

WANDA JESIONEK-SZYMAŃSKA

MORPHOLOGY AND MICROSTRUCTURE OF OLIGOLAMELLAR
TEETH IN PALEOZOIC ECHINOIDS. PART 2. GIVETIAN (MIDDLE
DEVONIAN) STAGE OF EVOLUTION OF OLIGOLAMELLAR TEETH

JESIONEK-SZYMAŃSKA, W.: Morphology and microstructure of oligolamellar teeth in Paleozoic echinoids. Part 2. Givetian (Middle Devonian) stage of evolution of oligolamellar teeth. Acta Palaeont. Polonica 27, 1-4, 195-211, December 1982. Issued January 1983.

Oligolamellar echinoid teeth, primitive in general morphology, are represented in the Givetian of the Skały beds (Grzegorzowice-Skały Section, Holy Cross Mts, Poland) by a few types differing mainly in fine details of their adaxial surfaces which may be smooth, ledged or denticulate. It is suggested that these characters reflect the adaptation to particular feeding habits. A new kind of Givetian echinoid teeth, closely related to the oligolamellar one is described. In some characters such as greater number of lamellae which also are thinner, they seem to be "intermediate" between oligolamellar and another group of Givetian echinoid teeth, for which the name multilamellar is proposed. It is newly recognized and briefly characterized.

Key words: echinoids, evolution, jaw apparatus, microstructure, Devonian.

Wanda Jesionek-Szymańska, Zakład Paleobiologii, Polska Akademia Nauk, Al. Żwirki i Wigury 93, 02-089 Warszawa, Poland. Received: March 1982.

INTRODUCTION

The study of Givetian echinoid remains resulting in the discovery of a primitive oligolamellar type of teeth (Jesionek-Szymańska 1979) has encouraged the author to look for new material in hope of finding more unknown types of the echinoid jaw elements. The most promising area for this purpose was the very fossiliferous Grzegorzowice-Skały Section in the Holy Cross Mts (Central Poland). Devonian deposits are there represented by several hundred meters thick and lithologically very diverse sediments grouped in 28 complexes (Pajchłowa 1957: fig. 1). Some of them, especially those belonging to the Skały beds of Givetian age appeared to be very abundant in echinoderm remains. A 120 kg sample of marls and weathered mudstones from complex XVI (shales with *Microcyclus eifeliensis*) at Ska-

ly locality (Pajchłowa 1957: fig. 3) has been examined. From the same locality about 250 kg of green mudstone mixed with marls, belonging to the complex XVII has been taken. An important part of material here described was derived from the vicinity of Miłoszów locality, a few kilometers west of Skały (Stasińska 1958: fig. 1). Easily accessible outcrops at Miłoszów, corresponding to Skały beds of Grzegorzowice-Skały Section, contain unnumbered amount of varied fossils constituting almost 90 percent of residua. Bryozoans, corals, brachiopods, ostracods are most common there but they also contain very important material of echinoid coronal plates, spines and elements of jaw apparatuses. Some 180 kg sample from Miłoszów was taken and this material contributed considerably to the knowledge of Givetian echinoids. All those samples were routinely processed, sometimes just washed with a solution of detergent, in other cases treated with Glaubert's salt or concentrated perhydrol. Echinoids, represented in residua by dissociated test plates, spines and elements of jaw apparatuses, were examined under binocular microscope, in thin sections under polarized light and with electron scanning microscope.

The work has been done in the Institute of Paleobiology of the Polish Academy of Sciences in Warsaw. The author is very indebted to Professor Zofia Kielan-Jaworowska for her constant interest and encouragement. The continued assistance of persons mentioned in Part 1 is gratefully acknowledged. Three more members of the Institute staff should be added to this list: dr J. Kaźmierczak who photographed the cross-sections of teeth, Ms E. Gutkowska and Mr W. Siciński who helped in preparation of the illustrations.

The collection described in this paper is housed in the Institute of Paleobiology of Polish Academy of Sciences in Warsaw, for which the abbreviation ZPAL is used.

REMARKS

In contrast to the material described in Part 1 (Jesionek-Szymańska 1979) where almost all echinoid material was assignable to the lepidocentrid genus and species *Kongielechinus magnituberculatus* (Jesionek-Szymańska 1979), the echinoid remains from the Skały beds have turned out to be so diverse that any attempt at a more precise taxonomic identification seemed very risky. Formerly expressed opinion (Jesionek-Szymańska 1979: 276) that much of identification work could be done by the method of comparison and elimination was probably too optimistic. When one has to do with relatively small number of for example, interambulacral and ambulacral plates all details of shape and/or tuberculations seem to be very distinct and taxonomically important. Matching them does not seem to pose a serious problem. However, when handling with several

scores of seemingly generically different plates one has to keep in mind that those plates may come from different areas of test or from juvenile individuals and these facts may influence the skeletal characteristics considerably. Formerly sharp morphological limits become more vague and provoke much uncertainty in identification.

Under these circumstances the decision was taken to examine the teeth separately, without suggesting the taxonomic position of echinoids from which they could possibly come. However, it should be pointed out that the majority of the examined ambulacral and interambulacral plates is assignable to common groups of Paleozoic echinoids typified by the flexible echinocystitoids and the rigid-sutured palechinoids. It is rather not surprising that in this vast material just one interambulacral plate of clearly cidaroid character has been found. Most probably these echinoids were yet not common in the Middle Devonian although their spines and isolated plates are known from the Silurian.

Preservation is also an important factor in the identification task and in the case of Skaly beds the material is in diverse condition. Many skeletal elements are well preserved (especially some elements of jaw apparatuses and coronal plates of palechinoids). However others are broken, abraded or corroded. Spines are always fragmented — no complete ones have been found.

The preservation of Aristotle lantern parts much depends on the morphology and structure of particular elements. In general, the rotulae are in the best condition especially those robust, blockshaped ones. They top the erect half-pyramids which before dissociating housed the broad and strongly built oligolamellar teeth. The rotulae are common in residua in contrast with epiphyses which, although twice the number in echinoids, are almost absent in fossil material. Fifteen more or less fragmentary epiphyses have been found.

Jaws are rather frequent among the examined material but the preservation much depends on their structure. Erect half-pyramids, corresponding to the oligolamellar teeth only very rarely are complete. Most often thin-walled aboral part, deeply excavated to accommodate muscle attachments area, are broken off. Only thick and broad oral endings, with a characteristic flange, probably supporting the teeth at work, are found.

Much more numerous and better preserved are small-sized, distinctly bent half-pyramids which, before dissociation of lantern, housed thin, lame-like, longitudinally bent and spinously ended teeth. The latter much resemble the "serrate" teeth described by Jackson (1912) and Bindeman (1938) from Permian and Carboniferous strata. The existence of this type of teeth in the Givetian material was mentioned in Part 1 of Jesionek-Szymańska (1979: pl. 24) paper. They are very numerous and well preserved in Givetian material from the Skaly beds and are also flourishing in Lower Carboniferous rocks at Czatkowice (near Kraków, Southern Poland).

They will be described in greater detail in the future. In order to compare them with oligolamellar teeth, in this paper they are discussed briefly (see p. 205). They are assigned to a separate type for which the name multilamellar is proposed.

Unfortunately, compasses have not been found in residua but of course there is no reason to infer that they were lacking in Givetian echinoids. In fact, they have but little chance to be preserved, as in most echinoids, both living and fossil, they are minute, slender, two-element rods, often strongly bent, and bifurcated abaxially. However, the single Givetian compass from a small sample of limestone derived from Marzysz locality (Holy Cross Mts) was etched with acetic acid. It is amazing that it withstood the harsh treating with acid, intensive washing and drying in high temperature. Its stereom is very fragile but it presents all the typical characteristics mentioned above, including long, hairlike bifurcating endings.

Although all the echinoid material merits a detailed description, the teeth have been given a priority because of the role they play in the better understanding of evolution and in classification of echinoids.

DESCRIPTION OF TEETH

In Skaly beds oligolamellar echinoid teeth are numerous but it would be very risky to perceive how many of them have been collected. None of them are complete because the growing zone — plumula, built of minute immature lamellae embedded in membraneous sac, is always absent. In some specimens however, aboral part of tooth displays a more loose arrangement of lamellae (fig. 4 B_1 ; 5 B_1) and is here considered as being part of tooth closest to plumula (plumula region). Not very frequent in the material are also oral ends but if present, they are sharp and generally the shape of tooth oral ending strictly corresponds to the shape of particular lamellae. Thus, most common in sediments are fragments of shafts and they are the base of her presented descriptions. Some isolated lamellae have also been found — especially those having greater thickness (pl. 70: 1—3; pl. 71: 1—4; pl. 74: 4).

On the base of these fragmentary lamellae and also after examining several more or less complete specimens, a model of basic unit of oligolamellar tooth has been reconstructed (fig. 1). The single lamella is elongated lame roughly triangular in outline, thickest at the region of apice and thinning up aborally. Its external side (fig. 1: A_1) is marked by a depression more or less strongly marked (pl. 70: 1—3), deepest aborally. The flattened end of lamellae is covered with calcareous crust of uniform appearance (pl. 70: 1, 3) but sometimes some linear elements appear (pl. 71: 5). Apice (fig. 1: A) may be uniformly rounded (pl. 70: 3) or flattened and

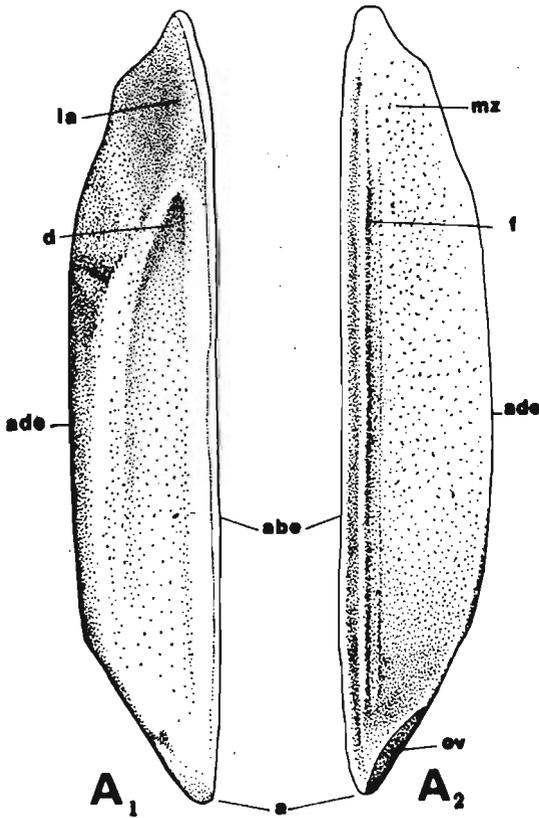


Fig. 1. Lamella of oligolamellar tooth. A_1 external view, A_2 internal view; *a* apice, *abe* abaxial edge of lamellae, *ade* adaxial edge of lamellae, *d* depression left by another lamella, *f* furrow left by adaxial edge of another lamella, *mz* meshwork zone, *ov* overlapping region. Reconstruction, no scale.

slightly twisted (pl. 71: 1—3) what influences the aspect of adaxial surface of teeth (pl. 70: 6; pl. 71: 1—3; pl. 72: 2, 3, 5). Inner side of lamellae (fig. 1: A_2) presents differently developed meshwork zone: it may be uniform (fig. 2: A) or present a linear structure (fig. 2: B) or form areas of thicker and thinner accumulation (fig. 2: C; pl. 74: 1). Narrow furrow runs along adaxial edge of each lamella (fig. 1: A_2 ; pl. 71: 3a, 4a; pl. 72: 1a) to accommodate the same element of neighbouring lamellae. Short overlapping region (fig. 1: A_2) is situated adorally (pl. 73: 3; pl. 76: 5).

Adaxial surface of teeth looks much alike in all types of oligolamellars (fig. 3: A, B; fig. 4: A_1 , B; pl. 72: 4; pl. 73: 3; pl. 74: 5) In contrast, adaxial surfaces differ considerably and this depends on the structure of adaxial edges (fig. 1: A *ade*) of particular lamellae. These edges may be rounded and covered with rather thick layer of calcareous crust (fig. 3: A_2 ; pl. 72: 1, 3, 5). This crust very often is weathered, showing proper edges of lamellae (fig. 3: C; pl. 70: 6; pl. 72: 2). This type of edge is here called smooth.

In other specimen the calcareous crust forms denticles of different appearances (fig. 4: A_2 , B_2 ; pl. 71: 1—2; pl. 73: 1—2, 4—6). This type of tooth is here given the name denticulate-edged. Another group, already

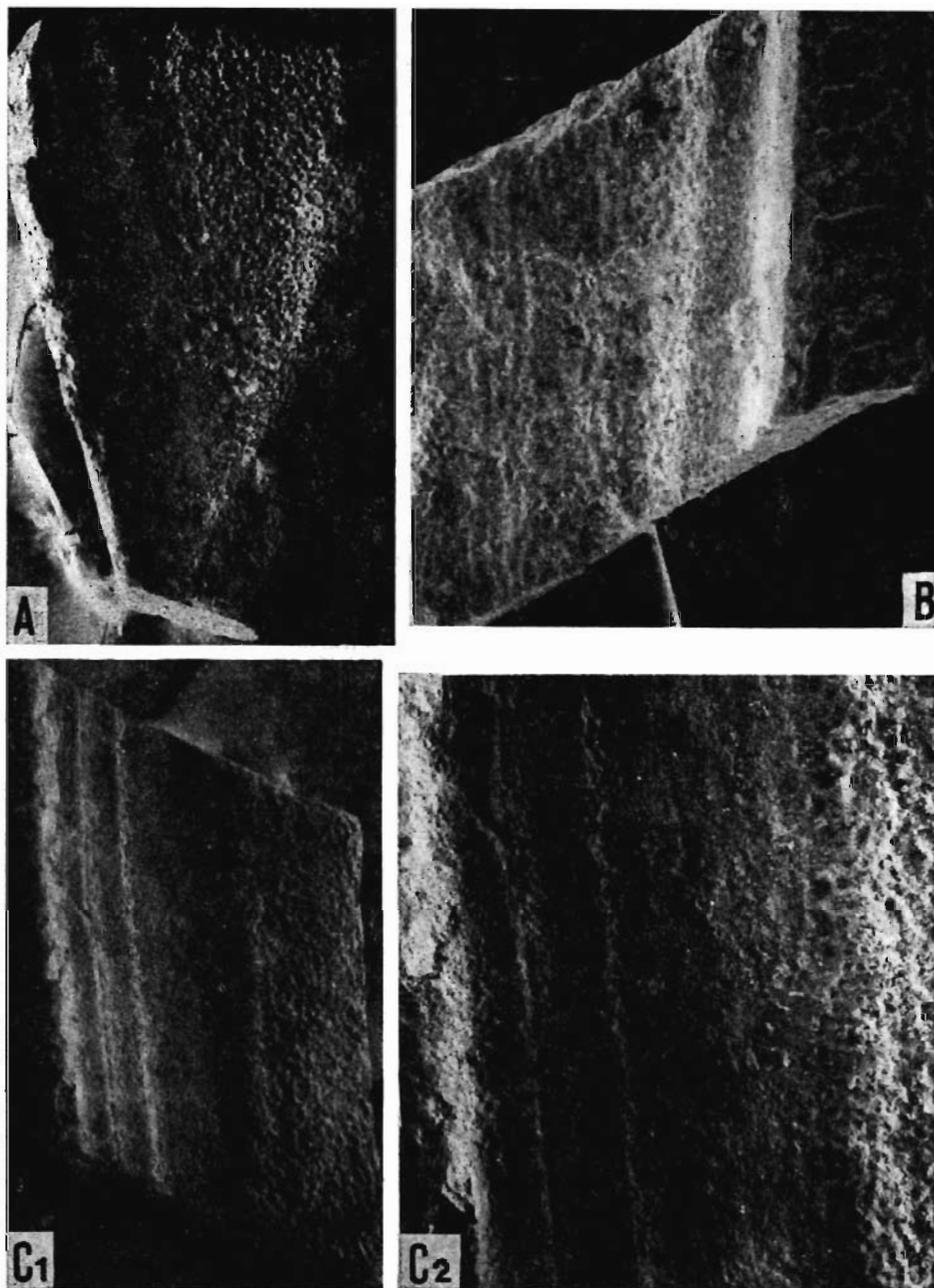


Fig. 2. A—C internal views of lamellae fragments showing differences in development and distribution of meshwork zone: A meshwork dense, uniform on smooth-edge lamella, Skały, complex XVI, $\times 45$, ZPAL E.III/D 201; B linear meshwork zone on ledge-bearing edge of lamellae, Skały, complex XVI, $\times 100$, ZPAL E.III/D 202; C₁ meshwork zone coarser and thicker abaxially on denticulate-edge of lamellae, Miłoszów, Skały beds, $\times 65$, ZPAL E.III/D 203; C₂ fragment of C₁ enlarged $\times 150$. All figures are SEM micrographs.

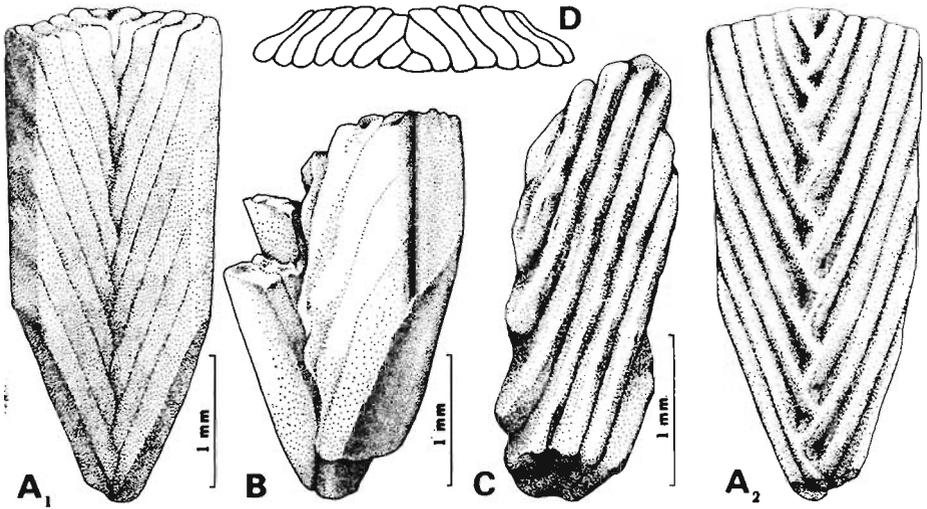


Fig. 3. A—C structure of smooth-edged oligolamellar teeth, slightly schematized: A₁ abaxial view, A₂ adaxial view; B fragment of tooth, abaxial view showing very thick lamellae; C fragment of specimen strongly weathered and broken off along overlapping zone and showing apices of lamellae; D schematized cross-section showing typical arrangement of lamellae in oligolamellar teeth.

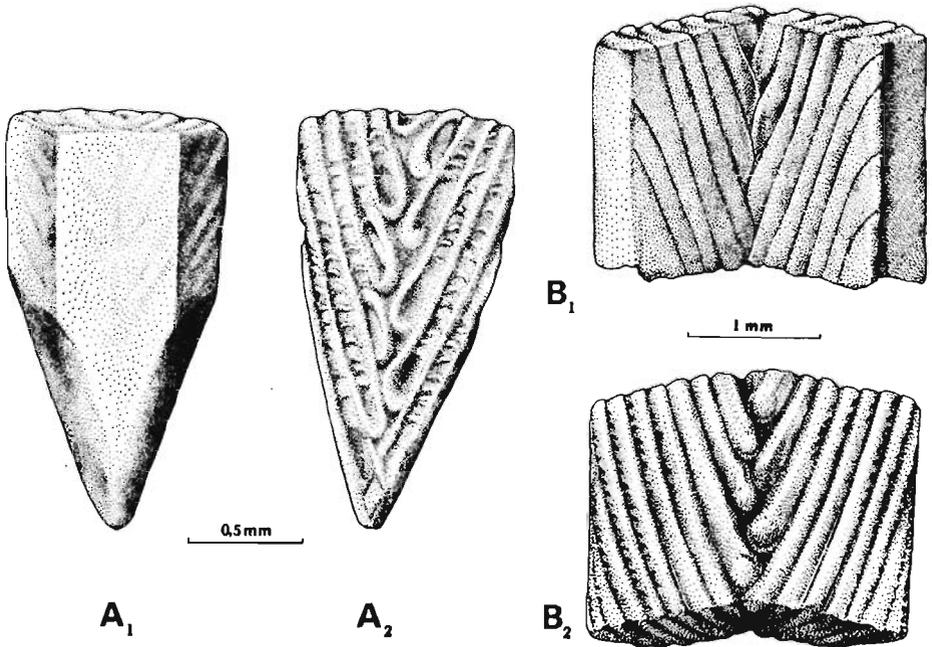


Fig. 4. A—B structure of denticulate-edge oligolamellar teeth; slightly schematized: A₁, B₁ abaxial views; A₂, B₂ adaxial views showing variable appearance of denticulation.

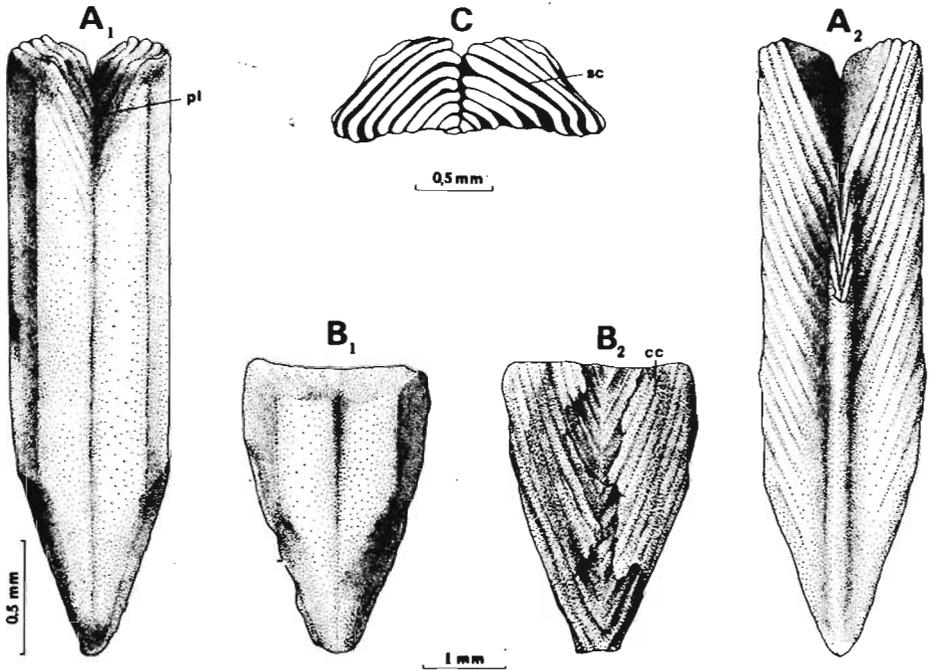


Fig. 5. A—C structure of more advanced oligolamellar teeth, slightly schematized: A_1 abaxial view of specimen with plumula region preserved; A_2 adaxial view of specimen immersed in xylen to show edges of lamellae covered with calcareous crust; B_1 abaxial view of larger specimen; B_2 adaxial view showing calcareous crust partially weathered; C cross-section showing characteristic arrangement and shapes of lamellae, cc calcareous crust, pl plumula region, sc secondary calcification.

described in detail in Part 1 (Jesionek-Szymańska 1979) presents flattened adaxial ledge-bearing edge (fig. 2: B; pl. 74: 2—3).

The question of how many plates may participate in construction of one oligolamellar tooth remains open until more and better preserved material is found. According to observations made on a few, almost complete teeth (both oral tip and plumula region are preserved) the number of lamellae does not exceed 25. In cross sections the number of lamellae is variable and amounts from 6 to 12. The smaller number of lamellae corresponds certainly to the teeth of young individuals (fig. 6: A; pl. 70: 4, 5; pl. 73: 4).

Among material from Skaly beds a small number of teeth, mostly in fragments, which in general morphology correspond to oligolamellar type (fig. 5; pls 75—76) was found. They differ from the formerly described in details which seem to have some importance. When complete (both chewing area and plumula region preserved) they are composed of around 40 lamellae (in material hitherto found) which are much thinner than those of other oligolamellar teeth. They also have very weak overlapping zone. The lamellae are bent inwardly particularly at their adaxial edges (fig. 5: C). The whole construction is kept together by secondary calcification

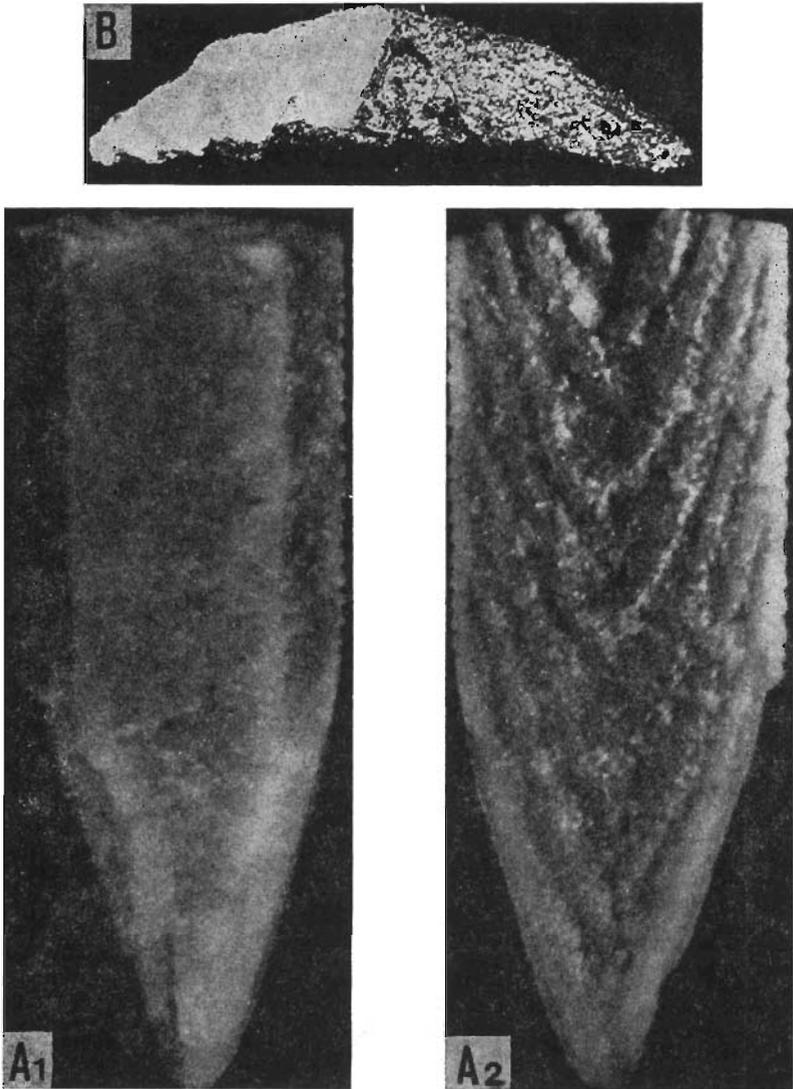


Fig. 6. Four-lamellae tooth (probably from a juvenile individual) of smooth-edge type; A_1 abaxial view; A_2 adaxial view, Skały, complex XVII, $\times 80$, ZPAL E.III/D 203; B cross-section through another specimen examined in polarized light, showing considerable thickness of lamellae, Skały, complex XVII, $\times 100$, ZPAL E.III/D S 204.

which is present between the lamellae and also evenly covers adaxial surface of tooth. This calcareous crust is however rather thin and fragile and in the majority of specimens it is at least partially weathered (fig. 5: B_2). The medially situated furrow — on abaxial surface of tooth seems to be more distinct on fragments of larger specimens (fig. 5: B_1). It is also noteworthy that the arrangement of lamellae in shaft seen in cross-section (fig. 5: C) is quite different from that of plumula region. The latter closely

resembles the same detail in formerly described simple, oligolamellar teeth (fig. 3: D). No special name for this type of teeth is here introduced as it is considered to be a member of oligolamellar group.

DISCUSSION

Despite the rather uniform appearance of the Paleozoic echinoid teeth reported by many authors, when closer examined, they reveal a great and significant diversity. This fact should not surprise if one take under consideration the morphological diversity of Paleozoic echinoids known since Jackson's (1912) famous *Revision*, with many later studies summed up by Kier (1965). This author in many other publications contributed considerably to the knowledge of this group (Kier 1968, 1973). The varied morphology of tests was certainly accompanied by different life style and feeding habits what in many ways had to influence the structure of jaw apparatuses. Looking at the Givetian variety of echinoid teeth which may be very simple, composed of few lamellae or multilamellar (see p. 205) we can infer that they went through long suite of evolutionary events before reaching the Givetian stage. The questions also arises how many types remain still unknown. No one is in position to present in this subject a well founded opinion.

All material described in this paper comes from very limited area and has been found in sediments of the same age, not much diverse lithologically. It would be very important to know the corresponding material from other region of the world. Still more pressing seems to be better knowledge of jaw apparatuses from older strata. From scanty material hitherto described one can infer that *Aulechinus* and *Ectinechinus* (Mac Bride and Spencer 1938) could have had very primitive oligolamellar teeth (Jesionek-Szymańska 1979: 281) but this inference needs to be confirmed on the better preserved material. The teeth of the Lower Devonian lepidocentrid *Rhenechinus hopstätteri* described and illustrated by Dehm (1953: 91, fig. 2) undoubtedly belong to the oligolamellar type. Only adaxial surface of teeth is visible but it presents the arrangement of tooth lamellae typical of here described oligolamellar group. Although Dehm (1953: 92), as far as the material allowed, accurately interpreted the structure of those teeth, his observations were overlooked and not commented upon by later authors.

Much more often in echinoid literature one meets with the mentions reporting, mostly very cursory, the presence of other group of echinoid teeth called sometimes "serrate" (Jackson 1912, Bindemann 1938, Kier 1965) in the Carboniferous and Permian strata. This group of echinoid teeth turned out to be very abundantly represented in the Skaly beds.

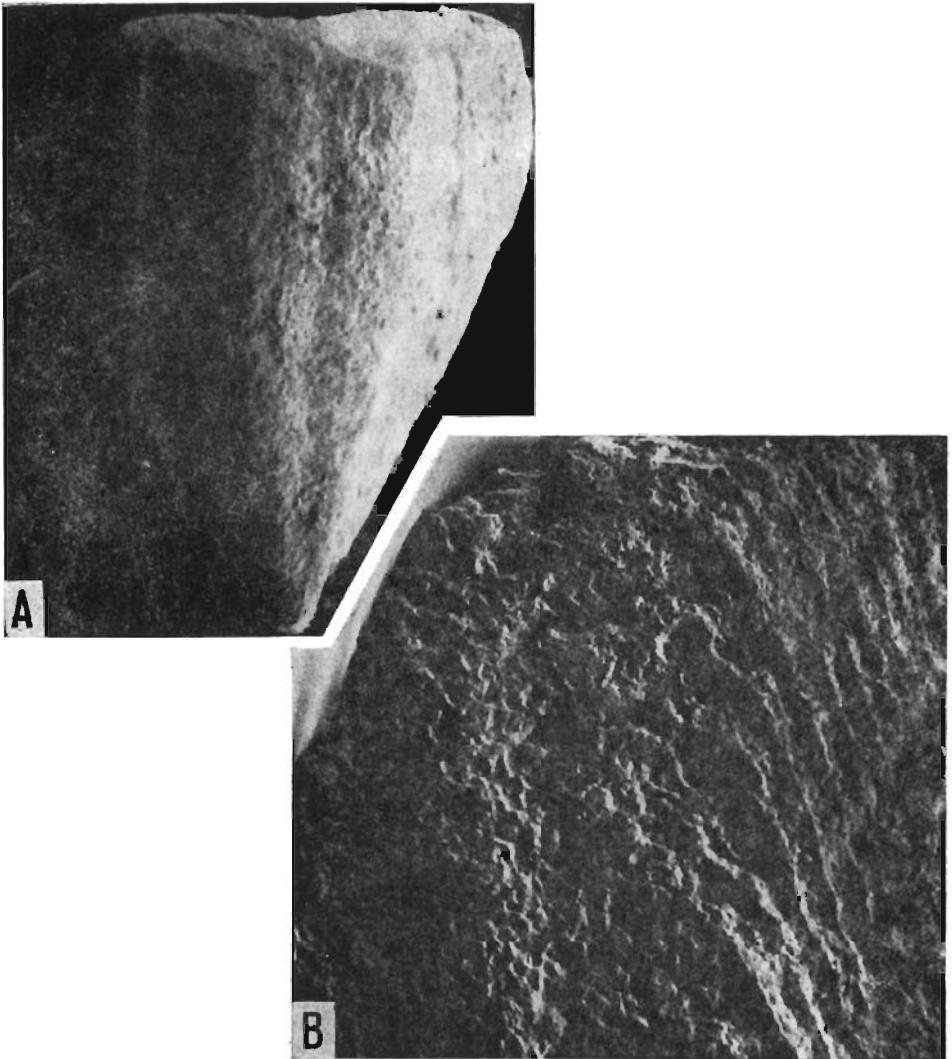


Fig. 7. *A* oral part of multilamellar grooved tooth, Skały, complex XVI, $\times 60$, ZPAL E.III/D 205; *B* fragment of aboral part of multilamellar grooved tooth showing very thin lamellae; also a stereom-like cover on lateral area is visible, Skały, complex XVI, $\times 200$, ZPAL E.III/D 206.

Not entering now into much detail it should be stressed that in microstructure they strongly differ from oligolamellar teeth. Most often they are not more than 2 mm in length (while oligolamellar teeth may reach about 4 mm). Having that small size they are built of much greater number of lamellae (up to 200 in material hitherto examined, in oligolamellar — up to 40) which are also much thinner (fig. 7: *B*). The tooth lamellae are often bent or even plicated. Cross-sections presented on fig. 8*A* show two types of these teeth found in the Skały beds. The type represented on fig. *A*,

distinctly grooved in cross-section is rather rare in the Givetian material from Skały beds. On the contrary the type presented on fig. 8B, flat in cross-section, is very common. These types of teeth, because of significantly large number of lamellae are here termed multilamellar. They will be examined more in detail later. As multilamellar teeth are very common in the Givetian echinoid material (ever 1000 specimens hitherto recorded in deposits from two localities in Holy Cross Mts.) one can infer that they could already have existed in the Silurian. Because of incompleteness of description (Salter 1899: 703; Spencer 1904: 37) it is difficult to interpret the structure of the teeth of the Silurian *Palaeodiscus ferox* Salter although their multilamellar structure is not excluded. The teeth of other Silurian echinoid *Aptilechinus caledonensis* described by Kier (1973: 660, pl. 83: 3) are simply impressions in silty shale and also need studies of more complete material. However from what is already known it is highly probable that they belong to multilamellar type.

There may be a little doubt that oligolamellar type of teeth is much more primitive than multilamellar one and that the latter had to have its origin in the formerly mentioned group. Such varieties of oligolamellar group as described on p. 202 and illustrated on fig. 5, where the tooth lamellae were more numerous, thinner, slightly bent and adaxially covered by the calcareous crust, may be the representatives of evolutionary line from which the multilamellar teeth originated. However, there exists a significant morphologic gap between those two types of teeth. Already in the Givetian they appear to be morphologically well distinct group.

Many questions concerning further ways (after Givetian) of teeth evolution arise. It seems that some characters of multilamellar teeth such as large number of lamellae, their thinness and plasticity resulting in

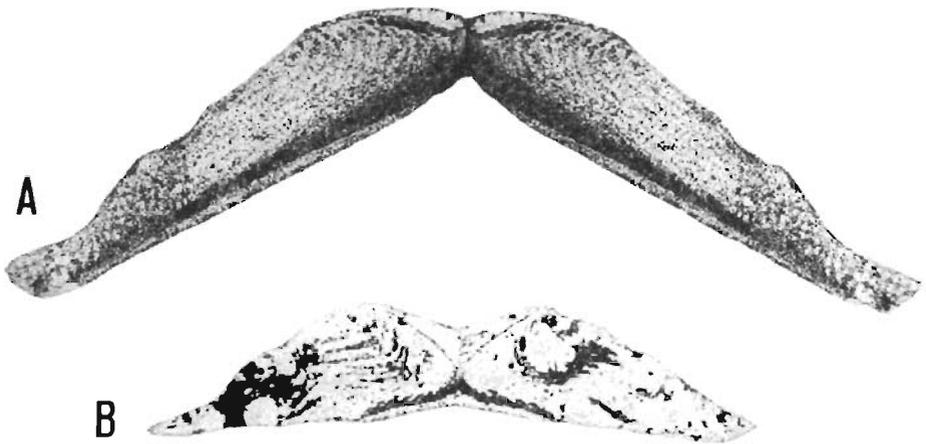


Fig. 8. A—B cross-sections through multilamellar teeth; A grooved tooth, slightly retouched, Miłoszów, Skały beds, $\times 110$, ZPAL E.III/D S 207; B flat tooth showing S-like bending of lamellae, Miłoszów, Skały beds, $\times 200$, ZPAL E.III/DS 208.

bending and plicating, point rather to multilamellar teeth as more successful in further echinoid evolution. It is significant that tooth of the recent *Echinus miliaris* is built of over 2000 very thin (not more than 0.00114 mm thick) lamellae (Giesbrecht 1880). It is also noteworthy that the peculiar spinous endings of multilamellar teeth (Jesionek-Szymańska 1979: pl. 24: 1) much resemble those observed in larval teeth of Recent cidarids (Lovén 1982: pl. 3: 22—23, Mortensen 1938: 24, fig. 10) and clypeasteroid (Théel 1892, pl. 9: 109).

Lately many papers dealing with microstructures of Recent (and some fossil) echinoid teeth have been published (Märkel 1978, Jensen 1979, 1981) revealing their diverse and complicated structure. The authors mentioned above presented far reaching conclusions concerning the origin of post Paleozoic echinoids. However, as long as the fossil material is only fragmentarily known (particularly that from the Permian/Triassic time) the conclusions of Märkel and Jensen cannot be confirmed nor discarded.

REFERENCES

- BINDEMANN, W. 1938. Ein Echinid mit Laterne aus dem Kulm von Herborn, *Mekechinus? herbornensis* n. sp. — *Senckenbergiana*, **20**, 3/4, 204—220.
- DEHM, R. 1952. *Rhenechinus hopstätteri* nov. gen. nov. sp., ein Seeigel aus dem rheinischen Unter-Devon. — *Notizbl. hess. L.-Amt Bodenforsch.*, **81**, 88—95.
- GIESBRECHT, W. 1880. Der feinere Bau der Seeigelzähne. — *Morph. Jb.*, **6**, 79—105.
- JACKSON, R. T. 1912. Phylogeny of the Echini, with a revision of Paleozoic species. — *Mem. Bost. Soc. Nat. Hist.*, **7**, 5—490.
- JENSEN, M. 1979. Primary plates of sea urchin teeth (Echinoidea) — *Vidensk. Meddr. dansk naturh. Foren.*, **141**, 7—27.
- 1981. Morphology and classification of Euechinoidea Bronn, 1860 — a cladistic analysis. — *Ibidem*, **143**, 7—99.
- JESIONEK-SZYMAŃSKA, W. 1979. Morphology and microstructure of oligolamellar teeth in Paleozoic echinoids, Part 1. Teeth of some early lepidocentrid echinoids. — *Acta Palaeont. Polonica*, **24**, 2, 275—293.
- KIER, P. M. 1965. Evolutionary trends in Paleozoic Echinoids. — *J. Paleont.*, **39**, 3, 436—465.
- 1968. *Nortonechinus* and the ancestry of the cidarid echinoids. — *Ibidem*, **42**, 5, 1163—1170.
- 1973. A new Silurian echinoid genus from Scotland. — *Palaeontology* **16**, 4, 651—663.
- LOVÉN, S. 1892. Echinologica. — *Bih. Svenska Vet.-Akad. Handl.*, **18**, 4, 1, 3—73.
- MÄRKEL, K. 1978. On the teeth of the Recent cassiduloid *Echinolampas depressa* Gray, and on some Liassic fossil teeth nearly identical in structure (Echinodermata, Echinoidea). — *Z. Morph. Tiere.*, **89**, 125—144.

- MORTENSEN, Th. 1938. Contributions to the study of the development and larval forms of echinoderms, IV. — *Mem. Acad. Roy. Sci. Lett. de Danemark* 9, 7, 3, 1—59.
- PAJCHŁOWA, M. 1957. Dewon w profilu Grzegorzowice—Skały. — *Biul. Inst. Geol.*, 122, 2, 145—254.
- SOLLAS, W. J. 1899. Fossils in the University Museum Oxford. 1. On Silurian Echinoidea and Ophiuroidea. — *Quart. J. Geol. Soc. London*, 55, 692—715.
- SPENCER, W. K. 1904. On the structure and affinities of *Palaeodiscus* and *Agelacrinus*. — *Proc. Roy. Soc. London*, 74, 31—46.
- STASIŃSKA, A. 1958. Tabulata, Heliolitida et Chaetetida du Dévonien moyen des Monts de Sainte-Croix. — *Acta Palaeont. Polonica*, 3, 3—4, 161—240.
- THÉEL, H. 1892. On the development of *Echinocyamus pusillus*. — *Nova Acta Roy. Soc. Scien. Uppsala*, 15.

WANDA JESIONEK-SZYMAŃSKA

MORFOLOGIA I MIKROSTRUKTURA OLIGOLAMELLARNYCH ZĘBÓW U JE-
ZOWCÓW PALEOZOICZNYCH. CZĘŚĆ 2. ŻYWECKI ETAP EWOLUCJI
OLIGOLAMELLARNYCH ZĘBÓW

Streszczenie

W żyweckich osadach serii skalskiej profilu Grzegorzowice—Skały (Skały, kompleks XVI i XVII) oraz Miłoszowa (Góry Świętokrzyskie) znaleziono obfity i zróżnicowany materiał jeżowcowy w postaci izolowanych płytek pancerza, kolców oraz elementów aparatu szczękowego. Kontynuując pracę nad ewolucją zębów jeżowców paleozoicznych (Jesionek-Szymańska 1979) w niniejszej pracy opisano 3 odmiany zębów oligolamelarnych różniących się głównie szczegółami budowy ich adaksjalnej powierzchni, która może być gładka, pokryta listewkami lub ząbkami, w zależności od wykształcenia adaksjalnych brzegów blaszek. To zróżnicowanie stanowi zapewne wyraz przystosowania do sposobu i rodzaju pożywienia. W pracy opisano również nieznaný dotąd typ zębów podobny w ogólnym planie budowy do zębów oligolamelarnych lecz o blaszkach zębowych nieco liczniejszych (do 40-tu), cieńszych, łukowato wygiętych. Powierzchnia adaksjalna jest całkowicie pokryta gładką wapienną polewą,

tak, że układ blaszek zębowych widoczny jest tylko na zwietrzałych okazach lub w pobliżu strefy wzrostu. Wspomniane cechy zbliżają nową odmianę do struktur obserwowanych w dużej grupie zębów nazwanych tu multilamellarnymi. Zęby te, bardzo liczne w żywocie serii skalskiej, zostały w niniejszej pracy po raz pierwszy zdefiniowane i krótko scharakteryzowane.

Opisane typy zębów pochodzą z warstw jednego wieku, co nakazuje ostrożność w wyciąganiu wniosków co do przebiegu ich ewolucji. Analiza porównawcza cech morfologicznych wykazuje jednak, że zęby oligolamellarne mogły być grupą wyjściową, która poprzez szereg przekształceń jak: powiększenie ilości blaszek, ich ścinienie i uzyskanie pewnego rodzaju plastyczności, oraz zwiększenie roli polewy spajającej poszczególne elementy, dały znacznie bardziej udoskonalony typ, za jaki można uznać zęby multilamellarne. Warto zauważyć, że ten kierunek ewolucyjny musiał być kontynuowany w późniejszej historii Echinoidea — wystarczy przypomnieć, że kilkunastomilimetrowy ząb współczesnego przedstawiciela jeżowców regularnych *Echinus miliaris* zbudowany jest z ponad dwóch tysięcy blaszek zębowych o grubości nie przekraczającej 0,00114 mm.

EXPLANATION OF THE PLATES 70—76

All specimens from Skały beds, Holy Cross Mts, Givetian
All figures are SEM micrographs

Plate 70

Teeth with smooth-edged lamellae

1. Fragment of lamellae with depression and lateral flattening, ZPAL E.III/D 210, Miłoszów, $\times 40$.
2. Fragment of lamellae with narrow depression, ZPAL E.III/D 211, Miłoszów, $\times 30$.
3. Almost complete lamella, external view, ZPAL E.III/D 212, Skały, complex XVII, $\times 60$.
4. Plumula region of juvenile tooth, abaxial view, ZPAL E.III/D 213, Skały, complex XVI, $\times 50$.
5. Fragmentary juvenile tooth with denticles on lateral area, abaxial view, ZPAL E.III/D 214, $\times 60$.
6. Adaxial view of 4-lamellae tooth, ZPAL E.III/D 215, a $\times 30$ b microstructure of calcareous cover, $\times 120$.

Plate 71

1. Adoral fragment of denticulate-edge lamellae, ZPAL E.III/L 216, Miłoszów, $\times 60$.
2. Fragment of another lamellae, ZPAL E.III/D 217, Miłoszów, $\times 50$.

3. Adoral fragments of lamellae, ZPAL E.III/D 218, *a* internal view $\times 60$, *b* side view, Miłoszów $\times 80$.
4. Internal view of lamellae showing furrow and apice, ZPAL E.III/D 219, Skały complex XVII, *a* $\times 40$, *b* $\times 120$.

Plate 72

Smooth-edged lamellae

1. Fragment of lamellae, internal view, *a* $\times 80$, *b* showing calcareous cover, $\times 240$, Skały, complex XVI, ZPAL E.III/220.
2. Fragment of tooth seen from overlapping side, calcareous cover weathered, ZPAL E.III/D 221, Miłoszów $\times 30$.
3. Arrangement of lamellae, fragment of tooth, adaxial surface, ZPAL E.III/D 222, Miłoszów $\times 25$.
4. The same, abaxial view, ZPAL E.III/D 223, Miłoszów, $\times 25$.
5. Large fragment of smooth-lamellae tooth, adaxial surface, ZPAL E.III/D 224, Miłoszów, $\times 25$.

Plate 73

Teeth with denticulate-edged lamellae

1. Fragment of tooth, adaxial view, ZPAL E.III/D. 225, Miłoszów, $\times 25$.
2. Enlargement of denticles, ZPAL E.III/D 226, Miłoszów, $\times 240$.
3. Adoral fragment of tooth with overlapping zone visible, ZPAL E.III/D 227, Skały, complex XVII, $\times 25$.
4. Juvenile tooth, ZPAL E.III/D 228, Skały, complex, XVII, *a* $\times 50$, *b* enlarged $\times 300$.
5. Two neighbouring denticulate lamellae *a* $\times 80$, *b* enlarged $\times 500$ ZPAL E.III/D 229, Skały, complex XVII.
6. Fragment of well preserved denticulate tooth, ZPAL E.III/D 230, Miłoszów $\times 40$.

Plate 74

1. Dense meshwork on ledge-bearing lamella, ZPAL E.III/D 231, $\times 80$.
2. *a*—*c* Fragment of tooth with ledge-bearing lamella: *a* $\times 40$, *b* $\times 120$, *c* $\times 160$, ZPAL E.III/D 232
3. Adaxial view of juvenile tooth, ZPAL E.III/D 233, $\times 50$.
4. Aboral fragment of ledge-bearing lamella, showing lateral flattening, ZPAL E.III/D 234.
5. Fragment of adaxial aspect of tooth, ZPAL E.III/D 235, $\times 50$.

All specimens from Skały, complex XVII

Plate 75

1. Transversal contour of tooth, ZPAL E.III/D 237, $\times 50$.
2. Fragment of tooth, calcareous crust partly weathered, ZPAL E.III/D 238, $\times 50$.
3. Half of tooth seen from overlapping region, ZPAL E.III/D 239, $\times 30$.
4. Fragment of tooth with median furrow, ZPAL E.III/D 240, $\times 30$.
5. Fragment of another tooth without median furrow, ZPAL E.III/D 241, $\times 30$.
6. Fragment of tooth showing arrangement of lamellae and lateral area covered with crust, *a* $\times 40$, *b* $\times 100$, ZPAL E.III/D 242.

All specimens from Skały, complex XVII

Plate 76

1. Juvenile tooth, ZPAL E.III/D 243, $\times 30$.
2. Fragment of tooth with traces of calcareous crust, ZPAL E.III/D 244, $\times 55$.
3. Upper part of tooth showing arrangement of lamellae seen from adaxial side, ZPAL E.III/D 245, $\times 60$.
4. Aboral part of broken tooth showing bent lamellae, ZPAL E.III/D 246, $\times 80$.
5. Oral end of tooth showing overlapping zone, ZPAL E.III/D 247, $\times 100$.
6. Fragment of large tooth with traces of calcareous crust, *a* $\times 60$, *b* enlargement of *a* showing fine detail of calcareous crust, ZPAL E.III/D 278, $\times 180$.

All specimens from Skały, complex XVII



