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MORPHOLOGY AND PALAEOECOLOGY OF THE PRODUCTID *HORRIDONIA HORRIDA* (SOWERBY) FROM ZECHSTEIN OF POLAND

Contents

Abstract. — The results of studies on the structure and palaeoecology of the brachiopod *Horridonia horrida* (Sowerby) from Lower Zechstein of the Holy Cross Mountains (Góry Świętokrzyskie) are discussed in the present paper. The life position preserved in some individuals, allowed the author to elucidate the adaptative character of several morphological elements of the shell and the range of their variability.

INTRODUCTION

The occurrence of *Productus horridus* Sowerby (recte: *Horridonia horrida*) in the area of the Holy Cross Mountains (Góry Świętokrzyskie) has already been mentioned by Pusch (1833). More detailed information on the Zechstein faunal assemblages of this region is given in the works by Czarnocki (1913, 1923) who also mentions *Productus horridus* found in the environs of Gałęzice and Kajetanów. Czarnocki's works are, however, geological in character and they lack descriptions and illustrations of the cited forms. A few specimens of the species referred to above have also been found by Czarnocki (1916) embedded in the cement of the Zechstein basal conglomerate in the region of Gałęzice, which was later confirmed in the work by Czarniecki, Kostecka and Kwiatkowski (1965).

The material, described in the present paper has been collected in summer of 1964, in an old quarry at Kajetanów and in the Zechstein outcrops in the western part of the Gałęzice — Kowala syncline (Sachty, Skałka and Besówka Hills). In the Holy Cross Mountains these are the sole surface exposures of the Zechstein deposits in the limy-marly facies which contain brachiopods.

The present work was prepared at the Palaeozoological Institute of the Polish Academy of Sciences, where also the described collection is kept, marked with catalogue numbers Z. Pal. Bp. IX/1—137.

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METHODS

The microfacies analyses of the deposit from the Gałęzice and Kajetanów sections have been carried out by the present author on the basis of 25 thin sections and of about 30 kg of rock samples, dissolved in the hydrochloric acid. The hydrochloric acid, used to dissolve the samples, had a concentration of 80 per cent and was mixed with water at a ratio of 1 part of acid to 10 parts of water. The dissolution process, started at an initial temperature of about 60°C, was hereafter continued for a week at 20°C. The application of this method allowed the author to leach fine organic particles and microfauna out of compact limestones. The specimens of *Horridonia horrida* were prepared by hand, partly by means of an electromagnetic vibrator of the "Vibro-tool" type. Serial sections of the studied brachiopods were fixed, by means of peels, on a diapositive microfilm and magnified by taking photographs, directly from the enlarger on the paper, from which drawings were made subsequently.

DESCRIPTION

Family **Dictyoclostidae** Stehli, 1954
Subfamily **Horridoniinae** Muir-Wood & Cooper, 1960
Genus *Horridonia* Chao, 1927
Horridonia horrida (Sowerby, 1823)

(Pl. I, Figs. 1—9; Pl. II, Figs. 1—12; Text-figs. 1—3)

1823. *Productus horridus* J. Sowerby; J. Sowerby, The Mineral Conchology... p. 17, Pl. 319, Fig. 1.

1961. *Horridonia horrida* (J. Sowerby); D. J. Gobbett, The Permian Brachiopod... p. 43, Pl. 3, Figs. 1—12; Pl. 5, Figs. 5, 7—8, 13 a-c. (with earlier synonymy).

1965. *Horridonia horrida* (J. Sowerby); S. Czarniecki, A. Kostecka & S. Kwiatkowski, *Horridonia...*, p. 468, Pl. 44, Figs. 1—5.

Material. — Thirty seven complete and 52 damaged specimens, as well as a few separate ventral and dorsal valves in different ontogenetic stages. The material comes from the Lower Zechstein bituminous limestones from Kajetanów and also Lower Zechstein, biodetritic limestones and marls of the environs of Gałęzice (Skałka and Sachty Hills). Elements of internal structure are, in many specimens, destroyed as a result of the recrystallization processes.

Measurements of the *Horridonia horrida* (Sowerby) shell (Table 1) and direction diagram of these measurements (Text-fig. 1) are given below.

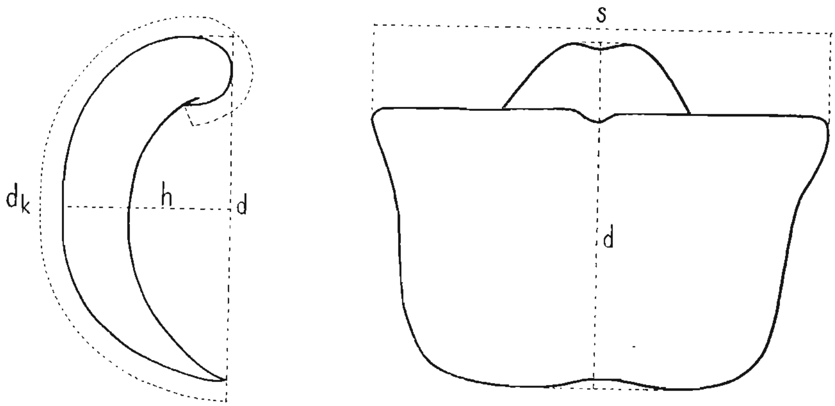

Fig. 1. — Diagram of the shell measurement directions: *d* length, d_k length of the ventral valve curvature, *s* width, *h* height.

External characters. — Concave-convex shell generally subpentagonal, sometimes suboval in outline. The largest width corresponds to the length of hinge margin. The largest convexity occurs in the middle part. Lateral and hinge edges of shell are sharp. Lateral lobes of valves strongly inflected towards the dorsal valve. Ears large, triangular in outline. Hinge margin straight. Anterior margin bent and forming a single fold. Trail moderately developed and, only in a few specimens, completely preserved.

Ventral valve strongly convex, now and then geniculate. Umbo large, broad, with a different degree of inflection, slightly protruding outside of the hinge margin. Umbonal angle, 78—80°. A broad shallow sulcus, running from the umbonal part and gradually disappearing near the anterior margin, is marked in the visceral region.

Dorsal valve slightly concave, seldom geniculate and, in visceral part, almost flat. In the middle, there is a slightly outlined not very broad fold, disappearing towards the trail. This fold corresponds to the sulcus of the ventral valve.

Table 1

Measurements of the *Horrridonia horrida* (Sowerby) shell (in mm)

Z. Pal, Cat, No. Bp. IX/	Length d	Length of arch of ventral valve d_k	Width s	Height h	Width-length ratio $\frac{s}{d}$	Ratio of convexity $\frac{d}{d_k}$
24 K	16	23	26	7	1.62	0.69
49 K	16	18	28	7	1.79	0.88
44 K	17	25	24	6	1.41	0.68
10 K	20	27	27	9	1.35	0.74
57 K	21	28	30	10	1.43	0.75
34 G	25	41	32	13	1.28	0.61
26 G	29	45	36	18	1.24	0.67
25 K	31	63	52	27	1.67	0.48
3 K	33	57	40	16	1.22	0.58
61 K	34	57	46	22	1.35	0.59
16 K	35	63	46	24	1.29	0.56
32 G	36	60	47	19	1.30	0.60
13 K	39	75	46	27	1.18	0.52
31 G	40	71	49	24	1.22	0.56
1 K	43	74	50	25	1.16	0.57
56 K	43	80	50	28	1.16	0.54
17 K	44	76	48	25	1.10	0.58
4 K	47	80	56	26	1.19	0.57

Ornamentation little varied, the shell is virtually smooth. Concentrical, irregular wrinkles are clearly visible. They are particularly well-outlined in the lateral and auricular region of the shell. Growth lines, irregularly spaced, are rather densely distributed. Towards the anterior part of the shell, their trace gradually becomes more and more irregular which results in the formation of numerous thickenings. In many specimens, in the anterior part of the valve, there are visible, more or less distinct, irregularly distributed radial costae. Monticules, occurring occasionally on some ventral valves, seem to be an initial phase of the formation of spines.

Spines are very characteristically distributed over the shell surface. On both valves, there occurs a row of spines running along the hinge margin, with 4—6 spines in each row. Thick, long, auricular spines occur on the ears of both valves. The length of spines increases from umbo to ears, the longest being the auricular spines which, in a few specimens, exceed the dimensions of the shell. On the valve, there occur single spines which, in general, are related with its anterior part, where sometimes they form irregular rows (Pl. I, Fig. 7). Inside of each spine, there

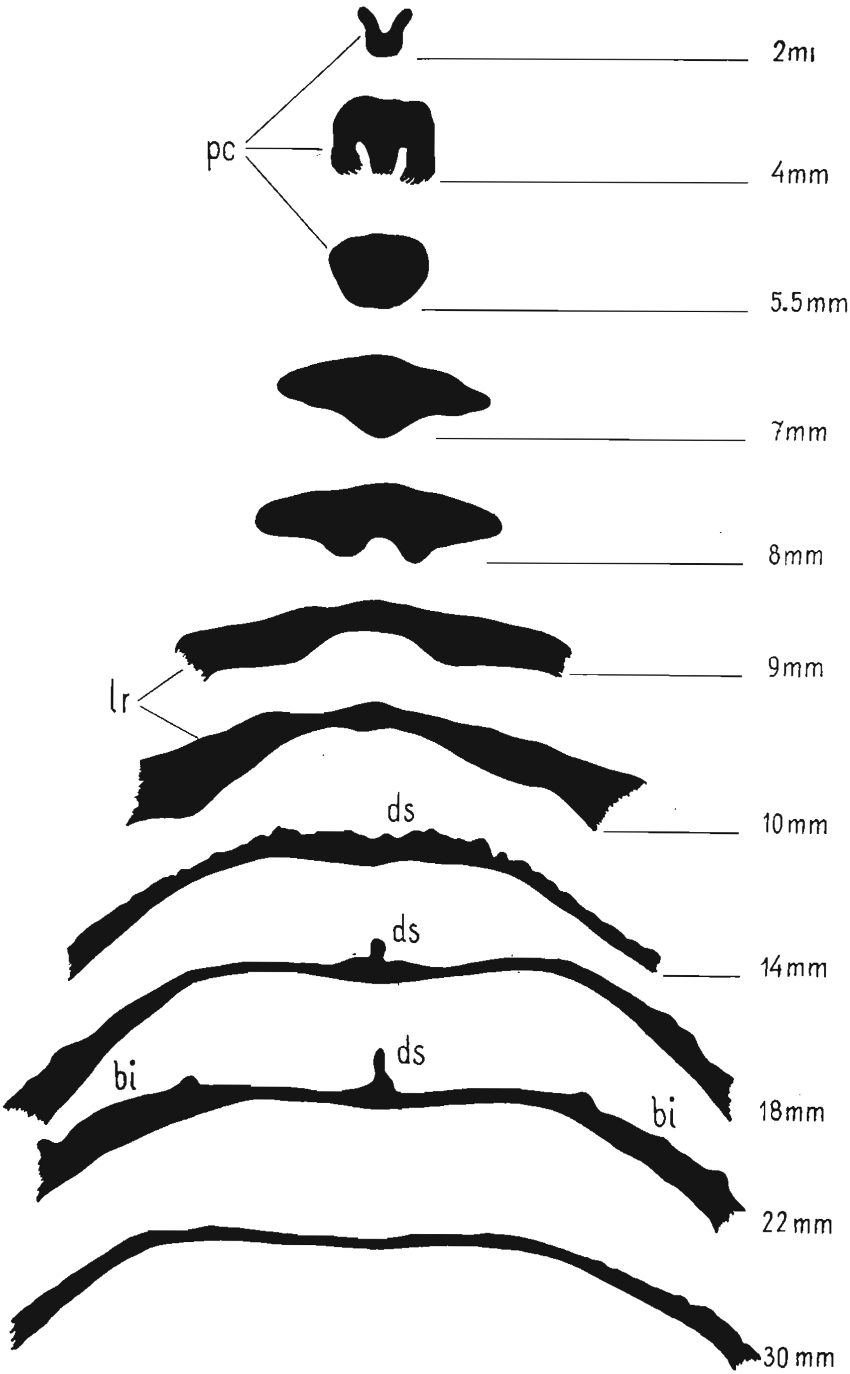

Fig. 2. — *Horridonia horrida* (Sowerby). Transverse serial sections through the dorsal valve: *pc* cardinal process, *lr* lateral ridges, *ds* dorsal septum, *bi* brachial impressions, × 6 (Bp. IX/125 K); Kajetanów.

occurs a central canal. The microstructure of spines does not differ at all from that of valves.

The thickness of valves, in particular that of the ventral one, is variable and depends on the ontogenetic stage. In general, ventral valves are more massive and reach a thickness of 1.0—5.3 mm, the umbonal part and the region of muscle fields being the thickest. The thickness of the dorsal valve amounts resp. to 0.8—3.0 mm and reaches its maximum in the anterior part.

Internal structure. — Ventral valve has a narrow elevated platform with oblong scars of adductor muscles, separated from each other by a shallow groove (Pl. II, Fig. 11). On both sides, in spacious depressions, there are visible radial marks of the diductor muscle fields.

Dorsal valve has triangular muscle fields, separated by a narrow, low septum (Text-fig. 2) of the breviseptum type, which does not reach the base of a cardinal process and is separated from it by a shallow alveolus. This septum is situated in a narrow groove and terminates at 2/3 of the length of the visceral region. The linoproductid (according to Muir-Wood's and Cooper's classification, 1960) type cardinal process is sessile, massive, with the median lobe more strongly developed and divided by a sulcus (Text-fig. 3). On the ventral face, it is bilobed and, on the dorsal, trilobed with muscle scars on myophores. It is connected with lateral ridges, running almost parallel to the hinge margin and gradually disappearing towards the ears. Brachial ridges indistinct, mostly not outlined at all. The entire visceral surface, except for muscle scars and brachial ridges,

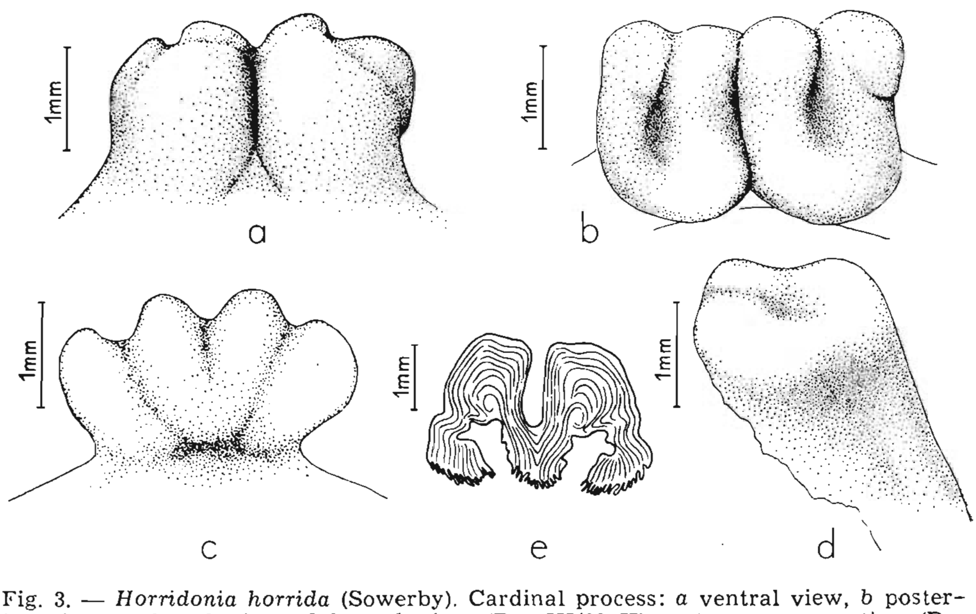

Fig. 3. — *Horridonia horrida* (Sowerby). Cardinal process: *a* ventral view, *b* posterior view, *c* dorsal view, *d* lateral view (Bp. IX/66 K), *e* transverse section (Bp. IX/125 K); Kajetanów.

is covered with nipple knobs, whose size increases towards the anterior margin and ears (Pl. II, Figs. 8 and 12). From the geniculate bent of the valve, these knobs pass into oblong endospines, with their sharp ends pointing anteriorly.

Variation. — The individual variation in adult specimens is displayed only in the external morphology of the shell, whose width is related to a different degree of the development of ears. In individuals with larger ears, the length of the hinge margin is slightly smaller than the largest width of the shell. The degree of the shell coiling is markedly variable (Pl. I, Figs. 1—3). The sulcus on the ventral valve displays a tendency to disappearance. Except for the hinge margin and ears, the spines occur irregularly, most individuals being devoid of them at all. In many cases, the costae are not outlined on the anterior part of the ventral valve.

The growth changes, observed in the external morphology, are expressed by a gradual increase in the degree of the shell coiling and by a successive decrease in the ratio of length. Certain disturbances in a concentrical disposition of the growth lines along the anterior margin and the formation of irregular, oblong costae (Pl. I, Fig. 4) are probably related to a gerontic stage.

Remarks. — The individuals of *Horridonia horrida* (Sow.), known from literature, display a great variation of the external morphology. In an extensive discussion, Gobbett (1961) analyzed the genus *Horridonia* Chao and declared the erection of several species and subspecies to be ill-grounded. According to this author, the changes in the external morphology of the shell, in particular such ones, as the number and manner of distributing the spines, are phenotypic in character. Gobbett refers to the idea of Chao (1927) and ascertains that only two species, that is *Horridonia horrida* (Sow.) and *Horridonia timanica* (Stuckenberg) should be left within the genus *Horridonia*. The forms, coming from Zechstein of the Holy Cross Mountains, display a complete similarity to *Productus* (*Horridonia*) *horridus* var. *hoppeianus* Eisel, described from Zechstein of Germany and Lithuania (Eisel, 1909, *fide* Malzahn, 1937; Stepanov, 1959). The specimens described are also identical with forms, known from Permian of Eastern Greenland (Frebold, 1931, 1933; Dunbar, 1935, 1961). The costae on the anterior part of the ventral valve, considered by Dunbar to be the most important character of the genus *Pleurohorridonia* erected by him, occur on many specimens of the collection of the present writer. The forms under study differ from other varieties of this species, distinguished by Eisel, in a lamellate micro-ornament and few spines in the visceral region of some ventral valves which — in var. *geranus* and *bufoninus* — cover the entire surface of the ventral valve. As compared with English forms, figured in King's work (1850, Pl. 11, Figs. 1—10), the specimens coming from the Holy Cross Mountains have only one row of hinge spines on both valves, a shallower sulcus and a smooth surface of the shell with widely scattered, long spines, occasionally occurring on the ventral valve. Nelson (1962) described — from Permo-Pennsylvanian of Yukon, Canada — two groups of forms which, in the shell morphology and distribution of spines, are similar to *Horridonia horrida* on the one hand, and to *Horridonia timanica* — on the other. In one of these groups, the hinge spines occur only along the hinge margin of the ventral valve and, in the other, along the dorsal. Numerous spines occur, in addition, in the visceral region of the ventral valve.

Horridonia timanica, occurring in the Permian-Carboniferous deposits of Arctic and the Ural Mountains, differs from *H. horrida* in the lack of hinge and aurical spines on the ventral valve, granular ornamentation of the shell, more massive hinge process and generally larger dimensions. Malzahn (1937) considered it to be a starting species for *H. horrida* and several of its varieties, separated by Eisel, as transitional forms.

Geographic and stratigraphic distribution. — *H. horrida* is a well-known index species for marine deposits of Upper Permian (Zechstein) of Europe and it has not been found so far in the Arctic Europe and Russia. It occurs almost always in the calcareous-marly facies and only few specimens have been found in the mudstone and coarse-clastic sediments.

In Poland, in addition to the Holy Cross Mountains (Gałęzice and Kajetanów), *H. horrida* occurs in Lower Zechstein (Werra cyclothem) of the Outer Sudetic Basin. Recently (Kłapciński, 1964), the representatives of this species have also been found in the bore-holes, drilled in the Zechstein deposits of the Fore-Sudetic Monocline.

Type specimens of this species come from Zechstein of Middle England (Marl Slate, Magnesian Limestone). In Germany, *Horridonia horrida* occurs in cupriferous shales (Kupferschiefer) and limestones (Zechsteinkalk) of Lower Zechstein. Of the North-eastern Europe's Zechstein, this species has been described from the bore-holes in Lithuania.

Outside Europe, *H. horrida* is known from Upper Permian of Eastern and Northern Greenland. In Arctic America, it has been described from the Permian deposits of Melville and Ellesmer islands.

The stratigraphic range of *H. horrida* has not so far been accurately determined because of difficulties of correlating the Permian deposits of Europe and Arctic Regions. On the basis of recent investigations (Dunbar, 1955), one may assume that faunal horizons of Permian of Arctic Regions which — among other species — contain *H. horrida*, probably correspond to Zechstein of Europe, although they also contain several faunal elements characteristic of the Sakmarian and Artinskian stages of the classical Permian of Russia.

GEOLOGICAL CONDITIONS AND PALAEOECOLOGY

STRATIGRAPHY AND FACIES

On the basis of lithological criteria, Czarnocki (1923) divided Zechstein of the Holy Gross Mountains into three members. Pawłowska (1964) who, in addition, had at her disposal materials coming from bore-holes, situated in the northern and southern parts of the Holy Cross Mountains, undertook an attempt to separate on this area four cyclothems corresponding to the division, accepted for the regions of evaporitic sedimentation of the Zechstein basin (Richter-Bernburg, 1955). The occurrence of *Horridonia horrida* in Zechstein of the Holy Cross Mountains is limited to Lower Zechstein, according to Czarnocki's division, or to the lowermost cyclothem (Z_1), according to Pawłowska's division.

Our remarks, concerning the lithology of Lower Zechstein are confined to the observation of sedimentological parts of the section, containing *H. horrida*, essential for the reconstruction of the environment of the productids described and characteristics of biocenotic conditions during the development period of these organisms. It has been to a considerable extent that the present writer suplemented his own studies by Czarnocki's (1923), Pawłowska's (1964) and Szaniawski's (1965) observations.

The lithological sequence in the two most important places of occurrence of *Horridonia horrida*, that is at Gałęzice and Kajetanów, is presented, together with the list of faunal assemblages, in the sections enclosed (Text-figs. 4 A-B).

The horizons of Lower Zechstein in which the specimens of *H. horrida* have been found, are developed on the whole in two lithofacies.

Clastic lithofacies

This facies is mostly represented by conglomerates and detritic limestones, widely distributed and with a variable thickness. A turbulent character of this environment was probably one of the factors which limited the development of life in this zone of the sea. Single specimens of *H. horrida,* found in these sediments, were probably redeposited — during the periods of more intensive turbulence of water — from nearby habitats. Such an interpretation is testified to by the sporadicalness of occurrence and fragmentary state of preservation of *H. horrida* found in these places. The occurrence of *H. horrida* in basal conglomerate of Zechstein allowed one to determine the age and marine character of the environment in which these sediments were deposited, at least for the western part of Gałęzice-Kowala syncline (Czarniecki, Kostecka & Kwiatkowski, 1965).

Calcareous and marly lithofacies

This facies is not only characteristic of the section of Gałęzice and Kajetanów, but also it constitutes an equivalent of the Zechstein limestone horizon with fauna, which directly overlays the basal conglomerate in other regions of Poland, in Germany and in Lithuania. The boundary between Lower and Middle Zechstein in the Holy Cross Mountains has been placed by Czarnocki (1923) in the top of deposits of this facies, assumed by him as such a boundary on the basis of the disappearance of fauna. It is also Pawłowska (1964) who considers these deposits to terminate the lowermost cyclothem (Z_1) in the environs of Gałęzice. This facies

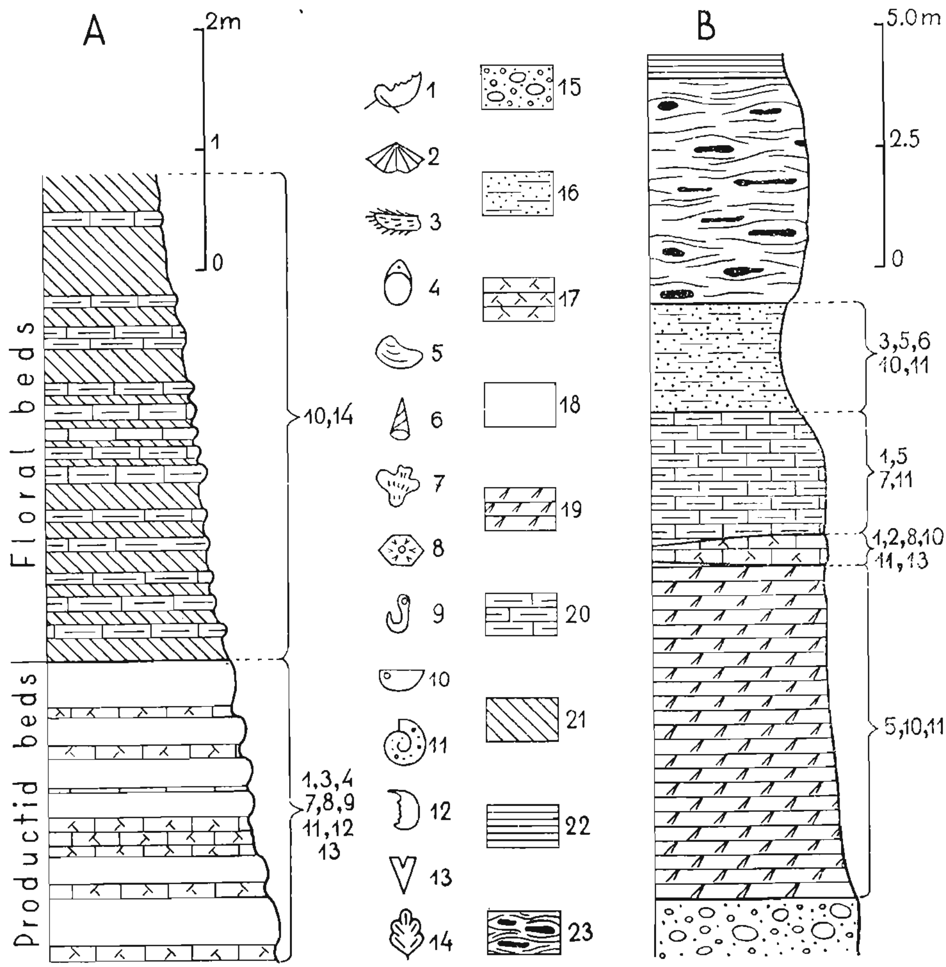

Fig. 4. — Sections through Lower Zechstein strata: *A* quarry at Kajetanów, *B* environs of Gałęzice (Skałka Hills); *1 Horridonia horrida, 2 Pterospirifer alatus, 3 Strophalosia, 4 Dielasma, 5* Lamellibranchiata, *6* Gastropoda, *7* Bryozoa, *8* Echinodermata, *9* Holothurioidea, *10* Ostracoda, *11* Foraminifera, *12* scolecodonts, *13* fish teeth, *14* remains of land plants, *15* conglomerate, *16* sandy marl, *17* biodetritic limestone, *18* pelitic limestone, *19* dolomitic limestone, *20* marly limestone, *21* limy siltstone, *22* shale, *23* laminated limestone with chalcedones.

comprises dark, often bituminous marly, dolomitic and biodetritic limestones. The occurrence of fauna is limited almost exclusively to the lowermost lithological members of the entire cycle of the Zechstein sedimentation which testifies to the fact that only during that period there existed conditions favourable to the development of few animal groups.

In the Zechstein profile of the quarry at Kajetanów, *H. horrida* occurs in a few beds of a black, bituminous, pelitic and biodetritic limestones (Text-fig. 4 A). The middle part of each bed forms an almost pure pelitic limestone, whereas towards the bottom and top, the structure of the rock passes into a more detritic and the colour becomes distinctly brighter. In this place, together with horridonias, there occur numerous brachiopods of the genus *Strophalosia* King and, less frequently, *Dielasma* King. Of other faunal elements, noteworthy are also abundantly occurring foraminifers of the families Ammodiscidae, Miliolidae and Lagenidae, often preserved in the form of galena and pyrite cores, fragments of the colonies of Bryozoans (Cryptostomata), various elements of the jaw apparatus of polychaetes (?Kalloprionidae Kielan-Jaworowska), plates, spines, pedicellariae of echinoids, sclerodermites of holothurians and, finally, teeth and scales of fish. In the detritic intercalations on the boundaries between beds, there also occur indeterminable remains of the carbonized plants. The pelitic cement contains a considerable admixture of clay particles, muscovite and terrigenous quartz that does not exceed the silt fraction. Within pelite, there are numerous threadlike or nestlike accumulations of organic matter to 0.7 mm in size.

The specimens of *H. horrida* from the Gałęzice section (Textfig. 4 B) have been found in bright biodetritic limestones forming intercalations within dark, dolomitic limestones. Of other brachiopods, in addition to horridonias, a few specimens of *Spirifer* (*Pterospirifer*) *alatus* Schlotheim have been found by the present writer. Crushed fragments of the Echinodermata 0.2—0.3 mm in size are microscopically the main faunal component of these rocks. Fairly fragment were foraminifers, among which such genera were identified as *Ammodiscus, Agathammina, Dentalina, Nodosaria* and *Geinitzina*. Fragments of valves and spines of brachiopods are also abundant and, occasionally, spicules of sponges may be found. Except for some foraminifers, all the biodetritic remains display a considerable degree of mechanical crushing. By chemical treatment some teeth and scales of fish were isolated, which should be probably assigned to the Paleoniscidae. In addition to organic remains, attention was also attracted by few intraclasts and grains of quartz to 0.5 mm in size, without signs of wear. The cement consists of a fine-grained calcite with a small admixture of a pelitic substance.

Grey marly limestones in which a few specimens of *H. horrida* have also been found, reposed on the section discussed above. This rock differs from that which underlies it in a much smaller content of detritic elements. The cement, developed in the form of a little-differentiated, pelitic groundmass, in which there are widely scattered foraminifers of the families of Ammodiscidae and Lagenidae, detritus of Echinodermata and fragments of valves of brachiopods, makes up in this place about 80 per cent of the entire volume. There is also a relatively high content of the terrigenous quartz of the silt facies and single grains to 0.4 mm in diameter. In thin sections, this rock displays an indistinct laminate texture, expressed by a parallel disposition of the detritus and a laminate character of the cement.

PALAEOECOLOGICAL CONCLUSIONS

Characteristics of biotopes

The sea transgression on the territory of the Holy Cross Mountains, that took place in Lower Zechstein, invaded an area morphologically differentiated by Hercynian folding (Czarnocki, 1923), which brought about the formation of a complex shoreline with the land deeply indented by bays. Faunistic observations, combined with a lithological analysis and distribution of facies, allow one to presume that, in contradistinction to central areas of the basin with an evaporative sedimentation, the Zechstein sediments in the Gałęzice and Kajetanów sections were formed in the littoral zone. The palaeoecological observations, made on the individuals of *H. horrida* and faunal groups, accompanying them, are in a complete conformity with Czarnocki's conclusion (1923) that in Zechstein of the Holy Cross Mountains there exists a littoral zone with two bays: the Gałęzice-Bolechowice and the Kajetanów bays, marked by a slightly different facial development.

All specimens of *H. horrida* in the Kajetanów section usually occurred on the lower surface of beds, forming characteristic, nodular swellings and always have preserved spines. The individuals, observed in beds were, in all cases, resting on convex ventral valves and the bending of layers, which preserved the imprint of their shape, testifies to the fact that such was their life position (Text-fig. 5). In addition to horridonias, numerously represented, bentonic foraminifers, built of a fine detritic material abundantly occurring on the bottom, were probably another component of the biocenose. A fragmentary preservation state and irregular distribution of other organic remains in the sediment indicate that they are rather allochthonous of this biotope and were driven here by water currents.

On the basis of a microfacial analysis of the deposit, containing horridonias, one may conclude that during the period of the existence of biobottom mud and turning in the axial plane. Such a distribution of spines is a common feature, met with in all the specimens examined, but a certain per cent of adult individuals has, in addition, long spines on the surface of the ventral valve, mostly in its anterior part (Text-figs. 6 and 7; Pl. I, Figs. 5—7). The last-named spines are disposed almost perpendicularly to the surface of the ventral valve and, on the whole, distributed very irregularly, sometimes forming larger groups. On the basis of the variable situation of these additional spines, one may draw the conclusion that they were formed as a supplementary resistance element since, with the growth of an individual, the anterior part of its shell was sunk in the sediment. In the case of the genera *Diaphragmus* and *Muirwoodia*, a similar role is ascribed by Muir-Wood and Cooper (1960) to single spines occurring on the anterior part of the ventral valve. The development of accessory spines was usually accompanied by an intensive increase in the degree of the shell coiling. On the basis of the material examined, the present author believes that, depending on effectivity, the first or the second of these two ways of protection against sinking was actually used and, sometimes, even both of them occur simultaneously. On the surface of the ventral valve of a few specimens, there occur variously sized monticules, which make up a sort of rudimentary spines, whose formation was arrested when the stability of the shell was obtained by an increase in the coiling (Pl. II, Fig. 9).

The material, reviewed from the viewpoint of the problems discussed, comes from one bed only and, therefore, an equal influence was exerted by abiotic factors on all individuals of the population. Thus, it should

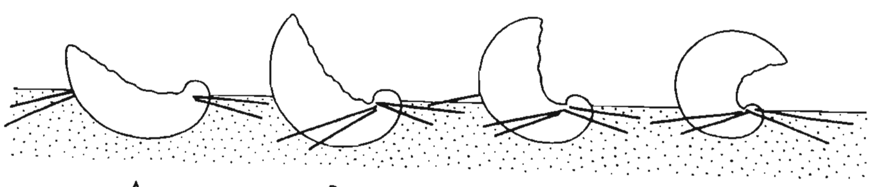

Fig. 7. — *Horridonia horrida* (Sowerby). Reconstruction of different life positions in sediment, made on the basis of field observations: *A—D* diagrams, showing a variable degree of coiling of the shell and the resistance role of spines; Kajetanów.

be assumed that within a homogenous biotope, there existed local differences in the hardness of the bottom, which exerted an influence on the morphology of shells reposing on it, or that the observed variability in the occurrence of accessory spines and in the degree of the shell coiling was a result of different positions of individuals in the sediment, taken in the earliest development stages. It should be also emphasized that the specimens, found in district limestones of the Gałęzice section, do not display the presence of accessory spines on ventral valves, and the degree of their shell coiling is much smaller. In their case, the bottom of the basin was covered with a sufficiently "harder" sediment as not to compel horridonias to use this additional protection.

The structure of the horridonias shells also reveals several other manners of adapting them to the life on a soft bottom. A large area of the ventral valve, increased by well-developed ears, formed a considerable resistance surface, while the geniculate, inflected lateral lobes and the anterior lobe of the shell assured a maximum rise of the mantle margin above the bottom surface. An almost tangent adherence of valves in the anterior and lateral parts provided a guarantee of a tight closure of the shell and — with an oblique position of the dorsal valve — helped remove the depositing clayey-mudy sediment, as it has been described by Grant (1966) in the genus *Waagenoconcha*. Nipples and fine spines, covering the inner surface of the anterior part of valves, might operate — with a small opening of valves — as a filtration system (Muir-Wood & Cooper, 1960, p. 34). The lack of costae on the surface of the specimens examined is probably secondary in character, since their function of a mechanical reinforcement of the shell structure was, with a partial burying of a horridonias in the sediment, unnecessary. The occurrence of indistinctly outlined costae on the anterior part of the ventral valve of adult specimens may be interpreted either as gerontic disturbances (Saritsheva, 1949), or as elongation of the mantle margin by folding, by which its respiratory area was increased (Schmidt, 1937).

Since, among Recent brachiopods, there are no ecological counterparts of productids, the attention of the present writer was focussed on other group of animals, with their mode of life and structure of shell similar to those of horridonias. The recent and fossil mussels of the genus *Gryphaea* Lamarck (Joysey, 1959; Hecker, 1962), whose structure, mode of life and plastic adaptability to abiotic factors display a far gone similarity to the brachiopods described, turned out to be a good comparative material. Grypheids, like horridonias, belong to the sessile benthos, free-laying on the bottom surface and, to a considerable extent, depending on its character. The bottom usually consists of a limy-clayey, quaggy sediment, on which the grypheid characters of these molluscs tend to develop to an extreme extent. The grypheoidal lines, occasionally developed from the conservative stem of *Ostrea*, as a result of an influence exerted by the environment have already become a classical material for the studies on interesting processes of the heterochronic parallel convergence (Urbanek, 1957). A lack of ornamentation, convex and strongly coiled ventral valve, well-developed ears and trail, as well as a relatively large dimensions of the shell, are the main morphological features of horridonias in which, among other characters, they are similar to grypheids. Such a great convergence with grypheids induced the present writer to presume that horridonias may constitute a counterpart of the "grypheoidal" line within Productoidea and, strictly speaking, Dictyoclostidae. On such an assumption, the most "grypheoidal" form should be ascribed to the most coiled forms with strongly developed ears and devoid of ornamentation. The forms with a small degree of the coiling and with the surface of both valves, ribbed and covered with spines, were probably the starting point of the "grypheoidal" line of horridonias. Hiatuses in records do not allow one to determine an accurate moment of the appearance of the "grypheoidal" trend and to trace successive development stages of this line. Several varieties, separated by Eisel (1909) from the individuals of *Productus (Horridonia) horridus*, which were collected in different Zechstein beds of the Gera Basin and, hereafter, identified by Malzahn (1937) as transitional forms from *Productus (Horridonia) timanicus* to *Productus (Horridonia) horridus*, seem to represent different stages of the functional adjustment to the environment conditions variable in time. The example of German form reveals also that the trend in morphological changes in *H. horrida* was marked by an adjustment character of acquired features, capable of recapitulation in the cases of changes, occurring in biotope. Such reversions consisted in the appearance of costae, decrease in the degree of the shell coiling and development of spines, distributed all over the valve surface. A similar capability of morphological reversions is also characteristic of the *Ostrea-Gryphaea* line (Joysey, 1959). The structure of the shell in the individuals, described in the present paper, seems to indicate that they represent this development stage rather distant from the hypothetical initial form.

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JÓZEF KAŹMIERCZAK

MORFOLOGIA I PALEOEKOLOGIA PRODUKTUSA *HORRIDONIA HORRIDA* (SOWERBY) Z CECHSZTYNU POLSKI

Streszczenie

Praca dotyczy gatunku *Horridonia horrida* (Sowerby, 1823) — brachiopoda charakterystycznego dla morskich osadów permu Europy i niektórych obszarów Arktyki; wykonana została na podstawie materiałów zebranych przez autora z cechsztynu Gór Świętokrzyskich (Gałęzice i Kajetanów). Występowanie gatunku ograniczone jest do dolnego cechsztynu (Czarnocki, 1923), wykształconego głównie w facji wapienno-marglistej.

Typowa *Horridonia horrida* opisana została po raz pierwszy pod nazwą *Productus horridus* Sowerby w 1823 r. z cechsztynu środkowej Anglii. W 1927 r. Chao utworzył w obrębie produktidów nowy rodzaj *Horridonia*, w którym *Productus horridus* przyjął za genotyp. Gobbett (1961), po rewizji rodzaju *Horridonia*, uznał za dobrze zdefiniowane jedynie gatunki *Horridonia horrida* (Sow.) i *Horridonia timanica* (Stuck.). Inne gatunki i podgatunki, wydzielone na podstawie różnic w morfologii zewnętrznej są, jego zdaniem, fenotypami wymienionych wyżej. Formy z cechsztynu Gór Świętokrzyskich są identyczne z *Productus* (*Horridonia*) *horridus* var. *hoppeianus* Eisel, opisanymi z cechsztynu Niemiec i Litwy. Od innych różnią się one, niekiedy znacznie, morfologią muszli, brakiem ornamentacji oraz ilością i rozmieszczeniem kolców.

Zmiany wzrostowe, jakim podlega muszla, są niewielkie i zaznaczają się w stopniowym wzroście skręcenia i stałym zmniejszaniu wskaźnika szerokości. Zmienność osobnicza zbadanych form dotyczy jedynie cech morfologii zewnętrznej muszli i jest wynikiem dużej podatności tych brachiopodów na zmiany biotopu. Zmienność ta uwidocznia się szczególnie w różnym stopniu skręcenia muszli i nieregularnym występowaniu kolców na obszarze wisceralnym skorupki wentralnej.

Występowanie horridonii w biocenozie umożliwiło autorowi przeprowadzenie obserwacji paleoekologicznych, wyjaśniających funkcjonalne znaczenie szeregu elementów morfologii zewnętrznej muszli. *Horridonia horrida* należy do grupy brachiopodów swobodnie spoczywających na dnie (Ivanova, 1958; Muir-Wood & Cooper, 1960). Paleogeografia cechsztynu świętokrzyskiego, powiązana z analizą mikrofacjalną sedymentu, wykazała, że horridonie żyły w przybrzeżnej strefie zbiornika, w którym deponowane były osady wapienno-ilaste, z dużą zawartością substancji organicznych i kwarcu terrygenicznego. Konstrukcja muszli horridonii, podobnie jak u innych produktidów należących do tej samej grupy ekologicznej (Saryčeva, 1949; Muir-Wood & Cooper, 1960, i in.), charakteryzuje się następującymi przystosowaniami, zabezpieczającymi przed pogrążaniem w miękki osad podłoża:

1) wydatny stopień skręcenia i zgrubienia w części dziobowej, ułatwiające uniesienie brzegu przedniego nad dnem;

2) duża powierzchnia oporowa muszli, zwiększona przez dobrze wykształcone uszka;

3) kolankowato zagięte płaty boczne i styczne przyleganie skorupek, zabezpieczające przed zanieczyszczeniem przez osad z boku i z góry;

4) welon oraz brodawki i drobne kolce, pokrywające gęsto wewnętrzną powierzchnię skorupek i funkcjonujące jako system filtracyjny;

5) wachlarzowato rozłożony system kolców zawiasowych i uszkowych, chroniący przed pogrążeniem i stabilizujący położenie w osadzie.

W wypadkach naruszenia równowagi osobnika w okresie wzrostu wytwarzane były przez brzeg płaszcza dodatkowe kolce na skorupce wentralnej, podpierające muszlę od strony przedniej. Częściej jednak w takich sytuacjach stabilność uzyskiwana była przez intensywniejsze skręcenie muszli. Asymetryczne skręcenie muszli niektórych osobników i wytwarzanie dodatkowych kolców z jednej tylko strony spowodowane zostało nierównomiernym pogrążaniem w osadzie.

Przeprowadzone obserwacje wykazały, że zmiany osobnicze związane były silnie z typem sedymentu, na którym leżały horridonie. Formy znalezione w wapieniach detrytycznych z Gałęzic nie mają dodatkowych kolców na skorupce wentralnej i skręcenie muszli jest u nich znacznie mniejsze. Ścisła zależność występowania kolców od warunków środowiskowych obniża znacznie ich przydatność jako diagnostycznej cechy gatunkowej.

Autor przeprowadził badania porównawcze z współczesnymi i kopalnymi małżami rodzaju *Gryphaea* Lamarck, których budowa, sposób życia i plastyczność przy zmianach czynników abiotycznych wykazują duże podobieństwo do horridonii. Główne cechy morfologii horridonii, upodabniające je do *Gryphaea*, to wypukła i wydatnie skręcona skorupka wentralna, brak urzeźbienia, wydatne uszka i duże rozmiary muszli. Autor wysuwa przypuszczenie, że horridonie mogą stanowić linię „gryfeidową", powstałą na przełomie karbonu i permu z pnia Productoidea. Na przykładzie osobników *Productus* (*Horridonia*) *horridus* opisanych z Niemiec (Malzahn, 1937) można sądzić, że zmiany morfologiczne w historii tego gatunku miały charakter przystosowawczy i, podobnie jak dla linii *Ostrea* — *Gryphaea*, mogły ulegać rewersji przy zmianach biotopu.

ЮЗЕФ КАЗЬМЕРЧАК

МОРФОЛОГИЯ И ПАЛЕОЭКОЛОГИЯ ПРОДУКТУСА *HORRIDONIA HORRIDA* (SOWERBY) ИЗ ЦЕХШТЕЙНА ПОЛЬШИ

Резюме

Работа посвящена виду *Horridonia horrida* (Sowerby, 1823) — брахиопода характерного для морских отложений перми Европы и некоторых районов Арктики. Исследования основаны на материале собранном автором из цехштейна Свентокржиских Гор (Галэнзице и Каетанув). Распространение вида ограничено к нижнему цехштейну (Czarnocki, 1923), развитому главным образом в известково-мергелистой фации.

Типичная *Horridonia horrida* была описана впервые под названием *Productus horridus* Sow. в 1823 г. из юехштейна центральной Англии. В 1927 г. Чао (Chao) установил в пределах продуктид новый род *Horridonia*, принимая *Productus horridus* как генотип. Гоббетт (Gobbett, 1961), после ревизии рода *Horridonia*, признал правильно определенными только виды *Horridonia horrida* (Sow.) и *Horridonia timanica* (Stuck.) .Иные виды и подвиды, выделенные на основании различий внешней морфологии, по мнению этого автора, являются фенотипами вышеуказанных. Формы из цехштейна Свентокржиских Гор идентичны с *Productus (Horridonia) horridus* var. *hoppeianus* Eisel, описанными из цехштейна Германии и Литвы. От иных они отличаются, иногда значительно, морфологией раковины, отсутствием скульптуры, а также количеством и размещением игл.

Возрастные смены раковины незначительные и проявляются в постепенном увеличении изгиба и постоянном уменьшении указателя ширины. Индивидуальная изменчивость изученных форм относится лишь к признакам внешней морфологии раковины и является результатом большой податливости этих брахипод на смены биотопа. Изменчивость эта проявляется особенно в различной степени изгиба раковины и нерегулярном расположении игл на висцеральной части вентральной створки.

Присутствие горридонии и биоценозе дало автору возможность провести палеоэкологические наблюдения, выясняющие функциональное значение ряда элементов внешней морфологии раковины. *Horridonia horrida* принадлежит к брахиоподам свободно расположенным на дне (Иванова, 1958; Muir-Wood & Cooper, 1960). Палеогеография свентокржиского цехштейна в увязке с микрофациальным анализом седимента указала, что горридонии обитали в прибережной области бассейна, в котором отлагались известково-глинистые осадки, богатые примесью органического вещества и терригенного кварца. Строение раковины горридонии, так как и иных продуктид принадлежащих к этой самой экологической группе (Сарычева, 1949; Muir-Wood & Cooper, 1960 и др.), характеризуется следующими приспособлениями, обеспечивающими перед погружением в мягкий осадок субстрата:

1) выдающаяся степень изгиба и утолщение полости около макушки, что облегчает приподнятие переднего края над субстратом;
2) большая опорная поверхность раковины, увеличена хорошо развитыми ушками;
3) коленчато согнутые боковые лопасти и тесное соприкосновение створок, обеспечивающее перед загрязнением осадком с верхней и боковых сторон;
4) шлейф и также бугорки и мелкие иглы густо покрывающие внутреннюю поверхность створок и действующие как фильтрационная система;
5) веерообразно расположенная система замочных игл и на ушках, обеспечивающая перед погружением и стабилизирующая положение в осадке.

В случае нарушения равновесия особи в течении роста, на вентральной створке были образованы мантийным краем добавочные иглы, которые поддерживали раковину с передней стороны. Однако чаще в таких случаях стабильность приобреталась более интенсивным изгибом раковины. Асимметрический изгиб раковины некоторых особей и образование добавочных игл только с одной störoроны вызвано было неравномерным погружением в осадке.

Проведенные наблюдения указали, что индивидуальные смены были сильно связаны с типом осадка, на котором лежали горридонии. Формы найденные в детритовых известняках из Галэнзиц не имеют добавочных игл на вентральной створке и изгиб раковины у них значительно меньший. Тесная зависимость присутствия игл от условий среды заметно понижает их диагностическое видовое значение.

Автор провел сравнительные изучения с современными и ископаемыми двустворчатыми моллюсками рода *Gryphaea* Lamarck, которых строение, образ жизни и пластичность при сменах абиотических факторов проявляют большое сходство к горридониям. Главные морфологические признаки горридоний, уподобляющие их к *Gryphaea*, это выпуклая и значительно изогнутая вентральная створка, отсутствие скульптуры, выдающиеся ушка и крупные размеры раковины. Автор предполагает, что горридонии могут представлять „грифеидную" линию продуктид, которая возникла на переломе каменноугольного и пермского периода. На примере особей *Productus* (*Horridonia*) *horridus*, описанных из Германии, можно полагать, что морфологические смены в истории этого вида имели приспосабливающий характер и, так как для линии *Ostrea-Gryphaea*, могли подвергаться реверсии при сменах биотопа.

PLATES

Plate I

Horridonia horrida (Sowerby)
(Kajetanów)

Figs. 1—3. Three adult specimens with a different degree of the shell coil, viewed laterally (Bp. IX/25 K, 19 K, 1 K).

Fig. 4. Adult specimen, viewed ventrally; in the anterior part, indistinct costae (Bp. IX/56 K).

Figs. 5—7. Three different specimens, viewed ventrally; irregular distribution of traces of ventral spines visible (Bp. IX/25 K, 106 K, 19 K).

Fig. 8. Adult specimen, viewed ventrally (Bp. IX/2 K).

Fig. 9. Adult specimen, viewed dorsally (Bp. IX/1 K).

All natural size

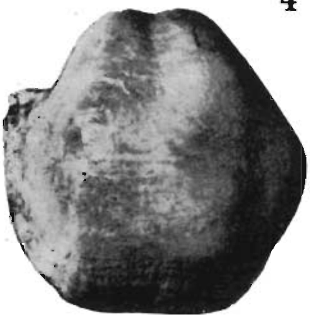

1


2


3


4


5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