability. Stereom and structure of both varieties is strongly reminiscent of ophicephalous pedicellariae.

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

Pedicellariae – morphotype III
(Text-figs 36, 37, 38)

1887. *Bursulella* gen. n.; Jones, pp. 1–8, figs 1–2.
1934. *Bursulella* Jones; Bassler and Kellett, p. 223.
1961. *Bursulella* Jones; Shaver (in: Benson *et al.*) p. Q412.
1978. *Bursulella* Jones; Kesling and Chilman, pp. 14–15, 115–116, 214–215, pls 6: 1–7; 106: 1–17.

Description. — Ophicephalous pedicellariae of bursulella-type. These pedicellariae consist generally of two, or rarely three, valves. In bivalved forms, each valve has two horns, commonly quite prominent and distally (apically) oriented (Pl. 13: 1–9; Text-figs 36, 41A–M, 42A–N, 43A–B, 44H–K). The outer surface of the valve is convex. Horns are half, usually one-third the height of a valve, but may form as much as two thirds of the height, and are commonly ornamented on their outer side (Pl. 13: 2–9; Text-figs 41A–F, 42H–L) with grooves, ridges, minute processes, pustulae or plicate crimps. Occasionally valves are totally smooth (Text-figs 36, 41I–M, 42M–N, 44H–K). On the inner side there are triangular, blunt teeth, laterally positioned and perpendicular or oblique to the valve wall; when the halves joined the teeth made a perfect fit (Pl. 13: 3–4, 8; Text-fig. 43A–B). Two rows of teeth can occur. Rows of teeth are better developed along the apical edge, and there are two to seven teeth in a row (Pl. 13: 1; Text-fig. 44H). Denticulation of this edge continues from one horn to another (Pl. 13: 3; Text-fig. $43A_2$). Adapically tooth size diminishes. The largest teeth are along the axial part of the valve (Pl. 35: 3; Text-fig. $44H_3$–H_5), where two to four teeth can be seen. On the lateral edge more delicate teeth may occur. These are weakly developed or coalesce into a single crest, of variable height (Pl. 13: 1c). In any case a narrow groove of varying depth develops between the inner edges of each pair of horns of adjoining halves; usually it can be clearly seen from the outside. The outer edge of horns commonly passes gradually into the marginal edge of the valve.

Just below the base of the small spines, on the edge of valve, the similar teeth can be seen again, two to five in number (Pl. 13: 1–9; Text-figs 36, 41A–M, 42A–N, 43A–B, 44H–K). Occasionally the marginal toothed edge (valve margin) adjoins not the lateral slat of the horns but the apical crest or to the middle part of

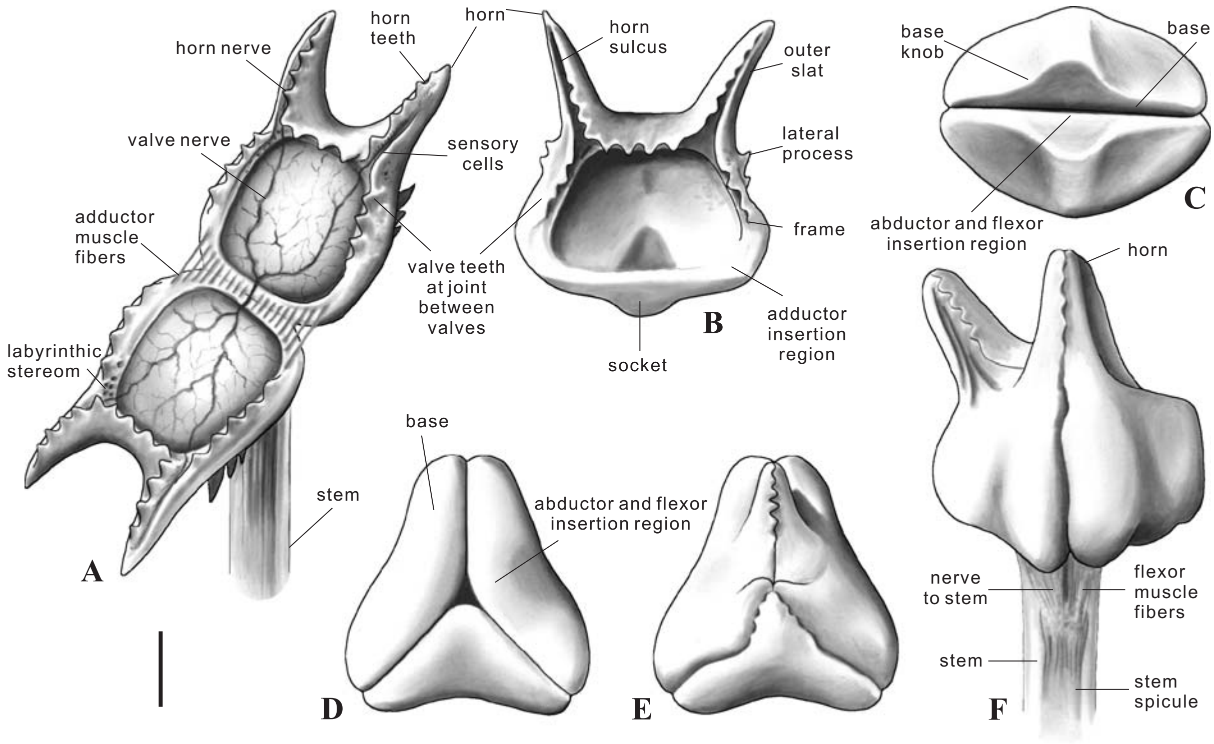


Fig. 36. Echinoid ophicephalous pedicellariae of bursulella type (morphotype III). **A**. Partial reconstruction of the bivalve pedicellaria. **B**. Details of a single valve, ventral view. **C**. Bivalve pedicellaria, proximal view. **D–F**. Trivalve pedicellaria, the body partially reconstructed; **D** proximal view, **E** distal view, **F** lateral view. Scale bar 200 μm.

the neural groove where it disappears (Text-figs 41A_1, C_2, 42H_3). Proximally tooth height is usually constant until they end. In some small (juvenile) specimens, or in specimens without external sculpture a lack of teeth is notable. In such cases a valve margin can be observed, with a somewhat sharpened and thinned edge (Text-figs 41F_2, G_2, H, 44J_2, K). At the base of the horn well preserved labyrinthic microstructure is usually visible. The same microstructure can be seen in large (> 0.5 mm) specimens at the base of teeth (Pl. 13: 1). When the valves are connected the line of contact is zig-zag in shape (Pl. 13: 3; Text-figs 36, 43A–B, 44K).

Proximal edge straight (Text-figs 41D, J_2, 42H_3), arched (Text-figs 42N, 44H) or wavy (Text-figs 41C_1, 43B, 44J). Sometimes, in small (juvenile) forms even straight edged valves were open proximally, along the whole width of the specimen (Text-fig. 41H). The larger valves with wavy margins, might be open proximally, the opening adjoining the short neck (Text-figs 41C, 44J). The neck was fixed to the centre of the basal surface (Text-figs 41J_2, 44K_2), in its axial part the base is usually expanded as an oval socket (Pl. 13: 1b, 2, 4; Text-figs 36C, 43A_1). On its outer surface its tapers to a narrow protuberance, the base knob, visible as a groove on the inner side (Text-figs 36B, 41A–B, D–F, 42B–L, O, 44H). In proximal corners on the inner side there is irregular labyrinthic stereom with characteristic needlelike calcite projections for adductor muscle attachment (Pl. 13: 1a).

Trivalved pedicellariae are generally similar, except for their base. In the only complete specimen no socket, but only a small, triangular pore can be observed (Text-figs 36D, 43B). The third valve of the pedicellaria has only one horn; the outer surface of all valves is concave (Text-fig. 36D–F). Possibly the trivalved forms are pathologic.

Globiferous pedicellariae of ladle type. These morphotypes differ from each other only in the relative development of blade and proximal edge. Attempted reconstructions are given in Text-figs 37 and 38. Basically the pedicellariae differ from the bursulella-type in having a single but very long horn (subsequently termed blade) and by the thin-walled structure of their valve. Only bivalved forms are known. Articulated valves are reported only from the Givetian of Siewierz (Boczarowski in Straszak 1986). Each half consists of three zones: valve, blade and terminal zone. The blade is a calcareous plate, ca. two-thirds to half of the specimen length. The valve is hemispherical in shape, with a more or less triangular outline. The entire element is ladle-shaped. Most specimens lack external sculpture.

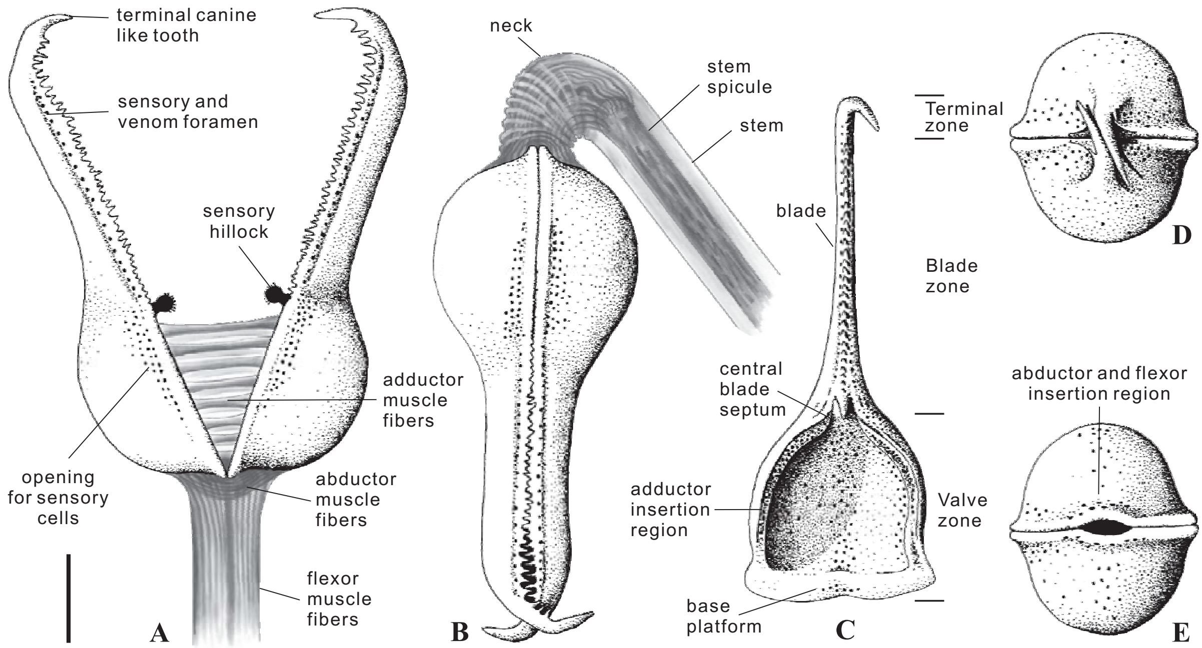


Fig. 37. Morphology of the echinoid bivalve globiferous pedicellariae of ladle type (morphotype III). **A**. Partial reconstruction of the pedicellaria with opened jaws. **B**. Partial reconstruction of the pedicellaria with closed jaws. **C**. Single valve, ventral view. **D**. Closed pedicellaria, distal view. **E**. Same in proximal view. Scale bar 200 µm.

The valve is thin-walled and built of simple perforate stereom (cf. Lawrence 1987). In the terminal zone the blade displays a single, sharp, usually hooked tooth (Text-figs 37, 38, 43C–O). When closed the terminal teeth of opposite valves fit tightly together (Text-fig. 37B, D). A blade can also be curved, with three to twenty subterminal teeth below the terminal tooth. Along the axis of a blade there are inner and outer teeth. The tooth edge occurs farther down the proximal part of blade, with accompanying increase of its height. In the blade zone a single median tooth and accessory teeth can be distinguish. Teeth are needle-like and circular in transverse section. In geologically older forms only big teeth occur, triangular in shape and devoid of accessory teeth (Text-fig. 42A–G). Also the double bladed channel of the venom vessels is lacking. The venom vessel and sensory nerve of the blade, together with venom nerves, lay in a partially covered perforated blade groove, the tooth row bordered the groove on one side. In more advanced forms there are two channels in the interior of a blade, separated by a central septum, developed as a simply perforate platelet (Pl. 13: 11–12, 16–17, 20; Text-figs 37, 38, 42A). The sensory and venom pores, piercing the ventral wall of a blade accompanied lumina in these channels. The central blade septum terminates at its base and only at this location can it be observed from outside (Pl. 13: 11; Text-fig. 38). The base of the blade and also the distal part of the valve zone externally is formed of irregularly labyrinthic stereom, without needle-like calcitic projections, passing into irregular perforated stereom. The wall is composed of simple perforate calcite. But the same zone on the inner side (edge part) has laminar stereom with characteristic needle-like projections. Adductor muscle attachment scar are prolonged as a valve margin towards the proximal part of the valve, forming a characteristic swelling of the marginal parts of the valves (Pl. 13: 10; Text-fig. 37D–E). The proximal edge is also swollen, but with the opposite relationships: the external microstructure is typical of the muscle attachment area, its presence may depend on preservation state of a given specimen. The internal one has a labyrinthic stereom. Fine pores (simple perforate stereom) penetrate throughout the valve. Most probably the pores were sensory ducts (Campbell 1973, 1974, 1976). The proximal edge of primitive forms is simple and has an eye-shaped plate, as in bursulella forms. On the other hand the basal knob is lacking, though, in some specimens slight deformation can be observed at the axis (Text-fig. 42C). More specialized forms have a basal platform in the proximal part of the base (Text-fig. 37C); its shape is diagnostic for the species. The basal platform usually has rounded corners and extends across the whole valve (seen internally). At the axial part there is oval incision forming an eye-like hole in closed valves, possibly a duct for nerves and

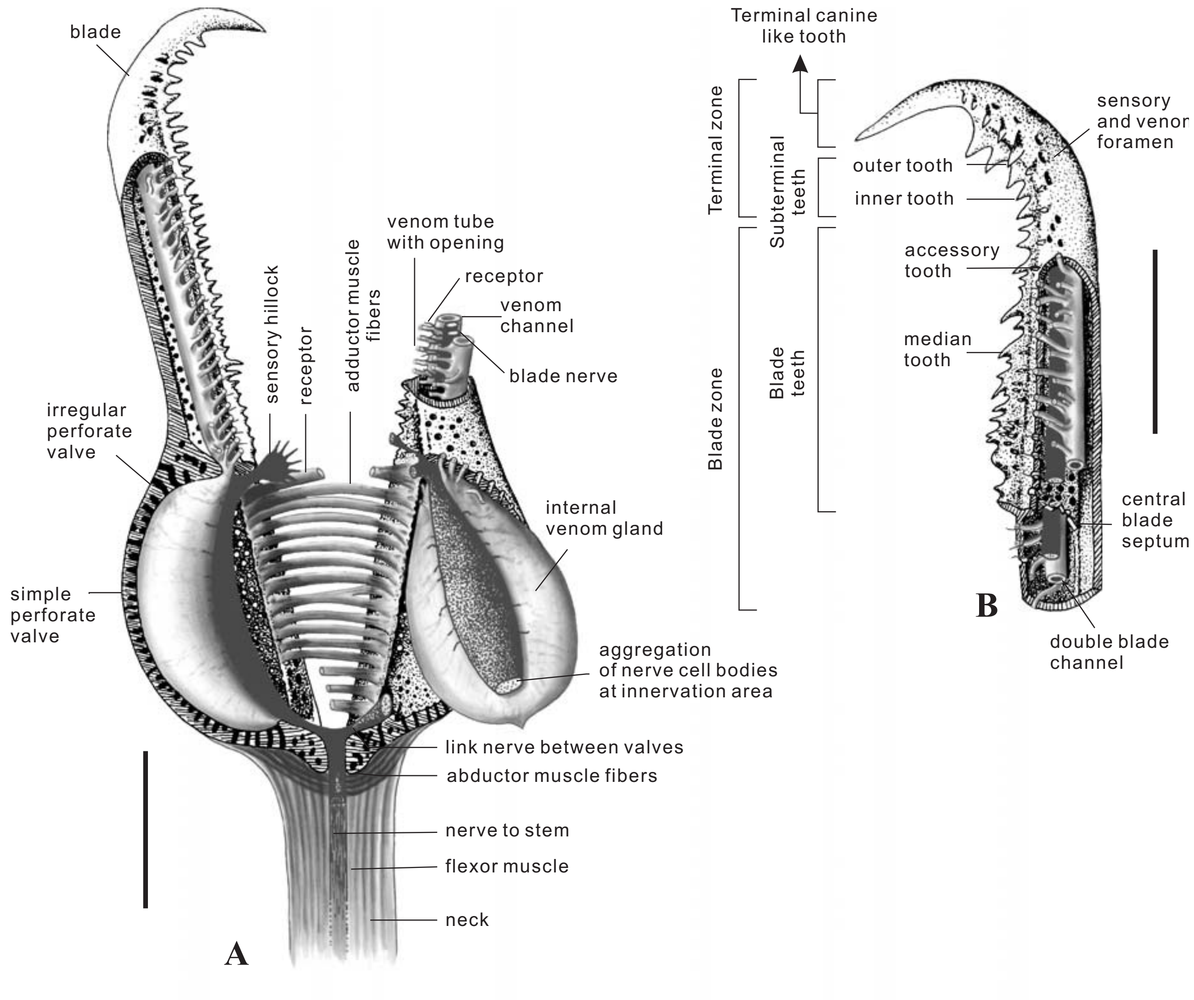


Fig. 38. Morphology of the echinoid bivalve globiferous pedicellaria of ladle type (morphotype III). Body in section. **A**. Reconstruction of pedicellariae body with opened jaws. **B**. Reconstruction of the blade. Scale bar 200 μm.

various vessels leading to the stem. The whole basal zone was also a region of insertion of the abductor and flexor muscles. Its shape enabled a very wide opening angle of the valves – 180° or even more.

Remarks. — As it will be concluded in the discussion below, *Bursulella triangularis* Jones, 1887 is a valid name for a Silurian echinoid. However, although the Devonian pedicellariae are closely similar to those from the type population of *Bursulella* it would not be reasonable to assume that their bearers were so similar also in other anatomical features. As a rule the ophicephalous pedicellariae have blunt jaws supplied with grasping teeth and each head sits on a flexible neck, which acts as a hydroskeleton and takes part in their proper orientation (Campbell 1973, 1974, 1976, 1983; Lawrence 1987). The teeth are also short and blunt (Lawrence 1987) and usually occur at the margins of jaws (Baker and Rowe 1990; McNamara and Henderson 1984). The pedicellariae described herein usually have similar teeth (Pl. 13: 1–9; Text-figs 36, 41A–M, 42A–N, 43A–B, 44H–K). Significantly, the collagen fibres, joining the stem skeleton with proximal parts of the valves (Lawrence 1987) transfer the activating and moving forces of these pedicellariae. Therefore the capturing force is not limited by the strength of the jaw's muscles alone. In bursulella-type pedicellariae a muscle insertion region can be clearly seen as an oval socket in the distal parts of the halves (Pl. 13: 2; Text-fig. 36C). In some specimens there is labyrinthic stereom with needle-like projections preserved on the outer surface of the socket, possibly the attachment area for the muscles. In both modern and fossil, pedicellariae of this type the structure of jaws allows for very tight and strong grip, especially the primitive pedicellariae of the bursulella-type of which large numbers with closed valves have been discovered (Pl. 13: 2–4; Text-figs 43A–B, 44K). Whereas in modern forms there is occasionally a small gap, opening towards the interior, midway up the valves, in the bursulella-type the valves are closed tightly. In extremely rare spec-

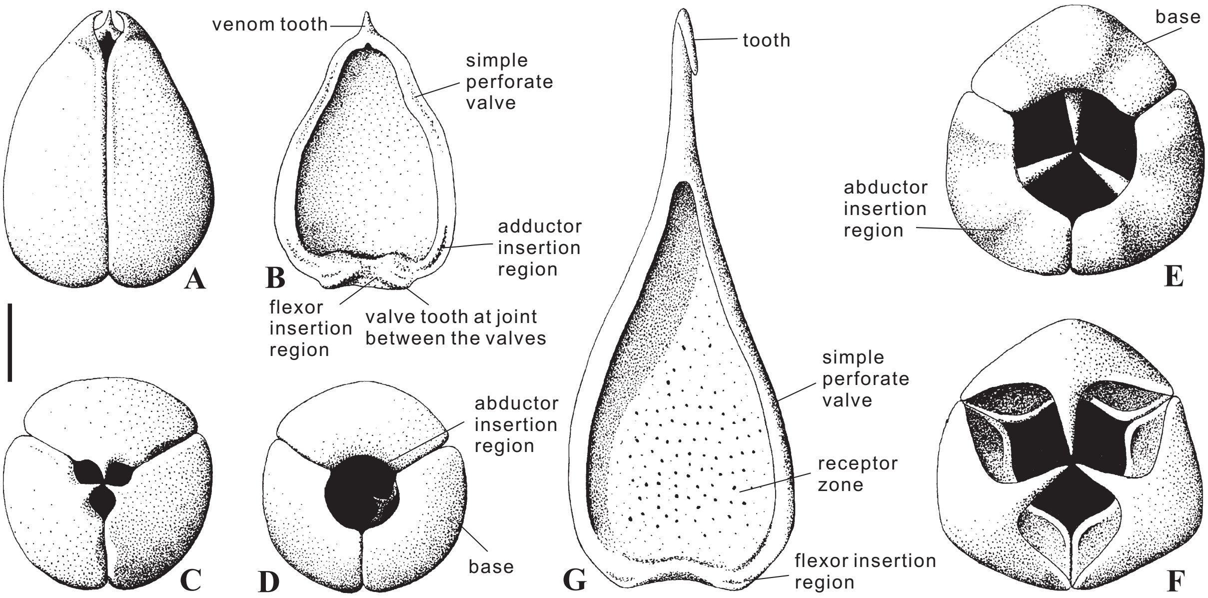


Fig. 39. Morphology and reconstruction of echinoid pedicellaria morphotype IV. **A**–**D**. Trivalve globiferous pedicellaria with closed jaws; **A** lateral view, **B** inner view, **C** distal view, **D** proximal view. **E**–**G**. Tridentate pedicellaria. **E**. Specimen with closed valves, proximal view. **F**. The same, distal view. **G**. Details of a single valve. Scale bar 200 μm.

imens with three valves (Text-figs 36C–F, 43B), there may be a small triangular opening, instead of a socket. The remaining margins of the valves fit closely, without any gap (Text-figs 36D–F, 43B).

Ophicephalous pedicellariae of the bursulella-type differ from the Silurian forms by their stronger development of horns and by their more complicated external sculpture (cf. Jones 1887). The Devonian forms from North America are most similar to morphotype IIId, but have a different outline and shape of horns, and different tooth arrangement. The American specimens have a much larger number of teeth and these teeth are not so sharp (cf. Kesling and Chilman 1978). In the groove on the inner surface of the horns there were most probably nerves, accompanied by the sensory cells. The receptors under consideration must have been of mechanical type so in the ophicephalous pedicellariae they were present in an open groove. Dissimilarity of the juvenile forms is not unusual (Mortensen 1928–1951; Tyler and Gage 1984). Labyrinthic stereom at the base of the horns suggests the presence of collagen microfibres.

Ladle-type pedicellariae are more numerous, and even mass-occur in some samples (e.g. Marzysz II/7, layer 7). Gradual differentiation of these pedicellariae is quite distinguishable. Their structure becomes gradually more complicated; as in the case of their ophicephalous counterparts, there is a gradual disappearance of external sculpture. Analogies in structure with the bursulella form suggest they belonged to the same echinoid species.

Discussion. — When in 1887 T. Rupert Jones discovered peculiar, small, horny valves in his samples from the Wenlock of Gotland Island, he classified them as ostracods, placing them in the genus *Bursulella*. Numerous, well preserved fossils of these forms from the Givetian Silica Formation of Michigan were described by Kesling and Chilman (1978), occasionally with closed valves.

For over 100 years the ostracode nature of these fossils was not questioned. On the other hand both microstructure and morphology indicate they are pedicellariae of Echinoidea. The following observations support their affinity to Echinoidea:

1. In thin section bursulella-type fossils, in polarised light, each sclerite is optically a single crystal, typical of echinoderm elements. This is not the case with ostracods, as their valves are composed of numerous and variously optically oriented calcitic prisms and lamellae. The bursulella sclerites exhibit echinoderm stereom: labyrinthic, laminar with or without the needle-like projections, simple perforate, both on the outer and at the inner surface of the valves (Pl. 13: 1). The valves of do not develop the laminated structure, typical of the Ostracoda (cf. Levinson 1961). Nor are they differentiate into external and internal layers.

2. No ostracod-type articulation (*vide* Scott 1961a, c) can be seen in the material studied. The bursulella-type articulation is unlike that of any ostracods.

3. Muscle scars and an ocular prominence on the internal surface of valves are lacking.

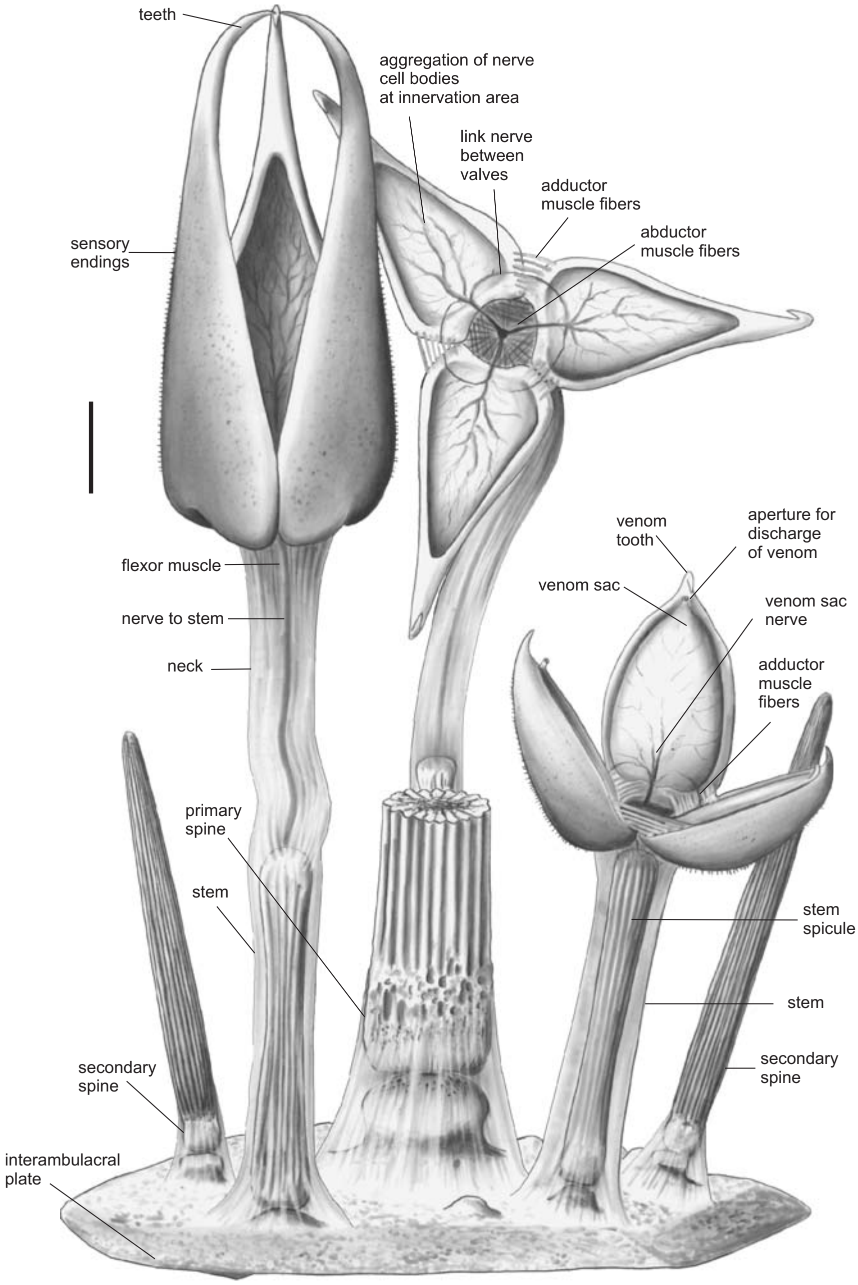


Fig. 40. Morphology of echinoid pedicellariae body (morphotype IV). Idealised reconstruction of the interambulacral plate with the primary and secondary spines. Scale bar 200 μm.

4. Occasional presence of trivalved forms, typical of pedicellariae, makes the ostracod interpretation impossible. The symmetry is biradial not bilateral (cf. Scott 1961b).

5. Fossils of the bursulella-type are accompanied by other echinoderm remains, particularly by the Echinoidea and Ophiocistioidea. They could not be found in assemblages dominated by the ostracods.

6. Numerous spiny forms of Ostracoda are known (Benson *et al*. 1961), but the distribution and development of the spines is different from that observed in bursulella.

Pedicellariae occur not only in the echinoids but also in starfish, but the bursulella-type display the following differences in respect to the starfish pedicellariae:

1. Elementary pedicellariae. Spiniform pedicellariae usually consist of six to eight weakly differentiated valves with small spines on their inner surface (Jangoux and Lambert 1988). In straight pedicellariae formed by two valves only, their base is massive, with an opening (cf. Jangoux and Lambert 1988; Roberts and Campbell 1988).

2. Alveolar pedicellariae. Complex pedicellariae developed within the alveolae do not resemble bursulella at all (cf. Jangoux and Lambert 1988). Although simple formsmay consist of two valves, their structure is more or less the same as the elementary pedicellariae.

3. Complex pedicellariae. The simple form in general outline resembles described bursulella but the third element forms a basis for the remaining valves. The cd pedicellariae type shows jaws resembling the blades typical of the globiferous bursulella, as they bear teeth, and their halves are similar rather to the arm hooks of the Ophiuroidea (cf. Jangoux and Lambert 1988; Lawrence 1987; Roberts and Campbell 1988).

The studied collection contains rare sclerites of possible starfish origin, but their taxonomic identification would require more numerous material. As pedicellariae are not known in the Ophiocistioidea, the only echinoderms possibly bearing elements of the bursulella-type remain the Echinoidea (?). Pedicelarial preservation requires special condition, relatively few species of echinoids from the palaeozoic have been reported with pedicellariae attached. So there is still a real possibility that they could come from Ophiocistioids. Echinoid remains often co-occur with ophiocistioid fossils, but in articulated fossils of ophiocistiods the pedicellariae are absent (e.g. Haude and Langenstrassen 1976b; Jell 1983).

Among them, cidaroids and the other Perischoechinoidea do not have ophicephalous pedicellariae, which are restricted to the Euechinoidea (Durham 1966b). Some forms have two types of them, e.g. *Arbacia* Gray, 1835 (cf. Campbell 1983). The bursulella-type pedicellariae are then the oldest ophicephalous forms. They may represent the ancestral form of pedicellaria of the modern Euechinoidea (cf. Durham 1966a–d; Durham *et al*. 1966; Durham and Melville 1957; Jensen 1981; Kier 1974). Among the oldest echinoids, closed pedicellariae are known in two Silurian species (Blake 1968). These pedicellariae do not differ significantly in their structure from spines. Therefore it seems probable that the pedicellariae are derived from spines (Blake 1968). In juvenile bursulella an eye-shaped opening occurs, visible in closed valves; with subsequent growth the opening disappeared. This also occurs in typical ophicephalous pedicellariae, where a duct is present at the proximal margin, which opens towards the neck. Although in some extant forms bivalved pedicellariae are not rare, e.g. in *Echinarachnius* Gray, 1825 (cf. Hyman 1955; Mortensen 1948b), no test can be matched with the bursulella-type pedicellariae. In the Devonian numerous echinoids with ophicephalous pedicellariae existed, as can be seen from the diversity represented in the present collection.

Globiferous pedicellariae of the ladle-type represent a new, earlier unknown variety. Stepwise etching of plates has revealed details of their internal structure. The frequency of these elements may be occasionally enormously high (e.g. Marzysz Ic/5), which suggests that the pedicellariae were capable of autotomy, as in living echinoids. The Devonian specimens are the oldest globiferous pedicellariae known to date; previously the oldest trivalved pedicellariae were described from the Pennsylvanian Graham Formation, Texas (Geis 1936).

Occurrence. — Bursulella pedicellariae. Wenlock: cephalopod limestone at Samsung (uppermost part of the Slite Beds) and Othem, Gotland. Givetian: Silica Formation of Michigan. Eifelian–Frasnian: various limestones and shales in the Holy Cross Mountains, Poland. Early Carboniferous: Dębnik, Poland. Ladle pedicellariae in the Eifelian–Frasnian: together with bursulellas in the Holy Cross Mountains, Poland. Givetian: Dziewki limestone at Siewierz, Poland.

Pedicellariae – morphotype IIIa
(Pl. 13: 1; Text-figs 41A–M, 42A–G)

Material. — Number of specimens and dimensions:

Material			Dimensions (μm)		
Number of specimens	Features		Minimum	Mean	Maximum
Ophicephalous pedicellariae: 48	Length (spiculate form)		170	605	1080
	Valve width (spiculate form)		215	540	835
	Length (smooth form)		355	540	835
	Valve width (smooth form)		365	490	790
Globiferous pedicellariae: 29	Length		650	1405	1715
	Valve width		325	580	890

Description. — Ophicephalous pedicellariae – spiculate form. Bivalved, both large and small (juvenile?) specimens have two horns on each valve, reaching from half to two-thirds of its height. On the inner side of the horns well developed neural grooves are visible, flanked laterally by sharp-edged ridges and adapically by five to eight teeth. The outer surface of horns is covered by sharp-edged riblets. On the outer surface of the valve there are numerous, long (up to 0.15 mm), apically oriented spines. In the axial part fine vertical riblets may occur. The margin of the valve bears four to six teeth. Smaller specimens do not have any teeth, the smallest ones lack even ornamentation of their horns. The basal knob is clearly differentiated and covered by pustulae and fine spines (Pl. 13: 1; Text-fig. 41A–H).

Ophicephalous pedicellariae – smooth form. Bivalved pedicellariae, with two horns on each valve, reaching up to one-third of its height (Text-fig. 41I–M). The horns have the inner neural grooves, flanked laterally by sharp-edged ridges and by apical teeth (two or three). At the distal edge there are large teeth (up to three). The outer surface is smooth. The valve margin has two to five denticles. There is no basal knob developed and the abductor and flexor insertion region is flat and eye-shaped (Text-fig. 41J_2). Valves, when closed, fit tightly together.

Globiferous pedicellariae. These are spoon-shaped bivalved forms (Text-fig. 42A–G). Juvenile specimens are in the shape of a narrow triangle (Text-fig. 42D). The blade is provided with large triangular teeth (eight to fourteen) and terminates with a tooth, of the same size as the others. In large specimens the teeth have deep grooves along their inner (osculation) surface. The groove housing the venom channel and neural stem is partly open, with a perforate bottom. The pores increase in diameter proximally. One incomplete specimen suggests that venom channels run side by side below the perforation (Text-fig. 42G). Closure of valves resulted in occlusion of the blades, along a zig-zag suture. A groove on the other side of the blades probably held receptors. The dense perforation typical for this morphotype is lacking on lateral surfaces, being replaced by large pores (Text-fig. 42G). The proximal edge is simple and forms an eye-shaped plate, similar to that in bursulella-type pedicellariae, but without the basal knob; in some specimens the axial part is deformed (Text-fig. 42C). Borders of the valve are armed with three to six strong, triangular teeth (Text-fig. 42A–G). In large specimens, ribs and furrows, connecting apically, are present internally (Text-fig. 42G). The proximal edge is straight or curved in older specimens. It forms an eye-shaped plate, similar to that in ophicephalous pedicellariae. A basal knob is lacking, although in some specimens a slight elevation can be observed in their axial part (Text-fig. 42C). The proximal surface is built of labyrinthic stereom with projections for muscle attachment (Text-fig. 42C_2), but the valves are devoid of any perforation, being thick-walled even in juvenile specimens (Text-fig. 42D). Small specimens of spiculate ophicephalous pedicellariae lack external sculpture, which thus developed gradually through ontogeny (Text-fig. 41A–H). With increasing size the proximal edge became more and more wavy (Text-fig. 41C), whereas the proximal openings gradually disappeared from both margins leading the centre. Neural grooves are clearly visible in all specimens. The occasional occurrence of trivalved forms is confirmed by the presence of some isolated valves with an angle of 120–140° between the arms of the proximal edge (Text-fig. 41C).

Remarks. — Morphotype IIIa ophicephalous pedicellariae differ from the others by prominent sculpture, although the smooth form of bursulella-type pedicellariae always co-occurs. Globiferous pedicellariae, however, are always sculpted of the second type seem thus missing. A similar relationships can be observed in other assemblages of pedicellariae (e.g. Marzysz). Type IIIa globiferous pedicellariae differ from others in having strong, triangular teeth along the valve instead of caninelike terminal, subterminal and accessory teeth. They also lack a curved distal end, have characteristically thick-walled valves, and lack a double channel in the blade, and lack valve margin and basal platform. Specimens from Siewierz are somewhat similar, but they lack teeth on the blade, teth being restricted to the valve.

Occurrence. — Late Eifelian: sets XIV, XV, XVII, XVIII of Skały. Early Givetian: outcrop III at Śniadka, Holy Cross Mountains, Poland.

Pedicellariae – morphotype IIIb
(Pl. 13: 5, 18; Text-fig. 43O)

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)		
Number of specimens	Features	Minimum	Mean	Maximum
Ophicephalous pedicellariae: 12	Length	330	370	400
	Valve width	410	505	545
Globiferous pedicellariae: 7	Length	565	715	745
	Valve width	270	300	325

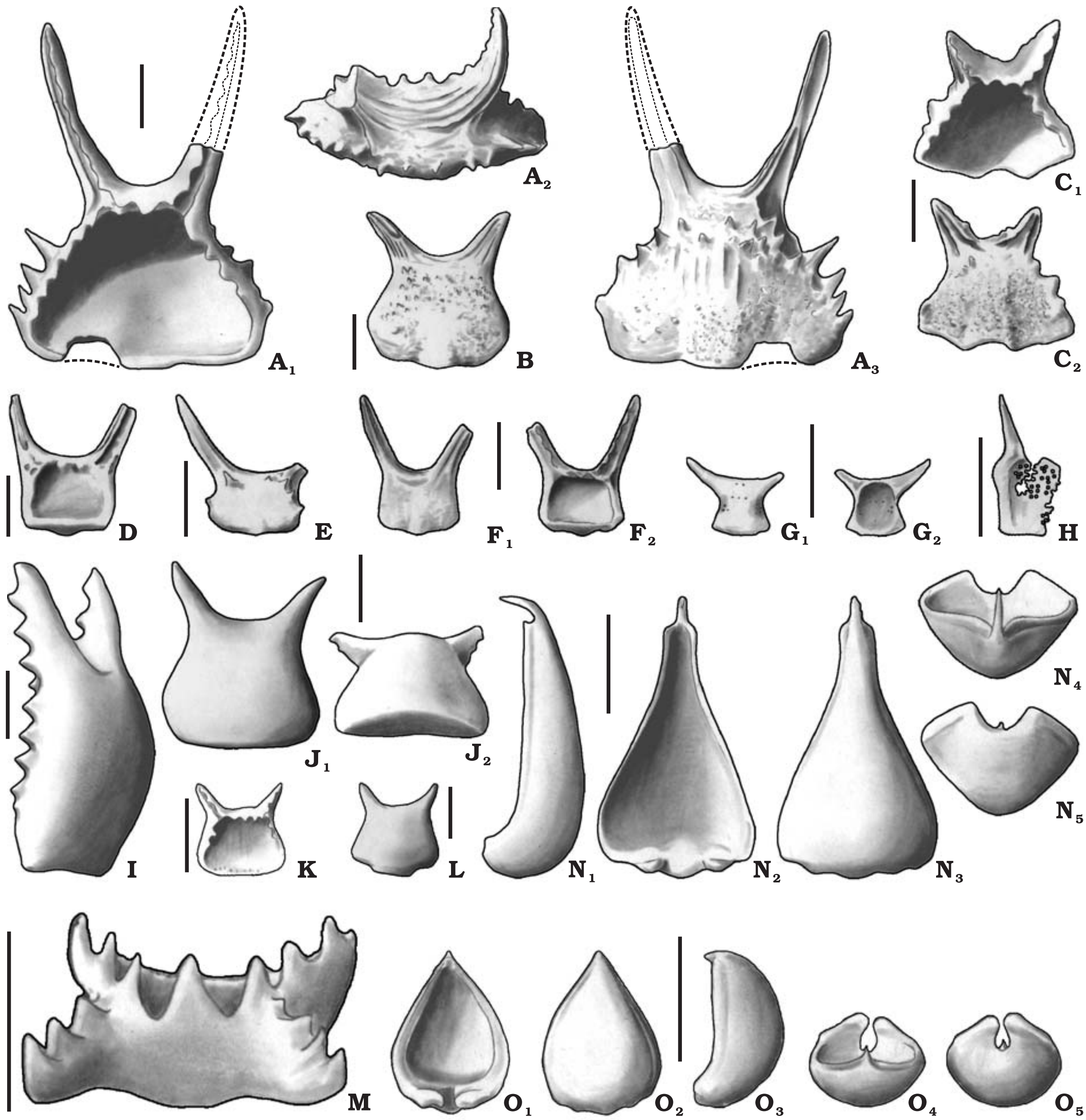


Fig. 41. Pedicellariae from the Early Givetian of outcrop III at Śniadka, Holy Cross Mountains. **A**–**H**. Echinoid ophicephalous pedicellariae of bursulella subtype. Spiculate form of morphotype IIIa. Ontogeny of these specimens is presented. **A**. Single valve GIUS 4-439 Śni./944/2, in partial reconstruction; A_1 inner view, A_2 proximal view, A_3 outer view. **B**. GIUS 4-439 Śni./944/3, outer view. **C**. GIUS 4-439 Śni./944/1; C_1 outer view, C_2 inner view. **D**. Small or juvenile form GIUS 4-439 Śni./944/8, inner view. **E**. Juvenile form GIUS 4-439 Śni./944/6, outer view. **F**. Juvenile form GIUS 4-439 Śni./944/5; F_1 outer view, F_2 inner view. **G**. Juvenile form GIUS 4-439 Śni./944/13; G_1 outer view, G_2 inner view. **H**. Juvenile form with very thin valve, GIUS 4-439 Śni./944/12, inner view. **I**–**M**. Echinoid ophicephalous pedicellariae of bursulella subtypem; sooth form (morphotype IIIa). **I**. Large single valve GIUS 4-439 Śni./944/4, lateral view. **J**. GIUS 4-439 Śni./944/7; J_1 outer view, J_2 oblique view. **K**. Single small valve GIUS 4-439 Śni./944/10, inner view. **L**. Small single valve GIUS 4-439 Śni./944/11, outer view. **M**. GIUS 4-439 Śni./944/9, proximal view. **N**–**O**. Trivalve pedicellariae (morphotype IVa); single valves. **N**. Tridentate elongate form GIUS 4-439 Śni./943/1; N_1 lateral view, N_2 inner view, N_3 outer view, N_4 distal view, N_5 proximal view. **O**. Globiferous dumpy form GIUS 4-439 Śni./943/2; O_1 inner view, O_2 outer view, O_3 lateral view, O_4 distal view, O_5 proximal view. Scale bar 200 μ.

Description. — Ophicephalous pedicellariae. They are bivalved, with two horns to each valve, up to quarter of their height. Short neural grooves are well developed on the inner side on the horns, bordered on each side by a toothed ridge, and apically by small teeth (2–3). The apical edge is usually long, with four or five teeth. On their outer side the horns are covered by riblets. The outer surface of the valve is covered in fine wrinkles and pustules. Margins of the valve have weakly developed teeth (0–2). Smaller specimens lack teeth, and the indistinct basal knob is covered by pustules. The proximal edge is somewhat wavy, so that axial parts of the valve did not fit tightly together, leaving a small eye-shaped slit.

Globiferous pedicellariae. These are bivalved, smooth, and thin-walled. The blade, forms ca. one-third of the height of the whole pedicellaria and has a flat terminal tooth. The distal end of the blade is slightly curved, but without any subterminal teeth. Mid-length there are occasionally fine median teeth, but accessory teeth are lacking. Along the lateral sides of some elements numerous venom and/or sensory pores may occur (Text-fig. 43O). The central blade septum is clearly distinguishable proximally. The marginal ridge of the valve passes onto the blade, so that three parallel blades are developed at its base. Teeth are lacking; only fine crenulation can be observed there. The base is straight, with an incision in its axial part (Pl. 13: 18).

Remarks. — Ophicephalous pedicaellariae of this type are similar to type IIIc of the ophicephalous pedicellariae. On the other hand the globiferous pedicellariae differ from all others by their relatively long distal edge and by the development of teeth (four or five in number) there. Neither their stratigraphical distribution nor analysis of frequency indicates relationship to any other skeletal elements. Moreover, in the Mid Givetian two distinct populations can be traced, represented by ophicephalous and globiferous pedicellariae. At Laskowa Góra (sample V/2) the morphotype IIIb occurs without any other types. Ophicephalous pedicellariae differ from the other types by development of the terminal tooth and structure of the basal platform.

Occurrence. — Mid Givetian: set B of Laskowa Góra. Mid–Late? Givetian: set A of Szydłówek, Holy Cross Mountains, Poland.

Pedicellariae – morphotype IIIc
(Pl. 13: 2–4, 6–17, 19–20; Text-figs 42H–O, 43A–N)

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)		
Number of specimens	Features	Minimum	Mean	Maximum
Ophicephalous pedicellariae: > 500	Length (spiculate form)	660	790	940
	Valve width (spiculate form)	410	545	600
	Length (smooth form)	295	330	410
	Valve width (smooth form)	305	465	550
Globiferous pedicellariae: 161	Length	570	1200	1745
	Valve width	275	585	820

Description. — Ophicephalous pedicellariae of spiculate form. These were bi- or trivalved. In the first case two horns occur on each valve, in the second case the third valve has one horn only (Text-figs 36E, F, 43B); the horns reaching up to half of the height of a valve. Horns, though usually radiating, may be parallel (Pl. 13: 7; Text-fig. 42K). The neural grooves are well developed, bordered laterally by a low, blunt ridge, and apically by distinct teeth (two to six). The apical edge (distal) may be short (Text-fig. 42K) and has three to four teeth. Horns are covered by riblets dorsally and the entire valve has fine wrinkles and pustules. The lateral edge of the outer surface of the valve may occasionally display numerous, short and sharp, apically oriented spines (Pl. 13: 4; Text-fig. 42H–L, O). Occasionally, fine spines occur over part of a valve (Pl. 13: 6). Sculpture of the external surface is strongly variable. The marginal ridge has variably developed teeth (two to four), disappearing proximally and lacking in smaller specimens. The basal knob is very distinct and either smooth (Text-fig. 42O) or pustulate (Pl. 13: 4, 8). The proximal edge is straight; in the axial part of a valve there occurs a distinct eye-shaped basal knob, marking the place of muscles attachment. In bivalved forms the valves are convex, in trivalved ones slightly concave in their axial parts (Text-figs 36E, F, 43B). Juvenile forms have finer sculpture, without the teeth and are always closed along the proximal side.

Ophicephalous pedicellariae – smooth from. Bivalved pedicellariae, each valve of which bears two very short and expanding horns, reaching up to quarter of its height. Neural grooves are almost invisible. Teeth occur only at the distal edge (seven to eight), although occasionally a single tooth is found near the base of the horn. The outer surface of the horns is covered by delicate riblets, the remaining surface is smooth. A basal knob does not occur. On the basal surface of each half a narrow, eye-shaped depression can

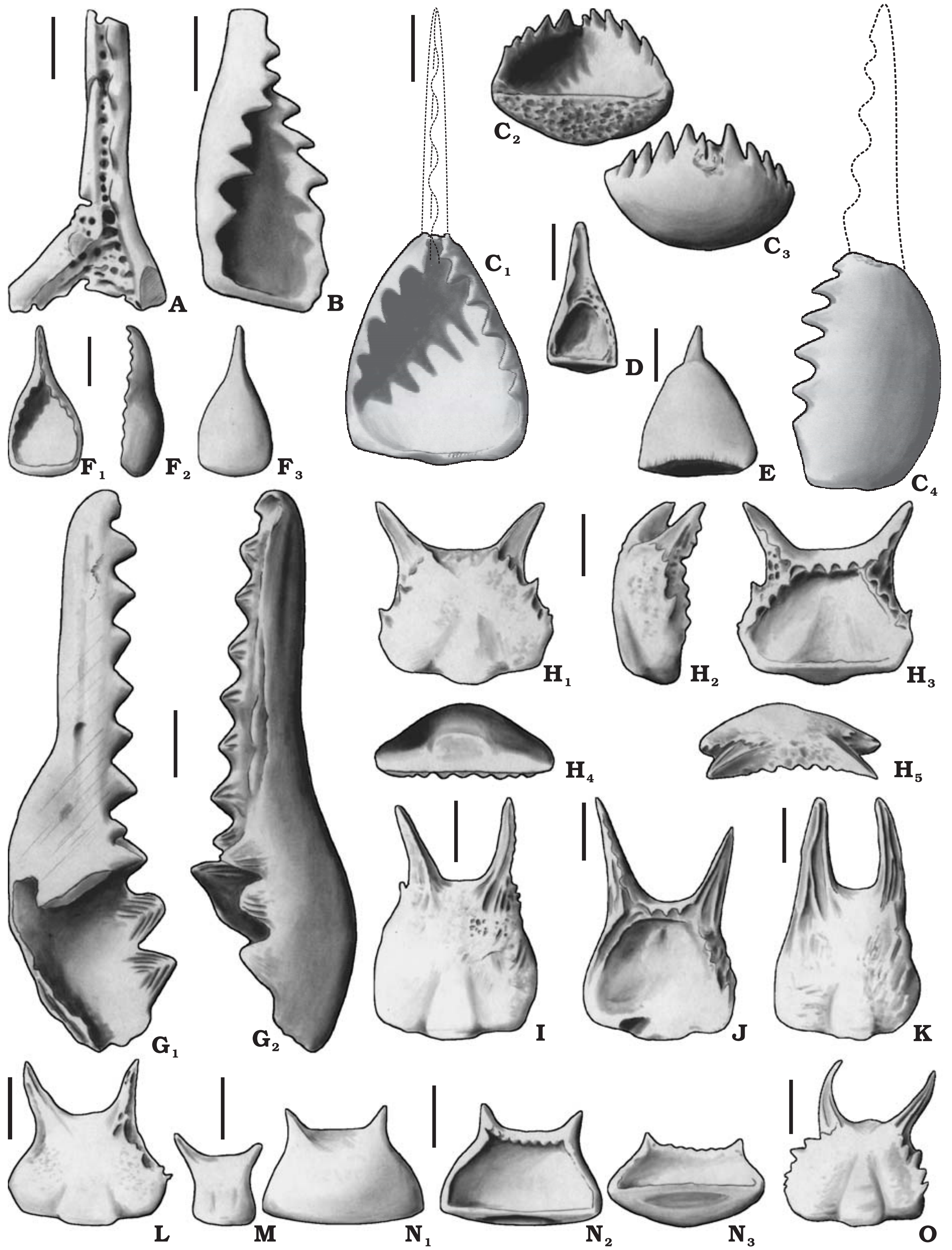


Fig. 42. Echinoid pedicellariae from the Givetian of the Holy Cross Mountains. **A**–**G**. Globiferous pedicellariae, ladle form (morphotype IIIa) from the Early Givetian of outcrop III at Śniadka. **A**. Fragment of a single valve with well preserved labyrinthic echinoderm microstructure, GIUS 4-439 Śni./942/1, inner view. **B**. GIUS 4-439 Śni./942/2, lateral-oblique view. **C**. Partially reconstructed smooth single valve GIUS 4-439 Śni./942/3; C_1 inner view, C_2 proximal-oblique view, C_3 distal-oblique view, C_4 lateral view. **D**. Small or juvenile form GIUS 4-439 Śni./942/5, inner view. **E**. Juvenile form GIUS 4-439 Śni./942/7, outer view. **F**. GIUS 4-439 Śni./942/4; F_1 inner view, F_2 lateral view, F_3 outer view. **G**. Fragment of very large specimen with ribbed teeth, GIUS 4-439 Śni./942/6. **H**–**O**. Echinoid ophicephalous pedicellariae of bursulella-type, single valves, ➛

be seen. The proximal edge is straight (Text-fig. 42N). These forms occur at low frequency, i.e. about 0.05% (Text-figs 42H–O, 43M–N). Juvenile forms are rare.

Globiferous pedicellariae. Bivalved form, thin-walled and ladle-shaped, with well developed blade usually forming two-thirds of its height. There is a terminal tooth and below it an accessory and median subterminal teeth. The subterminal zone is to a various degree curved (Pl. 13: 20; Text-fig. 43C–N). Occasionally, an expanded region with numerous subterminal teeth can be seen in the subterminal zone (Text-fig. 43L). Lateral surfaces of the blade are perforate, particularly near the central blade of a septum, the latter passes into the tooth ridge at the external surface. This simple perforate septum in the interior divides the blade into two channels (Pl. 13: 11–12, 16). The valve margin only partly coincides with the septum, as it terminates at the base of a blade and is bordered by very fine teeth. The valve has very numerous pores, especially along its lateral edges. The proximal edge is straight or slightly wavy. It has a delicate incision, leaving an eye-shaped when at closure of the valves are closed, a possible duct for nerves and the other internal systems. Also the basal platform is visible along this edge. The microstructure is as described for the main type above (see pedicellariae – morphotype III).

Remarks. — Ophicephalous pedicellariae are generally similar to the morphotype IIIb but differ in having more complicated external sculpture, stronger teeth and the presence of a short distal margin. The smooth form is only a morphological variation of the general type, as all the samples contain a single type of the corresponding globiferous pedicellariae, in an expected frequency (as found for the IIIa morphotype). The smooth variety has a somewhat narrower stratigraphic range – Late Givetian. Possibly this is an evolutionarily progressive form, the more so since Frasnian pedicellariae of this type lack any external sculpture. From the remaining types the globiferous pedicellariae differ in having a more complicated structure to their blade, a different valve shape and a flat basal platform. Pedicellariae of this type, occur in great abundance.

Occurrence. — Mid–Late Givetian: set A of Górno. Mid–Late Givetian: set B of Jaźwica. Late Givetian: set B of Czarnów; set A of Wietrznia Ia; set A of Wietrznia II; outcrop I, trench II at Marzysz; set B of Posłowice; set C of Sowie Górki set; sets B, C of Stokówka, Holy Cross Mountains, Poland.

Pedicellariae – morphotype IIId
(Text-fig. 44H–N)

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)		
Number of specimens	Features	Minimum	Mean	Maximum
Ophicephalous pedicellariae: 26	Length	580	485	330
	Valve width	515	400	270
Globiferous pedicellariae: 16	Length	810	580	410
	Valve width	500	329	215

Description. — Ophicephalous pedicellariae. Bivalved form, each valve having two long, arched and expanding horns, reaching from half to two-thirds of its height. Neural grooves are very distinct, flanked adapically by strong teeth (two to five), and laterally by a ridge where two short teeth may occasionally occur. Teeth on the distal edge (three to four) are well developed. Teeth are either lacking on the lateral edge (valve margin) of a valve (Text-fig. 44K) or there are two rudimentary ones developed (Text-fig. 44H). At the outer surface of the horns there can occur single, undivided grooves, which do not reach the distal tip. The remaining part of a valve is quite smooth. Only large specimens display the distinct basal knob (Text-fig. 44H). The basal surface is tightly closed; only in juvenile elements does it have an eye-shaped opening. The proximal edge is wavy in small specimens, but arched or straight in mature specimens.

morphotype IIIc from the Late Givetian of Marzysz, samples Marzysz II/13 (H–I, L–N), Marzysz II/7 (J–K), and Marzysz II/W/6 (O). **H**. Specimen GIUS 4-584 Mrz./235d/4; H_1 outer view, H_2 lateral view, H_3 inner view, H_4 proximal view, H_5 distal view. **I**. Elongate specimen with the normal horns, GIUS 4-584 Mrz./235d/6, outer view. **J**. Elongate specimen with the unequal horns, GIUS 4-578 Mrz./291/2, inner view. **K**. Elongate specimen with the parallel horns, GIUS 4-578 Mrz./291/3, outer view. **L**. Wide specimen with the short spines, GIUS 4-584 Mrz./235d/7, outer view. **M**. Smooth juvenile specimen GIUS 4-584 Mrz./235d/8, outer view. **N**. Smooth wide specimen with short horns, GIUS 4-584 Mrz./235e/5; N_1 outer view, N_2 inner view, N_3 proximal-oblique view. **O**. Irregular wide form GIUS 4-577 Mrz./55/6, outer view. Scale bar 200 μm.

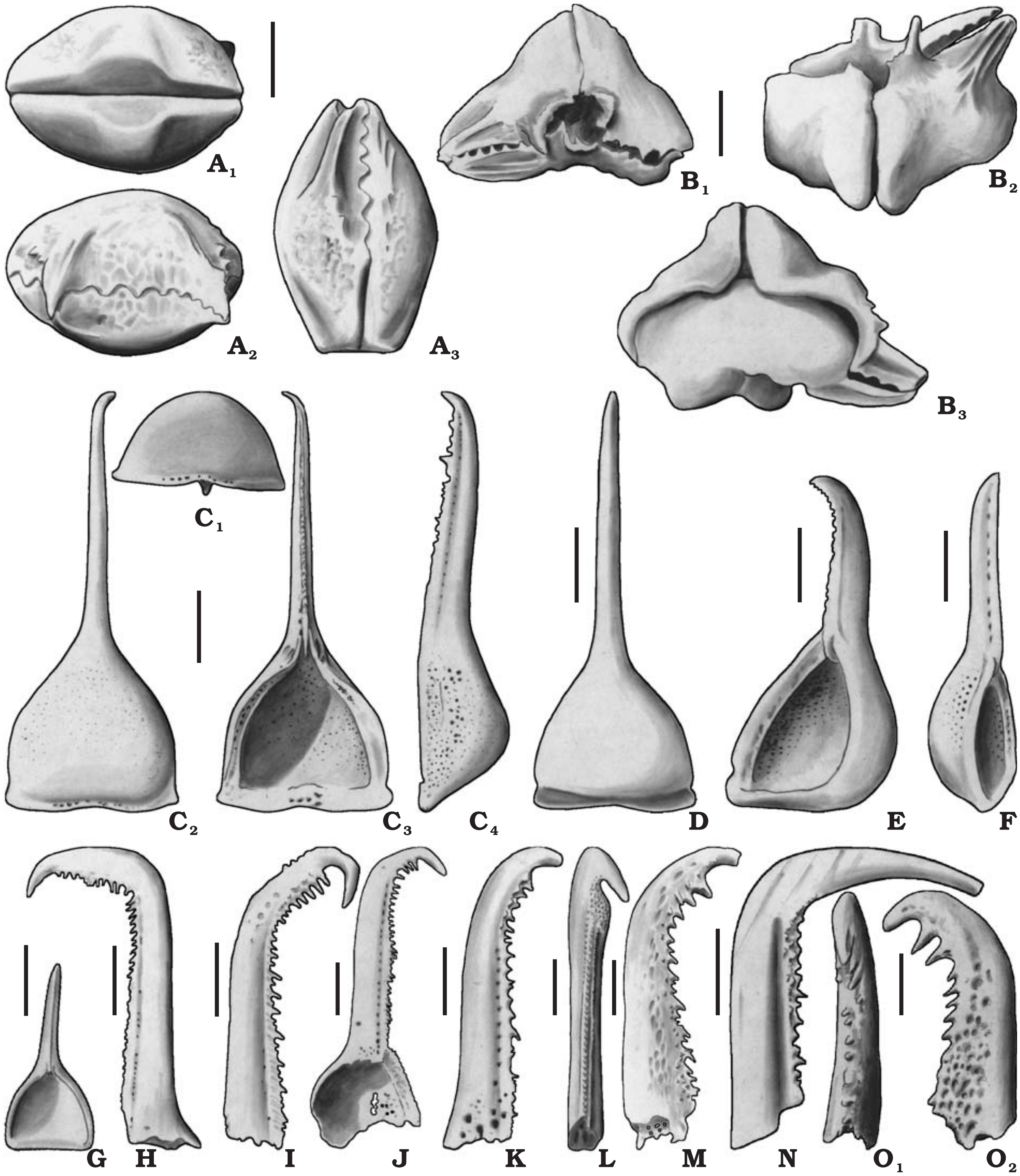


Fig. 43. Echinoid pedicellariae from the Givetian of the Holy Cross Mountains. **A**–**B**. Single valves of ophicephalous pedicellariae of bursulella type (morphotype IIIc) from the Late Givetian, sample Marzysz II/4. **A**. Complete, closed bivalved pedicellaria GIUS 4-575 Mrz./461/1; A_1 proximal view, A_2 distal view, A_3 lateral view. **B**. Complete, closed trivalved pedicellaria GIUS 4-575 Mrz./460/1; B_1 distal view, B_2 proximal view, B_3 lateral-oblique view. **C**–**N**. Globiferous pedicellariae, ladle type (morphotype IIIc); blades from the Late Givetian of Marzysz, samples Marzysz II/13 (C–D, F–H, J–L, N), Marzysz II/W/0 (E), and Marzysz II/4 (I, M). **C**. GIUS 4-584 Mrz./234/9; C_1 proximal view, C_2 outer view, C_3 inner view, C_4 lateral view. **D**. Specimen with a wide abductor and flexor muscle insertion regions, GIUS 4-584 Mrz./234/11, outer view. **E**. Specimen with a short blade, GIUS 4-562 Mrz./143/1, lateral-oblique view. **F**. Specimen without terminal, subterminal and blade teeth, GIUS 4-584 Mrz./234/16, lateral-oblique view. **G**. Young specimen GIUS 4-584 Mrz./234/17. **H**. Hooked blade with a short terminal tooth and long subterminal zone, GIUS 4-584 Mrz./234/10, lateral view. **I**. Hooked blade with a long terminal tooth and long subterminal zone, GIUS 4-575 Mrz./462/4, lateral view. **J**. Hooked blade with a long terminal tooth and short subterminal zone, GIUS 4-584 Mrz./234/14, lateral view. **K**. Curved blade with a blunt and short terminal tooth, GIUS 4-584 Mrz./234/12, lateral view. **L**. Curved blade with a wide subterminal zone, GIUS 4-584 Mrz./234/15, lateral view. **M**. Curved blade with long subterminal teeth, GIUS 4-575 ➛

Globiferous pedicellariae. Their valve is usually almost semiglobular in shape, thin-walled, and almost translucent (Text-fig. 44L–N). The blade is very long, up to two-thirds the height of pedicellariae. Subterminal and median teeth are present, but accessory lateral teeth along its entire length are lacking. Sensory pores are very small. The central blade of the septum passes into a high ridge, with very fine teeth. The proximal basal edge expands into two triangular lobes in its proximal corners. The valve is delicate and therefore, consequently usually badly preserved.

Remarks. — These ophicephalous pedicellariae differ from most others by the weak or absent sculpture on their outer surface. From the smooth forms they differ by having long horns and a basal knob. At Szczukowskie Górki these specimens are somewhat larger than in other localities. Globiferous pedicellariae are generally similar to the two types described above. From those of morphotype IIIc they differ by having almost hemispherical shaped valves, and by the structure of their basal platform, and from all others by the presence of the blade and their delicate structure.

Occurrence. — Mid Frasnian: set C of Górno; samples W5 and W6 from Szczukowskie Górki; set K of Góra Zamkowa, Holy Cross Mountains, Poland.

Pedicellariae – morphotype IV
(Text-figs 39, 40)

Description. — Globiferous pedicellariae. Exclusively trivalved, thin-walled pedicellariae, triangular in outline and with rounded corners (Text-figs 39A–D, 40). Individual valves are hollow inside, with a single, short venom tooth. No channels have been identified leading to the teeth. Walls of the valves are composed of simple perforate stereom. Teeth are curved towards the centre. The angle formed between the valves is 120°. On the proximal part of the valve, towards its outer edge, the stereom is irregularly perforate, with needle-like projections for muscle attachment. Similar stereom of the inner side is only rarely well preserved. Closer to the distal side the stereom gradually disappears and the valve margin becomes more and more solid. Adductor muscles were present in a shallow groove on the valve margin (Text-fig. 39B). When the head was closed, the valves formed a large, circular opening at the proximal side (Text-fig. 39D), at its borders the abductor and flexor muscles were presumably attached (Text-fig. 39B). A characteristic trilobate gap remains on the distal side after closure of valves (Text-fig. 39C).

Tridentate pedicellariae. These are trivalved forms, with convex, thin-walled valves, triangular in outline, with rounded proximal corners (Text-figs 39E–G, 40). Most commonly they are supplied with a single long blade, hooked distally. Stereom of the valve wall is simply perforate. The angle formed between the valves is 120°. The outer and inner surfaces of the proximal margin is composed of labyrinthic stereom with needle-like projections, presumably an attachment site for muscles. Distally such stereom disappears, and the adductor muscles may have attached to a shallow groove on the valve margin (Text-fig. 39G). The valves formed a large circular opening at their proximal margin after closure of the head (Text-fig. 39E), where abductor and flexor muscles were presumably attached. An additional point of contact of the valves was along a simple marginal ridge and their accompanying fossa (Text-fig. 39G). Closure of the valves creates a characteristic trifoliate gap at the distal side, between the teeth (Text-fig. 39F).

Remarks. — These various morphotypes of globiferous pedicellariae differ from each other in the outline of their valves, tooth arrangement and the structural details of the basal part. Most globiferous pedicellariae lack necks, and the head is adducted by a stem (Lawrence 1987) with some exceptions e.g. *Strongylocentrotus* Brandt, 1835 (cf. Geis 1936). The first pedicellariae derived from modified secondary spines must have been provided with the stem spicules (cf. Blake 1968). Thus the presence of a large basal opening might suggest that there was no neck and that the basal part of the head attached directly by muscles to the shaft of the stem. In the course of evolution the distance between the part of spine and its remaining part (a shaft) increased. It seems that the globiferous forms of morphotype IV lacked the neck. It was present, however, in type III pedicellariae (Text-fig. 40).

Tridentate pedicellariae of type IV consisted of three valves and differed in shape from ophicephalous pedicellariae, especially in the development of their proximal part and the long blade. Generally these are

Mrz./462/3, lateral view. **N**. Hooked blade with a very long and sharp terminal canine-like tooth, GIUS 4-584 Mrz./234/13, lateral view. **O**. Echinoid globiferous pedicellariae, ladle type (morphotype IIIb), curved blade with a blunt and short terminal tooth, GIUS 4-604 Las./1004/3, Middle Givetian set B of Laskowa Góra; O_1 ventral view, O_2 lateral view. Scale bar 200 μm.

small elements, though they may occasionally attain the largest dimensions among all the echinoid pedicellariae – up to 5 mm (Lawrence 1987). The specimens described here are typical tridentate pedicellariae and differ from their living counterparts in only their more simplified structure.

Discussion. — The venom tissue of this group of pedicellariae is variable both in development and position within an organ. Usually extant simple pedicellariae have their venom gland or venom tissue inside the valve (Cidaroida). In more complicated forms they occur in the proximal part, close to the base of the head (Echinida, Diadematoida, cf. Lawrence 1987; Mortensen 1928, 1943b) or a valve together with distal part of a stem are enclosed within the venom sacs (Lawrence 1987; Mortensen 1950, 1951). Among recent forms only the Echinoida show hollow valves. Burrowing echinoids as a rule lack such pedicellariae (e.g. Clypeasteroida, Laganoida) but some exceptions do exist (Clypeasteroida: *Fibularia* Lamarck, 1816, *Fibulariella* Mortensen, 1948 – Mooi 1989; Spatangoida – Lawrence 1987; Mortensen 1950, 1951). There is no strict correlation, however, between the mode of life and the presence or lack of pedicellariae (e.g. Arbacioida – Lawrence 1987). So far as can be judged from the scarce fossil material, the first echinoids lacked globiferous pedicellariae. The Devonian forms described herein are the oldest globiferous pedicellariae, up until now they were known from the Late Carboniferous of Texas, Illinois and Missouri (Geis 1936). This means that such highly specialised pedicellariae appeared at relatively early phylogenetic stages of the echinoids. Their simple structure and hollow interior indicate that the venom gland or sac lay inside the valve. In the cidaroids large globiferous pedicellariae surround the primary spines of the upper thecal area, but are not found on the ambulacral plates. The lack of skeletal elements specialised in transduction of a venom suggests that these pedicellariae were still very simple. A venom sac possibly occurred within the valve and had its simple aperture at the immediate vicinity of the base of the venom tooth. Similar Recent forms can be found among the Clypeasteroida (Fibulariidae), the difference is in presence of a keel running through the interior of an excavated valve (cf. Mooi 1989). All pedicellariae of this type have a very small or have simple perforate valve. Examples are in the Echinidae – *Paracentrotus* Mortensen, 1903, Glyptocidaroidae – *Glyptocidaris* A. Agassiz, 1853 (cf. Cherbonnier 1968; Jensen 1982), Loveniidae – *Echinocardium* Gray, 1825 and *Lovenia* Desor, 1847 (cf. Fischer 1966; Jensen 1982), Schizasteridae – *Schizaster* L. Agassiz, 1836 (cf. McNamara and Philip 1980; Mortensen 1951). They may show also smooth and convex outer surface, a very similar outline and presence of a single terminal tooth (Cidaridae – *Eucidaris* Pomel, 1883, cf. Hess 1975, Mortensen, 1928; Toxopneustidae – *Sphaerechinus* Desor, 1856). Some have a single terminal tooth (Glyptocidaridae – *Glyptocidaris* A. Agassiz, 1853, cf. Jensen 1982). The strongest morphological similarity can be found in *Strongylocentrotus* Brandt, 1835 (cf. Hyman 1955; Mortensen 1943b). Representatives of pedicellariae type IV are similar of construction to Triassic forms from the Alps described by Mostler (1972b: pls I: 8, II: 8). All the representatives of the order Cidaroida (with exception of Histocidarinae) have pedicellariae with a venom sac within the valve. The latter can be more or less broadly opened (Jensen 1982). Moreover, cidaroid valves are supplied with lateral and central cog-teeth (Jensen 1982), but in the Devonian pedicellariae described here there are only proximal valve teeth at the junction between the valves (Text-fig. 39B). Also in Cidaroida small and large pedicellariae of the same type are of a similar shape (Jensen 1982). The type IV pedicellariae from the Devonian are the most similar to those from modern representatives of the Cidaroida and Echinoida. Tridentate pedicellariae occur in the majority of echinoids, with exception of the cidaroids and arbacioids (Lawrence 1987). Tridentate morphotype IV is generally similar to the globiferous pedicellariae of the morphotype IV. They always occur together.

Occurrence. — Eifelian–Frasnian: widespread in the Holy Cross Mountains, Poland.

Pedicellariae – morphotype IVa
(Text-fig. 41N–O)

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)		
Number of specimens	Features	Minimum	Mean	Maximum
Globiferous pedicellariae: 22	Length	230	245	270
	Valve width	115	180	195
Tridentate pedicellariae: 16	Length	290	445	570
	Valve width	205	265	325

Description. — Globiferous pedicellariae. Small, thin-walled, droplet-like specimens, with rounded corners (Text-fig. 41O). Strongly convex valves have a single, adaxially bent, short terminal tooth. Their valve margin is fairly distinct but narrow. At the proximal part of the valve there are two teeth and pits, forming a sort of articulation. After the closure of valves the proximal sutures formed a trilobate gap. A similar opening can be observed at the distal margin, among the terminal teeth.

Tridentate pedicellariae. They are also thin-walled, but triangular or bottle-shaped in outline, with proximal corners rounded. The convex valve has a short, adaxially curved, tooth-like blade. The distal part of the valve is strongly compressed laterally, so the blade is not sharply distinct from the valve (Text-fig. $41N_3$). The valve margin is narrow, in its proximal part it has narrow grooves for adductor muscle attachment. Just below this location are well-developed fossae and teeth with rounded terminations, which, at the wavy proximal edge, joined both valves. The proximal opening of the base is circular, the distal one is trilobate.

Remarks. — This form differs from other ones by the shape of its valve, the wavy proximal edge with three convexities: one at the axis, the other two symmetrically at the sides of the former; they are formed by exceptionally large basal teeth, which form the hemispherical knobs.

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

Pedicellariae – morphotype IVb
(Pl. 34: 1–4; Text-fig. 44A–G)

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)		
Number of specimens	Features	Minimum	Mean	Maximum
Globiferous pedicellariae: 66	Length	630	815	985
	Valve width	340	655	610
Tridentate pedicellariae: 43	Length	1005	1410 (?)	2930 (?)
	Valve width	485	640	1270

Description. — Globiferous pedicellariae. They are thin-walled, triangular in outline, with rounded corners (Text-fig. 44A–D). The valves are of uneven convexity, being most convex at their proximal side, at ca. quarter of their height. They are provided with a single, short, adaxially bent terminal tooth. The valve margin is very distinct, usually broadest at ca. half of height of the valve (Text-fig. $44B_1$). In the proximal part of a valve two teeth and fossae can be seen; they form wrinkles. A circular proximal opening is typical for this variety.

Tridentate pedicellariae. They are thin-walled pedicellariae, of triangular outline, shovel-shaped, with rounded corners (Text-fig. 44E–G). The valves are somewhat convex, with a long blade (up to half the height) gradually passing into a valve. The blade, similar to a terminal tooth, is to a various degree adaxially bent along whole its length (Pl. 13: 2–4; Text-fig. 44E), or forms a hook only at its termination (Text-fig. 44F, G). The hooks may also be curved laterally. Proximally and axially there is a hemispherical convexity, absent in large specimens, and then the proximal edge is straight and a triangular opening can be seen at the base. The valve margin is narrow and locally absents at the distal part. In the proximal part of the valve there are delicate teeth and a fossa, connecting the valves. The basal pore is circular, the distal pore trilobate, occasionally asymmetrical.

Remarks. — Globiferous forms differ from other subtypes by the shape of their valve, the presence of a wide valve margin and more delicate teeth at the proximal margin of a valve. This margin is slightly wavy. Their trilobate distal opening and circular proximal one is also characteristic. In some specimens the teeth may be more strongly expressed (Text-fig. 44D) or whole the valve may be laterally compressed in its proximal part, as can be seen in the tridentate pedicellariae of morphotype IVa, but its blade does not pass from the distal side to the valve wall, and the general outline of a complete specimen is pear-shaped. Tridentate forms differ from the latter in the shape of the valve, narrow valve margin and weak teeth joining the valves. Large specimens, which are known only from fragments (Text-fig. 44G) have straight or slightly wavy proximal edge, flat valve and a triangular basal pore.

Occurrence. — Late Givetian: trench II at Marzysz. Mid Frasnian: samples W5, W6 from Szczukowskie Górki, Holy Cross Mountains, Poland.

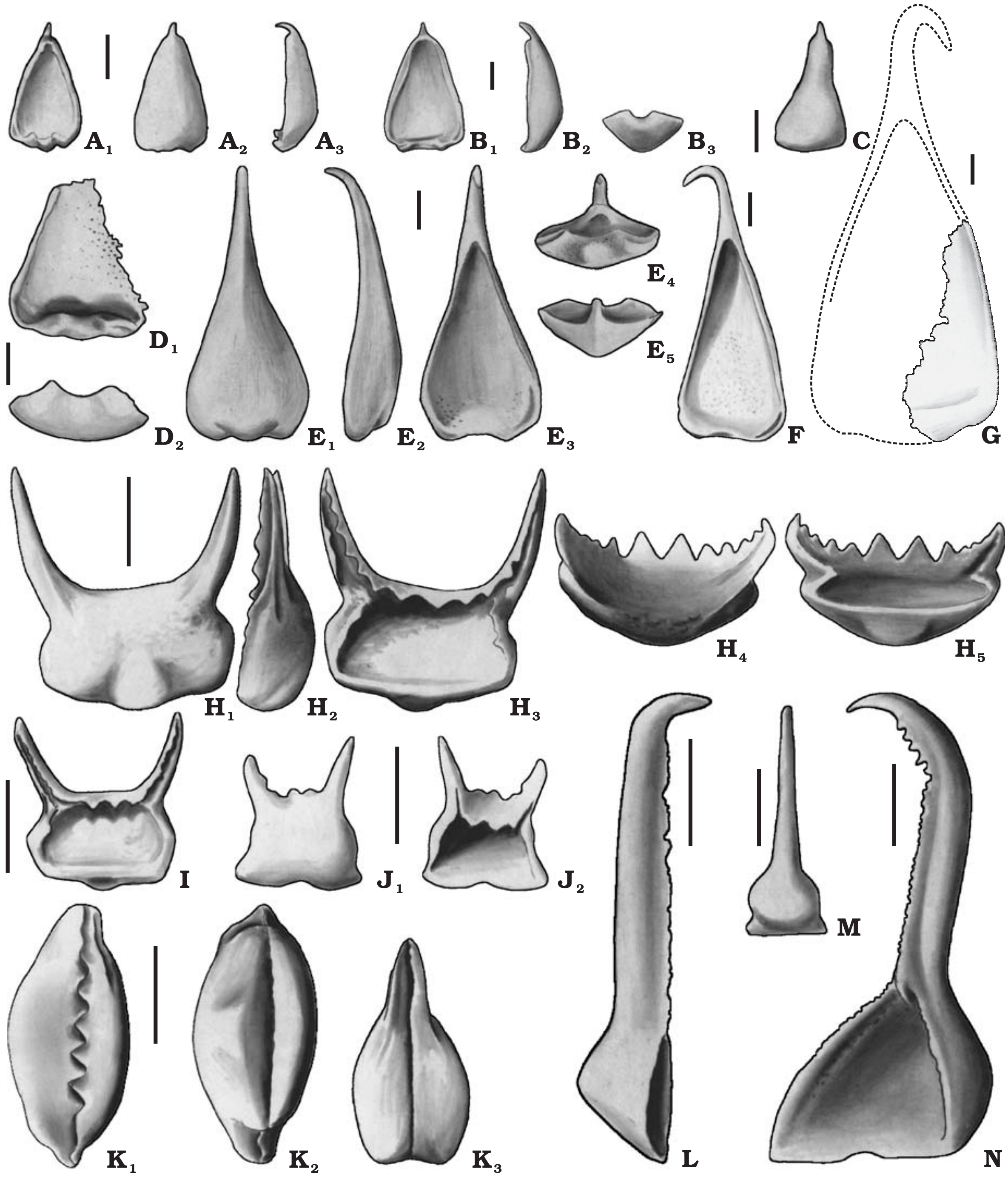


Fig. 44. Echinoid pedicellariae from the Devonian of the Holy Cross Mountains. **A**–**G**. Trivalve pedicellariae (morphotype IVb), single valves from the Late Givetian of Marzysz, samples Marzysz II/W/6 (A–E) and Marzysz II/13 (F–G). **A**. Small globiferous valve GIUS 4-568 Mrz./46a/3; A_1 inner view, A_2 outer view, A_3 lateral view. **B**. Globiferous pedicellaria GIUS 4-568 Mrz./46a/2; B_1 inner view, B_2 lateral view, B_3 proximal view. **C**. Narrow specimen of globiferous pedicellaria GIUS 4-568 Mrz./46a/5. **D**. Fragment of large valve, globiferous pedicellaria, GIUS 4-568 Mrz./46a/4; D_1 inner view, D_2 proximal view, angle between the valve border 120°. **E**. Tridentate pedicellaria GIUS 4-568 Mrz./46b/1; E_1 outer view, E_2 lateral view, E_3 inner view, E_4 proximal view, E_5 distal view. **F**. Tridentate pedicellaria GIUS 4-584 Mrz./236/3. **G**. Reconstruction of large tridentate pedicellaria, GIUS 4-584 Mrz./236/2. **H**–**K**. Echinoid ophicephalous pedicellariae of bursulella type (morphotype IIId) from the Middle Frasnian, set C of Górno. **H**. Specimen GIUS 4-607 Grn./1058/1; H_1 outer view, H_2 lateral view, H_3 inner view, H_4 distal view, H_5 proximal view. **I**. Specimen GIUS 4-607 Grn./1058/2, inner view. **J**. Small valve GIUS 4-607 Grn./1058/3; J_1 outer view, J_2 inner view. **K**. Complete, closed bivalved pedicellaria GIUS 4-607 Grn./1058/4; K_1 distal view, K_2 proximal view, K_3 lateral view. **L**–**M**. Echinoid globiferous pedicellariae, ladle type (morphotype IIId) from the Mid Frasnian, set C of Górno. **L**. Specimen with hooked blade, GIUS 4-607 Grn./1057/, lateral view. **M**. Specimen GIUS 4-607 Grn./1057/2, outer view. **N**. Specimen with curved blade, GIUS 4-607 Grn./1057/3, lateral-oblique view. Scale bar 200 μm.

Table 1

Comparison of basic features of living and fossil echinoid pedicellariae. Data on Recent echinoids from Campbell (1973, 1974, 1976, 1983); Geis (1936); Hyman (1955); Jensen (1982); Lawrence (1987); Mooi (1989); Mortensen (1928–1951).

Features	Type of pedicellariae					
	Globiferous		Ophicephalous		Triphyllous	Tridentate
	typical	ladle form	typical	bursulella form	typical	typical
sharp teeth	present	present	absent	absent	absent	present
blunt teeth	absent	absent	present	present	absent	present
many teeth	yes	yes	yes	yes	no	yes
number of terminal teeth	single or more	one	absent	horn teeth only	absent	single
handle	absent	absent	present	absent	absent	absent
venom teeth	present	present	absent	absent	absent	absent
subterminal teeth	present	present	absent	absent	absent	absent
jaw edge crenation	various	present	present	present	absent	absent
central grasping tooth in the centre of gripping area	absent	absent	present	absent	absent	absent
distal point of the valve contact	present	overlapping terminal teeth	present	present	absent	present
typical number of the head valves	3	2	3	2	2 or 3	3
number of head valves (min.–max.)	2–5	2	2–3	2–3	2–4	2–5
venom tissue	present	present	various	absent	absent	absent
angle between the valves	120° or other	180°	120° or other	120°, 180°	180°, 120° or other	120° or other
opening angle	90–180°	90°–160°	180°	90°–160°	180°	180°
neck	various	present	present	present	present	long
stem	present	present	present	present	present	short
autotomy	present	?	?	?	?	?
activity	stimulating	?	stimulating	?	continuous	stimulating
stimulation	chemical	?	mechanical	?	spontaneous	mechanical
functions	defensive, using venom against biological stimuli	probably defensive using venom against biological stimuli	defensive, against mechanical stimuli	?	protective, keep the test clean, defensive	defensive, against biological stimuli

Class **HOLOTHUROIDEA** de Blainville, 1834

Holothuroid remains are quite common among fossils although rarely reported in literature. Ironically, fossil sclerites attributed to holothurians frequently represent other echinoderm groups, as suggested by Pawson (1966, 1980); e.g. the representatives of the Triassic family Calclyridae, have been proposed to be arm spines of the ophiuroids (Mostler 1971b), or even sponge spicules (Mostler 1971c).

The first description of Devonian holothuroids was given by Martin (1952) although his paper contains descriptions of specimens far from complete. Subsequently Devonian holothuroids have been described and revised by Gutschick and Canis (1971), Frizzel and Exline (1966) Gilliland (1993), Lehman (1958), Seilacher (1961), Smith (1988b), and Haude (1983, 1992). Beckmann (1965) identified in the Givetian of the Renish Slate Mountains several types of the holothurian sclerites, e.g. *Achistrum multiperforatum* and *Devonothyonites* (included into *Tetravirga* Frizzell *et* Exline, 1955) and some other, mostly synonimized by the subsequent authors. The only description on the fossil holothurians from the Devonian of the Holy Cross Mountains was presented by Matyja *et al*. (1973), who described a material of *Eocaudina*. Garcia-López and Truyols (1974) reported, on incidentally found material, new forms from the Cantabrian Mountains, Spain. Langer's (1991) holothurian remains from the Devonian of the Rhenish Slate Mountains show strong affinities to those from the Holy Cross Mountains. Haude (1983, 1992) reported an occurrence of completely preserved *Eocaudina* and reviewed fossil sclerite aggregates from the Lower Givetian of the Rhenish Slate

Mountains, Germany. Among the oldest completely preserved fossil sea cucumbers is *Palaeocucumaria hunsrueckiana* Lehmann, 1958 from the Early Devonian of the Hunsrück Mountains, Germany.

Holothurian sclerites are known also from the Ordovician (Schallreuter 1968, 1975) and Carboniferous (Alexandrowicz 1971; Etheridge 1881; Gutschick *et al*. 1967; Hanna 1930; Hui 1985; Langenheim and Epis 1957). Sroka (1988) described complete holothuroids of the genus *Achistrum* from the Mid Pennsylvanian of Illinois. Reviews of earlier literature were offered by Croneis and Mc Cormack (1932), Deflandre-Rigaud (1962) and Frizzell and Exline (1955, 1966). Gilliland (1992a, b, 1993) attempted to unify taxonomy of fossil and living sea cucumbers, an approach which is followed in the present paper.

Order **Arthrochirotida** Seilacher, 1961

Family **Palaeocucumariidae** Frizzell *et* Exline, 1966

Remarks. — Isolated plates of these sea cucumbers can be classified as *Etheridgella* (Frizzell and Exline 1966; Gilliland 1993). Having a fully plated body seems to be a primitive feature. One might expect intermediate forms to exist between these fossils and the primitive Echinocystitoida; indeed, representatives of the latter were originally described as holothurians (MacBride and Spencer 1938). A similar imbrication of plates in tentacles can be observed in ophiocistioids *Sollasina*, *Eucladia*, and *Gillocystis*. This is a common feature for the two groups and suggests close relationships within the Echinozoa, as concluded by Smith (1988b). It is to be noted also, that in the ophiocistioids plates from the tube feet may have short spines, e.g. *Sollasina*. The presence of sclerites similar to those of the Holothurioidea in the ophiocistioids suggests closer affinities of the two groups than suggested by Smiley (1988). Seilacher (1961) considered *Palaeocucumaria* to be affiliated with the Synaptidae based on its numerous interradial plates in the calcareous ring (Gilliland 1993). The presence of sclerites of this type in extant sea cucumbers is probably a relic (Pl. 14: 1–2).

Genus *Palaeocucumaria* Lehmann, 1958

Type species: *Palaeocucumaria hunsrueckiana* Lehmann, 1958.

Palaeocucumaria ancile sp. n.
(Pl. 14: 3–15)

Holotype: GIUS 4-802 Ska./826/4, Pl. 14: 6.

Type horizon: Late Eifelian, set XVII of the Skały Beds, *Tortodus kockelianus* Zone.

Type locality: Skały, Holy Cross Mountains.

Derivation of the name: From Latin *ancile* – the holy shield from the times of king Numy, its shape can be seen in scales, covering the body wall.

Material. — Number of specimens and dimensions:

Material		Dimensions (µm)			
Number of specimens	Features	Holotype	Minimum	Mean	Maximum
ghtRods: 2500	Length	–	430	760	920
Plates from body wall: 1300	Diameter	–	575	715	1015
Perforate plates: 4500	Diameter	–	380	480	510
Arches: > 5000	Length	–	320	390	420
Plates from tentacles: 350	Length	430	370	410	530
	Width	410	380	420	500

Diagnosis. — Main perforate plates from the outer ring of tentacles tongue shaped. Ventral side smooth.

Description. — Plates from the body wall. These plates, most probably derived from the proximal part of the body, are perforated right through and are shield – shaped (Pl. 14: 8–10). Juvenile plates are oval and built of a delicate lattice with serrated margins (Pl. 14: 13–15). Plates presumably from the posterior part of the body have blind pores, and are polygonal or triangular (not rounded) in shape; all have short spines at one of their borders (Pl. 14: 12).

Rods from the tentacles. These elements are only weakly curved; their middle part is stocky (Pl. 14: 3–5, 11). Perforation can be seen only at margins. Lingulate main plates from the tentacles have straight proximal side.

Remarks. — This species differs from *Palaeocucumaria hunsrueckiana* Lehmann, 1958 by the more delicate structure of its plates and by the presence of short, instead of long, processes on the distal plates (cf. Frizzel and Exline 1966; Gilliland 1993; Lehman 1958; Seilacher 1961; Smith 1988b). From *Palaeocucumaria delicata* sp. n. it differs by the outline of the main plates from tentacles and the lack of ridges on their ventral surfaces. All these remains, irrespective of rock matrix, are of brown colour.

Occurrence. — Late Eifelian: sets XIII–XIX of the Skały Beds at Skały. Early Givetian: outcrop III at Śniadka, Holy Cross Mountains, Poland.

Palaeocucumaria delicata sp. n.
(Pls 14: 16–21; 15: 1–15; Text-fig. 69K–S)

Holotype: GIUS 4-578 Mrz./286/1, Pl. 15: 15.

Paratype: GIUS 4-584 Mrz./228/5, Pl. 14: 20.

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

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

Derivation of the name: From Latin *delicatus* – delicate, due to its plates being more delicate than those of other species.

Material. — Number of specimens and dimensions:

Material		Dimensions (µm)			
Number of specimens	Features	Holotype	Minimum	Mean	Maximum
Rods: > 5000	Length	–	260	920	1100
Plates from body wall: 5000	Diameter	–	620	890	1340
Perforate plates: > 10000	Diameter	–	290	485	540
Arches: > 5000	Length	–	400	450	540
Plates from tentacles: 750	Length	–	325	375	420
	Width	–	360	480	540
Fragment of tentacle: 28	Diameter	700	–	–	–

Diagnosis. — Perforate plates from the outer ring of tentacles polygonal or shield-like in shape; their ventral margins with two parallel, axially situated ridges.

Description. — Plates from the body wall. These elements are perforated right through and of highly variable shape: shield-like, plate-shaped, trapezoidal, triangular and irregular (Pl. 15: 1–7). Juvenile plates irregular or elongate, built of a delicate network with uneven margins (Pl. 14: 16–18). Minutely perforate plates are the only ones with short, undetached spines (Pl. 15: 7).

Rods from the tentacles. Sclerites are arch-like, their middle parts are imperforate or weakly perforate (Pl. 15: 8–10); also small rods have been found, commonly with few perforations at their ends (Text-fig. 69K–S), with the intermediate forms being represented. Their colour is dark-brown. The rod illustrated in Text-fig. 69R, is of exceptional morphology, being flat and with a central opening.

Articulated elements. Numerous specimens partially articulated derived from tentacles have been found, with elements in life arrangement. This has allowed reconstruction of tentacles to be made (Pl. 15: 9–15). Tentacles of *Palaeocucumaria* are composed of an internal skeleton consisting of twelve triangular scales, arranged in pairs (Pl. 15: 15) disposed in a rosette pattern. Subsequent rosettes are stacked. The axial skeleton was surrounded and framed by a peripheral skeleton, consisting of arch-like plates, which partly overlapped over their thinned margins (Pl. 15: 8, 9, 13). The whole structure formed a sort of tube, surrounding the axial skeleton; the tentacles, though armoured must have been flexible. In the outer rings of the peripheral skeleton one side displayed the imbricating pattern of the main plates of the tentacles.

Remarks. — The present species differs from other *Palaeocucumaria* by the extremely delicate structure of its plates and by having the shortest processes on the plates in almost horizontal arrangement.

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

Order **Dendrochirotida** Grube, 1840

Family **Cucumariidae** Ludwig, 1894 emend. Pawson *et* Fell, 1965

Subfamily **Devonothyoninae** subfam. n.

Diagnosis. — Sclerites trizonate, their perforated central part forming a lamella bordered by a ridge. Lateral processes with similar structure provided with an outgrowth, in shape of a comb or a rod with lateral spines. The sklerotome also includes dagger-shaped anal teeth and branching, perforated, commonly spine-bearing blades. All elements with elevated peripheral ridges.

Remarks. — Anal teeth have been recognised in numerous representatives of Dendrochirotida and other holothuroids but so far they have not been identified in Apodida, Dactylochirotida, and Elasipodida (Gilliland 1993). In modern sea cucumbers these structures commonly form large, elongated, perforated scales, 400–1000 mm in length. Most commonly they are Y-shaped, as in some Molpadida, e.g. *Trochostoma* Danielsen *et* Koren, 1878 (Ekman 1927) or *Cherbonniera utriculus* Sibuet, 1974. Some anal teeth are similar to those from the Devonian (cf. Sibuet 1974), and they even have similar spine-bearing, asymmetrical outgrowths. Living species show a wide range of morphological variability and the elements are of significant diagnostic value. Closest analogies of the Devonothyoninae subfam. n. among the extant holothurioids can be seen in the Dendrochirotida and particularly in the Cucumariidae, e.g. *Cucumaria spatha* Cherbonnier, 1941; *C. georgiana* (Lampert, 1886); *C. denticulata* Ekman, 1927 or *Paningia curvata* Cherbonnier, 1958, and *P. bispicula* Cherbonnier, 1965 (cf. Cherbonnier 1941b, 1958a, 1965; Ekman 1927). Plates from their body wall have very similar, protruding processes of solid calcite. In juvenile specimens, e.g. of *Cucumaria steineni* Ludwig, 1898, these processes protrude outward from the body bristled with sclerites (cf. Ekman 1927). Among the species of the new subfamily is probably the ancestor of the Cucumariidae. In the Devonian they underwent a gradual simplification of their skeletal structure. *Ballistocucumis* gen. n. might be the most primitive, being the geologically oldest, although its plates are small and of the most complicated structure (Text-fig. 76).

Genus *Ballistocucumis* gen. n.

Type species: *Ballistocucumis bimembris* sp. n.

Derivation of the name: From Latin *ballista* – catapult, due to the similarity of shape; the second part of the name refers to its affinity with the recent family Cucumariidae.

Diagnosis. — Centre of the sclerite crescentic in shape; lamella perforated; head with processes at both ends, in a comb-like arrangement.

Ballistocucumis bimembris sp. n.
(Text-fig. 45A–C)

Holotype: GIUS 4-779 Zba./354/1, Text-fig. 45A.

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

Type locality: Zbrza, Holy Cross Mountains.

Derivation of the name: From Latin *bimembris* – double-shaped, due to two kinds of sclerites.

Material. — Number of specimens and dimensions:

Material		Dimensions (μm)			
Number of specimens	Features	Holotype	Minimum	Mean	Maximum
Plates: 45	Width	340	290	330	350
	Height	290	240	250	265

Diagnosis. — As for the genus.

Description. — Sclerites L-shaped. Central lamella perforated by a few to more than ten pores. Flanks, forming the lateral processes, are cylindrical in shape and may be perforated. Their height is similar to the height of the head-shaped process (Text-fig. 45A–C).

Remarks. — This type of the sclerites is the most primitive in the whole subfamily. Anal sclerites have not been found.

Occurrence. — Late Emsian: set V of the Grzegorzowice Beds at Grzegorzowice. Early Eifelian: brachiopod *Chimaerothyris dombrowiensis* Zone (*Polygnathus partitus* Zone) of Zbrza; set VIII of the Grzegorzowice Beds at Grzegorzowice, Holy Cross Mountains, Poland.

Genus *Devonothyonites* Langer, 1991

Type species: *Devonothyonites triangularis* Langer, 1991.

Devonothyonites accipitris sp. n.
(Pl. 16: 1–2, 9; Text-figs 45D–F, 47A, 48A–I, 49V–W)

Holotype: GIUS 4-618 Grz./380/2, Text–fig. 45E.

Type horizon: Early Eifelian, set VIII of the Grzegorzowice Beds, *Polygnathus partitus* Zone.

Type locality: Grzegorzowice, Holy Cross Mountains.

Derivation of the name: From Latin *accipiter* – hawk, shape of sclerites somewhat resembles the hawk.

Material. — Number of specimens and dimensions:

Material		Dimensions (µm)			
Number of specimens	Features	Holotype	Minimum	Mean	Maximum
Plates with head: 19	Width	530	425	510	700
	Height	775	600	720	980
Anal teeth: 58	Width	–	365	410	450
	Length	–	900	1120	1242
Plates with processes: 3	Diameter	–	870	930	960
	Length of process	–	190	220	230

Diagnosis. — Sclerites from the body wall with weakly perforated lateral processes, shorter than the axial processes.

Description. — Sclerites from the body wall. They are in the shape of a flying bird; their central portion may be as thick as the flanking regions. The head has scarce lateral branches, and it can be bifurcated (Text-fig. 45D–F). The central lamella if present, is flat. Other sclerites from the body wall have a large, thick and centrally placed vertical spine. Perforated lamella of these sclerites with four branches and surrounded by a marginal thickening (Text-fig. 47A).

Anal teeth. The sclerites have, on average, four lateral spines always pointing towards the narrower part of the sclerite. The number of lateral spines can be from two to six. The processes can be asymmetrically arranged. An additional, vertically arranged central spine may occur in some lamellae. The lamella in itself is relatively thick and commonly perforated even at its periphery (Pl. 16: 1–2; Text-fig. 48A–I).

Remarks. — Sclerites from the body wall differ from those of other species in having short lateral processes. The anal teeth of this species are very peculiar, as no other species has such numerous lateral processes arranged in a row and these are directed in the direction opposite to that of other species, i.e. toward the narrower end. Larger anal teeth are perforated and spatula-shaped (Pl. 16: 9; Text-fig. 49V–W).

Occurrence. — Only known from the type locality.

Devonothyonites avis sp. n.
(Pl. 16: 3, 4, 6–8, 11–14, 17, 18, 20; Text-figs 46A–R, 47B–E, 48P–AC, 49E–S, X–Z, 50M–O)

Holotype: GIUS 4-584 Mrz./209/1, Text-fig. 46A.

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 *avis* – bird, as it is bird-shaped.

Material. — Number of specimens and dimensions:

Material		Dimensions (µm)			
Number of specimens	Features	Holotype	Minimum	Mean	Maximum
Plates with head: 248	Width	880	350	780	995
	Height	985	590	890	990
Anal teeth: 186	Width	–	115	300	360
	Length	–	360	980	1750
Plates with processes: 21	Diameter	–	360	380	460
	Length of process	–	175	190	200

Diagnosis. — The sclerites from the body wall with long lateral and axial processes; inner lamella and marginal thickening perforated. Similar structure in other skeletal elements; typical anal teeth with two processes directed always toward the broader segment of the plate.

Description. — Sclerites from the body wall. Head of sclerites from the body wall commonly have with long, irregularly distributed lateral spines, sometimes merging with the main lamella (Text-fig. 46M–R). The head may display a few isolated pores (Text-fig. 46C, D, K). Plate pores may reach a hundred;

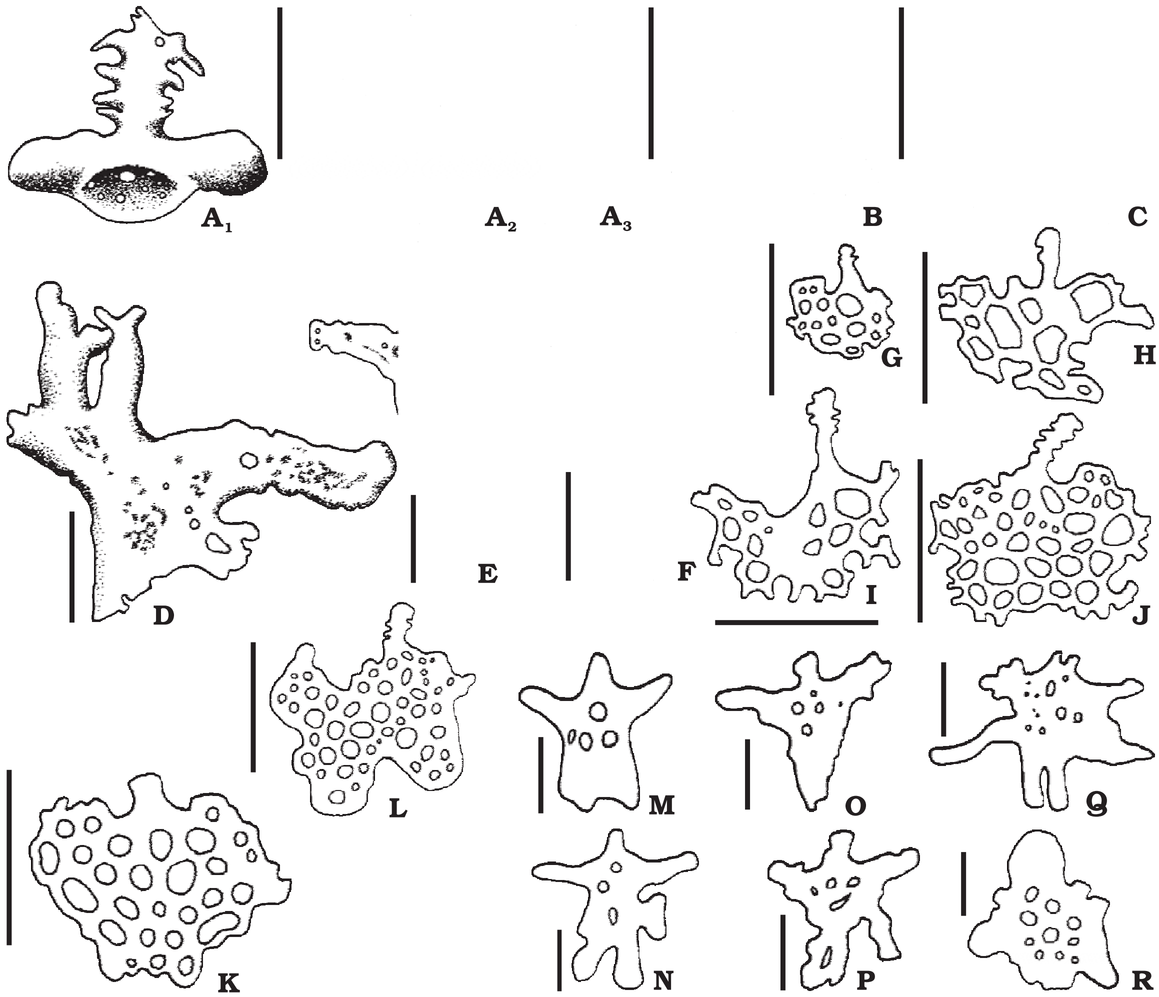


Fig. 45. Holothurian sclerites from the Devonian of the Holy Cross Mountains. **A**–**C**. *Ballistocucumis bimembris* sp. n. from the earliest Eifelian *Chimaerothyris dombrowiensis* horizon of Zbrza. **A**. Holotype GIUS 4-779 Zba./354/1; A_1 side view, A_2 oposite side view, A_3 lateral view. **B**. GIUS 4-779 Zba./354/2, side view. **C**. GIUS 4-779 Zba./354/3, side view. **D**–**F**. *Devonothyonites accipitris* sp. n. from the earliest Eifelian *Chimaerothyris dombrowiensis* horizon set VIII of Grzegorzowice, side views. **D**. Fragment of sclerite GIUS 4-618 Grz./380/1. **E**. Holotype GIUS 4-618 Grz./380/2. **F**. GIUS 4-618 Grz./380/3. **G**–**L**. *Devonothyonites exporrigus* sp. n. from the Early Givetian, outcrop III, Śniadka, side views. **G**. GIUS 4-439 Śni./963/1. **H**. GIUS 4-439 Śni./963/2. **I**. GIUS 4-439 Śni./963/3. **J**. Holotype GIUS 4-439 Śni./963/4. **K**. GIUS 4-439 Śni./963/5. **L**. GIUS 4-439 Śni./963/6. **M**–**R**. *Devonothyonites spiritus* sp. n. from the Late Frasnian set H of Kostomłoty IV, side views. **M**. GIUS 4-801 Kos./534/1. **N**. Holotype GIUS 4-801 Kos./534/2. **O**. GIUS 4-801 Kos./534/3. **P**. GIUS 4-801 Kos./534/4. **Q**. GIUS 4-801 Kos./534/5. **R**. GIUS 4-801 Kos./534/6. Scale bar 200 µm.

commonly these pores are located in depressions on the sclerite surface, as in the holotype. Large pores can be flanked by smaller ones (Text-fig. 46H). Invariably the ends of lateral processes are transformed into flattened, perforated plates (Pl. 16: 17, 18; Text-fig. 46A–K). Rarely specimens with more than two lateral and one axial process occur (Text-fig. 46B, I). Plates with arched and thin central spines are similar to those described above, but with more numerous processes. Also some three-rayed plates, devoid of any processes may occur (Pl. 16: 20; Text-fig. 50M–O). The marginal thickening of lateral processes in all types of sclerites (the anal teeth including) are parallel to each other along the greater part of their length.

Anal teeth. These sclerites display significant morphological variation but they are always strongly perforated and bordered by the marginal thickening. Their narrower end is never bifurcated, unlike the broader end. Forms with two lateral processes have them in form of sharp-edged spines, crossbow or dagger-shaped (Pl. 16: 4; Text-fig. 48P–U). The processes may occasionally occur as variously shaped lamellar outgrowths. Sporadically a third, vertically oriented process can be seen (Text-fig. 48R). All these elements are symmetrically arranged in half of all sclerites. Exceptionally elements have one of their processes underdeveloped or totally lacking (Pl. 16: 6–8; Text-figs 48AB–AC, 49E–S).