SHELL STRUCTURE OF THE DEVONIAN RETZIID BRACHIOPOD *PLECTOSPIRA FERITA*

by GERTRUDA BIERNAT *and* ANDRZEJ BALIŃSKI

ABSTRACT. Electron microscope studies of *Plectospira ferita* (von Buch) show the presence of two inorganic layers, primary and secondary, as well as a third, outermost one interpreted here as a periostracum. This is the first time a periostracum has been recognized in the fossil state. The structure of the periostracum of *P. ferita* is described and a comparison is made with periostraca of living brachiopods. The micro-ornamentation of the shell of *P. ferita* is described; pits and tubercles occurring on the surface of the primary layer are considered in detail.

THE minute Middle Devonian retziid brachiopod *Plectospira ferita* is a remarkable, but poorly known, species originally described by von Buch (1834). One of its characteristics is a differentiated surface ornamentation. The shell is folded with a zig-zag anterior commisure and bears distinct and numerous trunk-like surface tubercles. The most interesting are very fine, densely spaced pits looking like puncta (text-fig. 1).

No detailed observations were made during study of the Middle Devonian brachiopods from the Holy Cross Mountains (Biernat 1966) because this species is very rare in the Devonian of Poland, being then known from only one specimen. Since 1966 only three additional shells have been found during field-work, one of them with an exceptionally well-preserved shell exterior. This shell, together with some others of the same species from West Germany, have allowed detailed electron microscopic studies.

Material

The collection studied includes specimens of *P. ferita* (v. Buch) from Poland and West Germany. The specimens from Poland come from brachiopod-bearing marly shales of the Skały Beds, Holy Cross Mountains (exposure 83), where they occur together with other rare brachiopods such as *Uncinulus primipilaris* (v. Buch), *Kayseria lens* (Phillips), *Undispirifer* sp., *Cyrtina intermedia* (Oehlert), *Squamulariina parva* (Gürich) (see Biernat 1966, text-figs. 1-3). One of the four Polish specimens of *P. ferita*, the best-preserved of those studied up to now, has been broken into small pieces and investigated with the SEM.

Nine out of forty-nine specimens from the Middle Devonian of Eifel, West Germany, have been studied with the SEM. They are not so well preserved, usually with an exfoliated primary shell layer. In some specimens the primary layer is preserved only in the form of small patches between the ribs in the anterior part of the shells. Complete shells as well as sections and fragments of shells have been studied. The specimens from West Germany are housed at the Palaeontological Museum of the Humboldt University in Berlin (cat. nos. MB. B 303-306). The specimens from the Holy Cross Mountains are housed at the Institute of Palaeobiology of the Polish Academy of Sciences in Warsaw (cat. no. ZPAL Bp VII).

SHELL STRUCTURE OF *PLECTOSPIRA FERITA*

Shell structure of *P. ferita* is easily comparable with that of other Spiriferida. What is more, exceptionally well preserved specimens of this species enable correlation of each shell layer with

[Palaeontology, Vol. 25, Part 4, 1982, pp. 857-867, pls. 92-95]

particular stages of exoskeletal secretion in the Recent brachiopods, including an initial stage of forming an outermost organic sheet.

The specimens under study reveal two inorganic layers, the primary and the secondary ones, the latter being endopunctate. A most exciting and interesting discovery is the recognition of the third, outermost layer, which probably corresponds with the outermost organic layer of the Recent brachiopods, i.e. the periostracum. It is preserved either as a very thin layer overlying the calcitic primary layer and/or as more or less circular isolated patches filling the cup-shaped pits on the primary layer (e.g. Pl. 92, figs. 2–5).

A preserved periostracum within the Palaeozoic brachiopods is a new record. There is no other evidence for such a layer, except for the moulds of protegular parts of periostracum on some inarticulate brachiopods (Biernat and Williams 1970; Poulsen 1971). However, one can suggest that the preservation of periostracum on fossil brachiopods is not so rare. The specimens of *P. ferita* from West Germany kindly loaned to us by the Palaeontological Museum of the Humboldt University in Berlin also possess similarly preserved periostracum.

The shell exterior is covered by tubercles—a characteristic shell ornamentation for *P. ferita*. Depending upon the state of preservation, the shell surface can be ornamented also by pits or patches of periostracum filling them (Pl. 92, figs. 2, 4; Pl. 95, fig. 1).

Primary layer. The outer surface of the primary layer is finely granular without evident traces of the radial lineation described in some Spiriferida (Mackinnon 1974, p. 193, pl. 1, figs. 1, 4; pl. 15, fig. 4). Such lineation only rarely occurs in *P. ferita* and may be partly due to some recrystallization and weathering (Pl. 92, fig. 1).

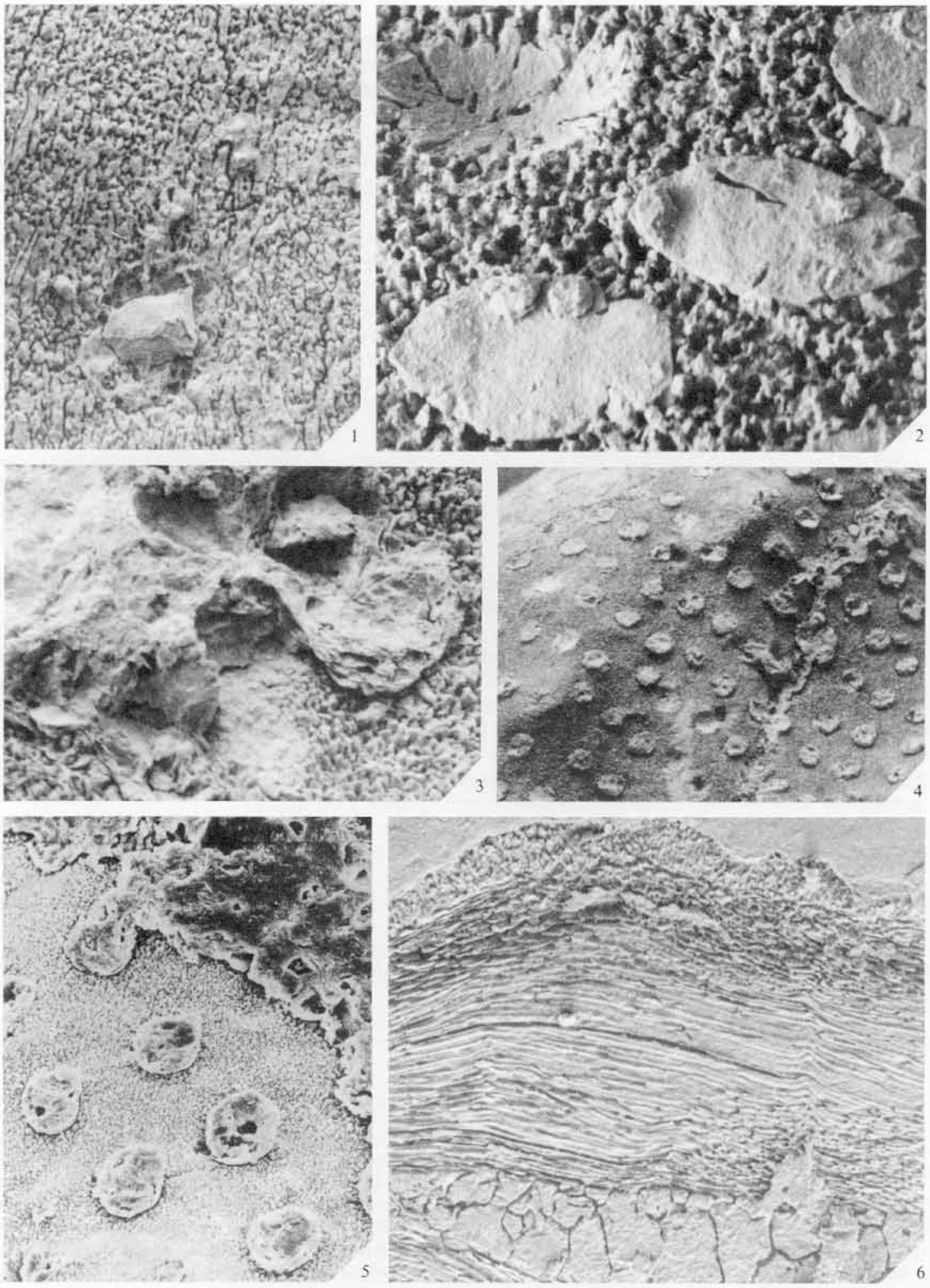
The thickness of the primary layer can vary from about 17 to 35 μm, without taking into account the pits and tubercles. It is composed of crystallites having their long axes more or less normal to the plane of junction between the primary and secondary layers (Pl. 93, fig. 1). Fine depositional banding with a periodicity of about 0·3 to 0·8 μm occurs sporadically. This banding may be explained by diurnal changes in the rates of deposition, as is the case in Recent, and some fossil articulate brachiopods (Williams 1968*a*; Mackinnon 1974).

Secondary layer. The structure of the secondary layer of *P. ferita* strongly resembles that of other spiriferides. This layer is made up of stacked fibres which measure up to 20 μm in width. Fibres may exhibit a fine banding with a periodicity of about 0·3 to 0·6 μm, which may be the daily amount of deposition. The inner surface of the secondary layer shows a standard secondary shell mosaic pattern. The secondary layer contains lenses of coarsely crystalline calcite which can pass peripherally into standard fibrous calcite (Pl. 92, fig. 6). The endopunctate condition greatly resembles that of other Retziidina and Recent Terebratulida. The puncta are widely spaced, very thin, and measure 3 to 8 μm in diameter (Pl. 93, fig. 2).

Periostracum. Well-preserved specimens show a third layer overlying the calcitic primary shell layer. The third layer is very thin, usually reaching a thickness of 1·5 to 2·0 μm (Pl. 93, fig. 1); exceptionally, it can be as thick as 6 μm.

EXPLANATION OF PLATE 92

Figs. 1–6. *Plectospira ferita* (von Buch). 1, view of the external surface of the primary layer showing traces of fine radial lineation (running from bottom to top). ×600. ZPAL Bp VV/663a. 2, view of slightly inclined external surface of primary layer showing patches of periostracum filling cup-shaped pits; an empty pit at top left corner. ×600. MB. B 303. 3–6, ZPAL Bp VII/663a: 3, view of fragmentarily preserved periostracum overlying the granular surface of the primary layer; lamellar structure well seen at the right of micrograph. ×1000. 4, view of the external surface of shell showing patches of petriostracum and two tubercles. ×100. 5, view of the external surface of shell showing the formation of patches of periostracum. ×300. 6, section through a tubercle showing the primary (top) and secondary layers; the latter with a lens of coarsely crystalline calcite (bottom of micrograph). ×300.



BIERNAT and BALIŃSKI, brachiopod *Plectospira*

In the specimens of *P. ferita* from West Germany, the primary structure of the outermost thin layer is obliterated (Pl. 92, fig. 2). More details on the structure of this layer can be seen on the well-preserved specimen from the Holy Cross Mountains. Here the outermost layer shows a distinct lamellar structure (Pl. 92, fig. 3; Pl. 94, fig. 2). The lamellae are about 0·1 to 0·2 μm thick. There are also sporadic, fine vesicles approximately 1 μm in diameter.

A somewhat different structure is to be found in characteristic hemispherical or somewhat lens-like thickenings of the outermost layer, which fill in the pits on the primary layer. Alongside thin lamellae there are numerous vesicles. They show wide variation in size, but extremely large vesicles, up to 20 μm or more in diameter, are typical (Pl. 92, figs. 3, 5–6; Pl. 94, fig. 6). The base of the hemispherical thickenings is formed by a somewhat thicker lamella, which pads the smooth surface of the pit bottom on the primary layer (Pl. 93, fig. 4; Pl. 94, fig. 1). This smooth surface of the pits (Pl. 94, fig. 3) suggests that the inner padding lamella was strongly cemented to the pit bottom, unlike the rest of the junction surface of the outermost and primary layers. This may explain, at least in part, the formation as a result of weathering of characteristic patches of the outermost layer on the surface of the primary one (Pl. 92, figs. 4–5).

Origin of the outermost layer

On the basis of the morphology described above it seems most likely that the third, outermost layer corresponds to the periostracum. The thickness of periostracum in Recent brachiopods rarely exceeds a micron, but in *Macandrewia* it can attain more than 8 μm (Williams and Mackay 1978, 1979). The thickness of periostracum of *P. ferita*, although undoubtedly much reduced during fossilization, could fall within these limits.

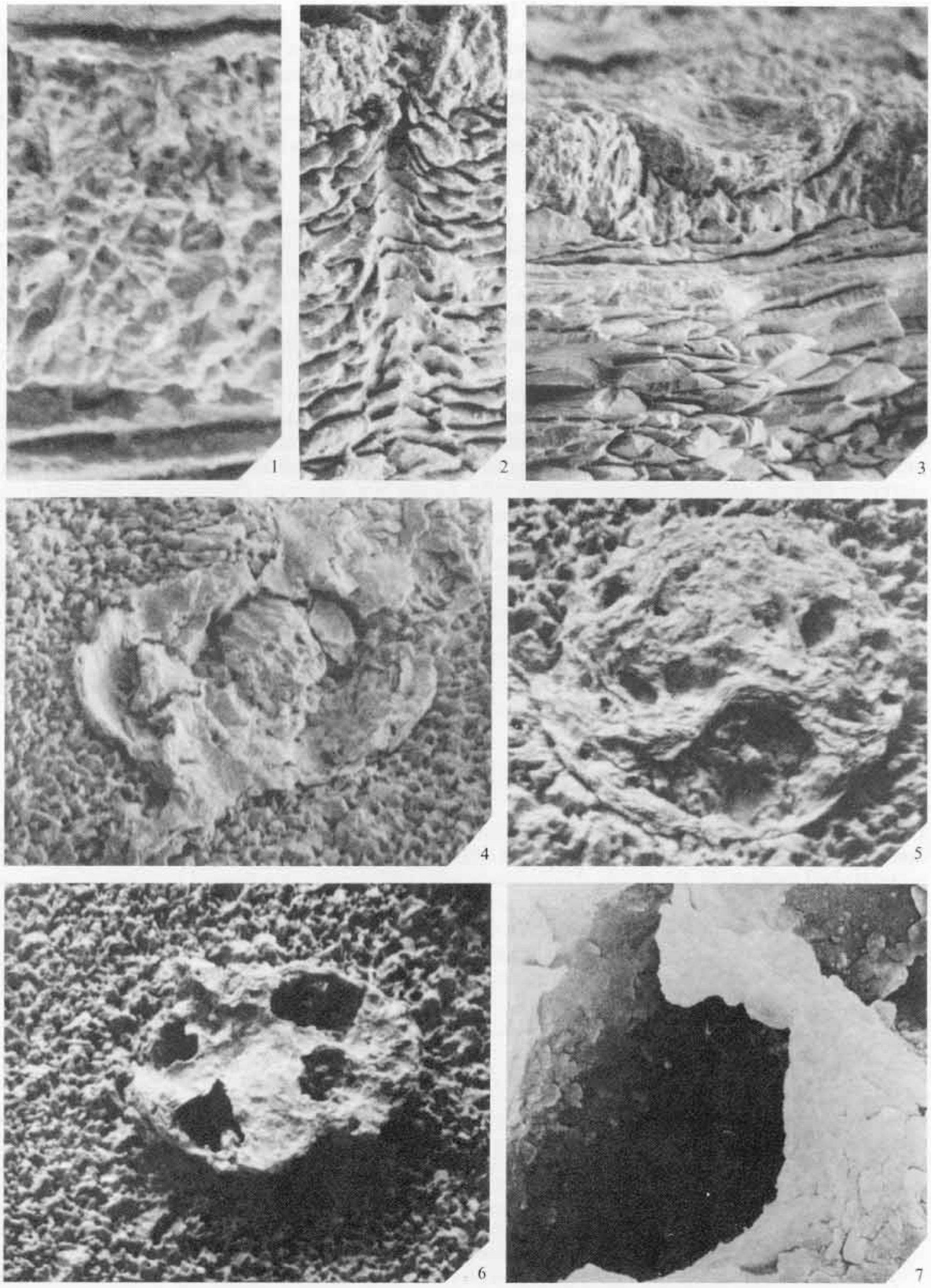
The recognized structural elements of this layer—such as lamellae and vesicles—can be compared with analogous structures of the known periostraca of Recent brachiopods.

One of the essential arguments convincing us that the layer in question can be interpreted as a periostracum is its place in the exoskeletal secretory regime of *P. ferita*. As has been shown by studies on the ultrastructure of the calcareous shell of living and fossil articulate brachiopods, that part of the secretory regime has been remarkably stable throughout the known history of this group of brachiopods (Williams 1968*a*, *b*; Mackinnon 1974). Moreover, secretion of an outermost organic sheet must always have been an integral phase of the entire secretory regime (Williams 1968*b*, p. 1). From this point of view, the outermost thin layer covering the primary shell layer of *P. ferita* can correspond only with the outermost organic sheets of other brachiopods.

As far as we know, a preserved periostracum has never been observed in fossil brachiopods. The periostracum mentioned by Ivanova (1971, pp. 14–15) for a number of fossil brachiopods in fact corresponds to the calcitic primary layer. Jope (1965, 1969), on the other hand, recognized proteinaceous fragments from decalcified fossils of inarticulate and articulate brachiopods. There have also been reports of organic matrices in other fossil invertebrates, for example, ammonoids and pelecypods, some of them remarkably well preserved (e.g. Grégoire and Voss-Foucart 1970; Grégoire and Teichert 1965; Grégoire 1966; Erben, Flajs and Siehl 1969; Mutvei 1969; Pugaczewska 1976).

EXPLANATION OF PLATE 93

Figs. 1–7, *Plectospira ferita* (von Buch). 1, section through the secondary (bottom) and primary layers and a thin periostracum (top). × 2000. ZPAL Bp VII/663a. 2, section through the primary (top) and secondary layers showing punctum. × 1000. MB. B 304. 3–7, ZPAL Bp VII/663a. 3, fracture through a patch of periostracum filling a pit on the primary layer. Secondary layer at the bottom half of micrograph. × 1000. 4, view of the abraded patch of periostracum showing well-developed inner sealing membrane. × 1000. 5, view of the slightly abraded patch of periostracum showing its lamellar-vesicular structure. × 1500. 6, general view of a patch of periostracum showing a few slightly damaged large vesicles. × 1000. 7, more detailed view of the vesicle-bounding membrane. × 10K.



BIERNAT and BALIŃSKI, brachiopod *Plectospira*

This allows the supposition that the preservation of periostracum in fossil brachiopods is also to be anticipated if the right preservation is available. More attention must be paid in future to the shell surface when studying existing fossil collections. The periostracum may be preserved as its original material, with some diagenesis; it may also have undergone pseudomorphosis or impregnation, still preserving some of its original structure. This latter case may be exemplified by *P. ferita*.

Discussion

The present studies on periostracum of *P. ferita*, although fragmentary, throw some light on the degree of differentiation of the organic exoskeleton within the brachiopods. The lamellar structure recognized in the periostracum investigated may, to some extent, reflect its original structure. Particular lamellae may correspond to some of the periostracal elements of living brachiopods, such as the outer and inner bounding membranes (or basal membrane), the fibrillar mat, as well as the protein labyrinth changed due to compaction and the vacuoles bounded by triple-layered membranes (Williams and Mackay 1978, 1979).

Small vesicles in the periostracum of *P. ferita* correspond presumably to the mucin inclusions and vacuoles (Williams 1968*b*). But hemispherical periostracal thickenings densely and regularly distributed have not, so far, equivalents within the known periostraca of Recent brachiopods. The presence of such structural elements is suggestive of further possibilities both in specialization and secretory differentiation of the mantle edge cells. As the best-preserved fragments of the shell from Poland show, these thickenings appear to be made up, in their greater part, of vesicular tissue (Pl. 93, figs. 5-7; Pl. 94, fig. 6), underlain by a thickened inner sealing membrane (Pl. 93, fig. 4; Pl. 94, fig. 1). Among living articulates a vesicular periostracum is the more prevalent condition (Williams 1968*c*, p. 274; 1968*b*, p. 8; Biernat and Williams 1970, p. 502). However, the vacuoles of the periostracum within living brachiopods may approach about 3 μm in diameter, in contrast to *P. ferita*, where they may be more than 20 μm. If these vesicles really correspond to the original structure of the periostracum, they may be treated as a secretory result of a few, or perhaps of many cells. By comparison with the vacuoles in Recent forms, these vesicles must have contained the discarded cell constituents, and in all probability were bounded by triple-layered membranes.

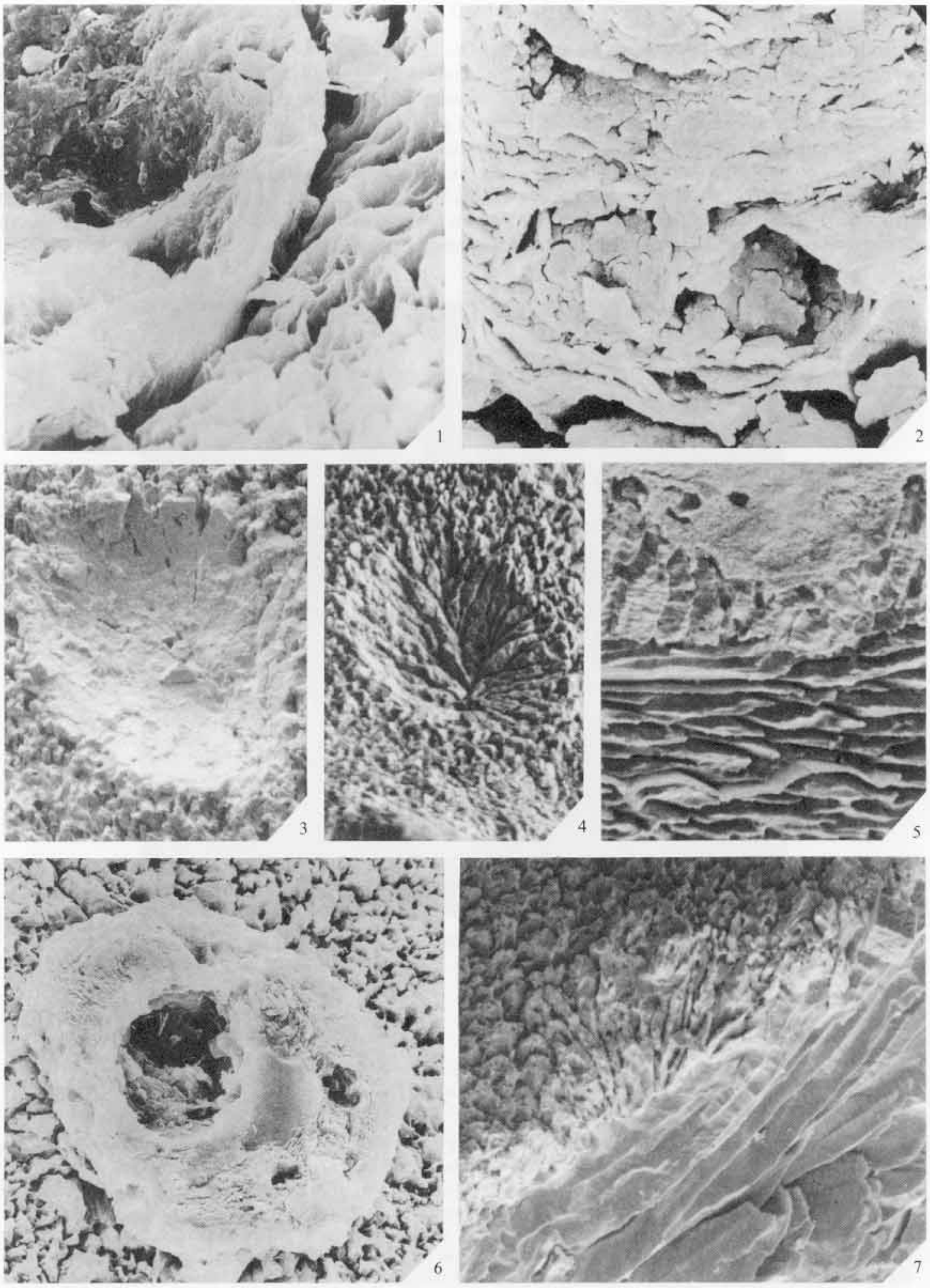
ORNAMENTAL FEATURES OF THE MINERAL SHELL SURFACE

Pits

Pits, which are moulds of hemispherical thickenings of periostracum on the surface of the primary layer (Pl. 93, fig. 2), constitute one of the most characteristic elements of micro-ornamentation of the mineral shell surface (Pl. 95, fig. 1). Their distinctness and appearance depend very much upon the state of preservation of periostracum. The most common is the case when the shell is devoid of periostracum and the pitted surface of the primary layer is then well seen. Pits, densely spaced over the whole shell surface, are arranged in regular oblique rows (Pl. 95, fig. 1). Their regular concavity shows only little variation in outline from rounded to longitudinally elliptical, ranging from 45 to

EXPLANATION OF PLATE 94

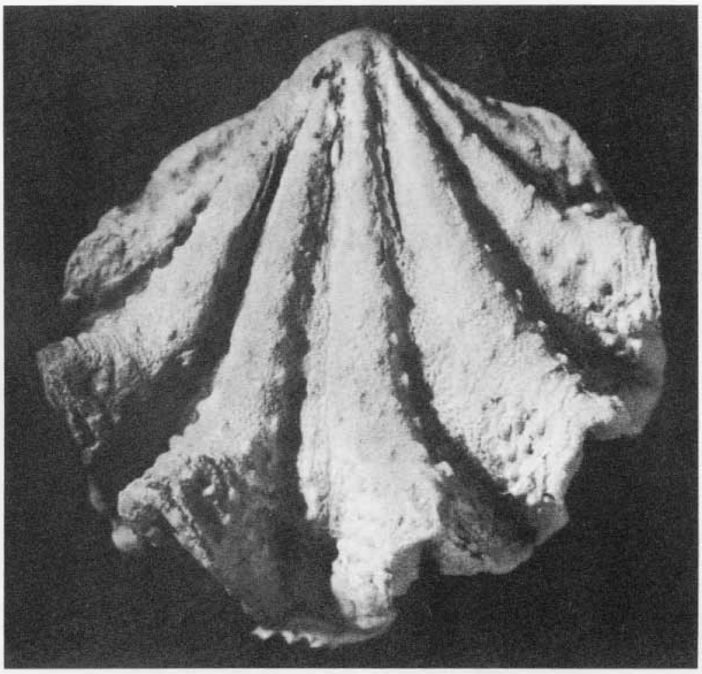
Figs. 1-7, *Plectospira ferita* (von Buch). 1, detailed view of edge of a patch of periostracum showing the inner sealing membrane. × 3600. ZPAL Bp VII/663a. 2, detailed view of a fragment of periostracum showing its lamellar structure. × 10K. Same specimen as fig. 1. 3, view of a pit on surface of the primary layer with well-preserved smooth pit bottom. × 600. MB. B 303. 4-7, ZPAL Bp VII/663a. 4, view of a pit with somewhat weathered bottom showing a characteristic rosette-like pattern of crystalline arrangement. × 1000. 5, section through a pit showing arrangement of crystallites of the primary layer (top). Secondary layer at bottom half of micrograph. × 1000. 6, view of a patch of periostracum showing its vesicular-lamellar structure. × 1500. 7, external view of the primary (top) and secondary layers; a part of the pit is seen in the centre; notice the lack of connection between the pit and endopunctation. × 1000.



BIERNAT and BALIŃSKI, brachiopod *Plectospira*

75 μm in diameter and from 12 to 17 μm in depth. The bottom of the pit, if well preserved, can be smooth (Pl. 94, fig. 3), but if somewhat weathered it shows a rosette-like pattern (Pl. 94, fig. 4) because of a specific arrangement of crystallites of the primary layer (Pl. 94, fig. 5).

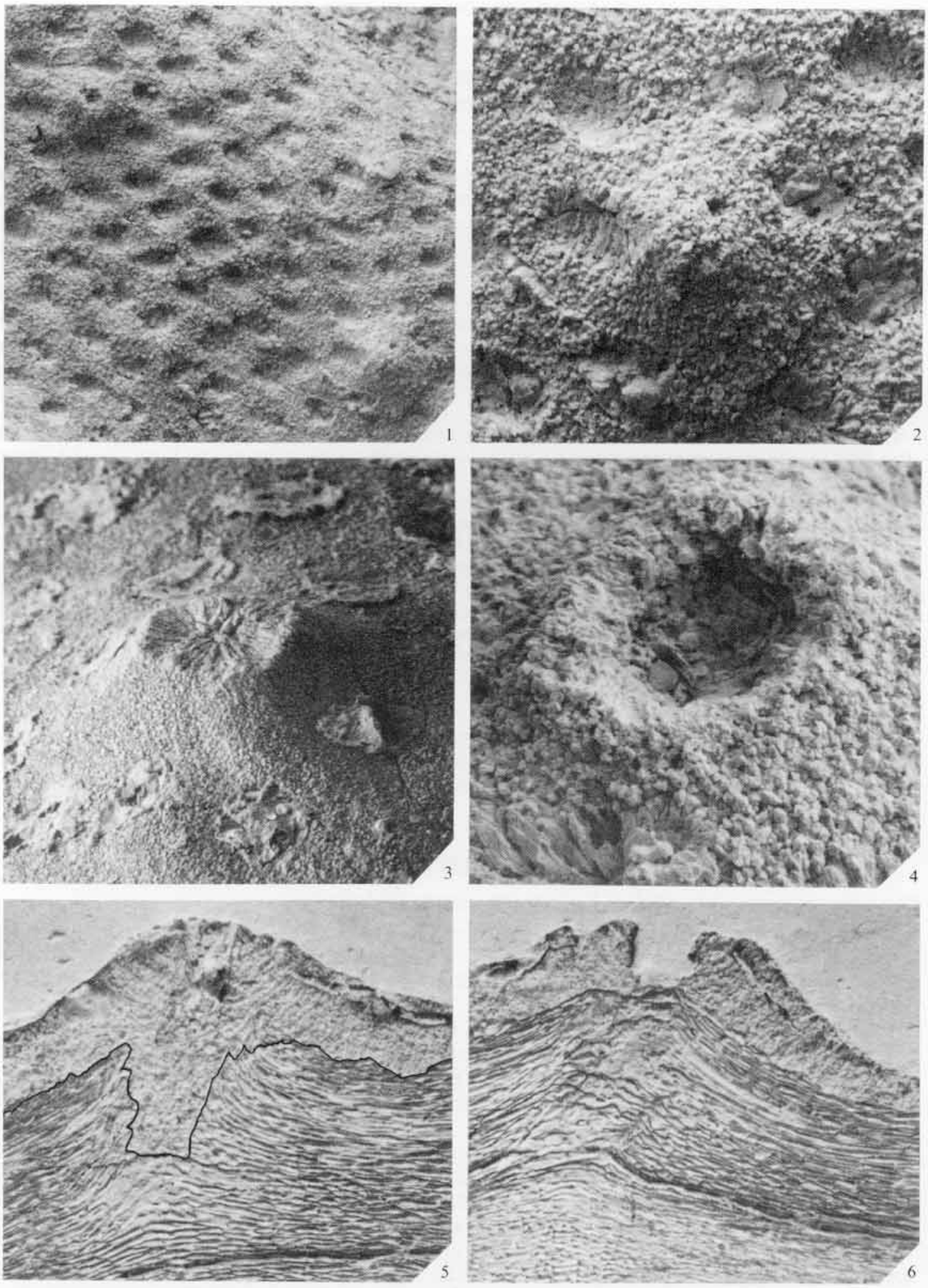
In many cases, however, the pattern of the shell surface is peculiar. There occur small patches of periostracum, similar to the pits in their arrangement and outline (Pl. 94, fig. 4). These patches are remnants of the periostracum that fills in the pits. Such a preservation is due to gradual weathering as well as to the disintegration of periostracum (Pl. 92, fig. 5). There are also a few places where the shell surface is smooth, being covered by periostracum which screens the presence of pits. It is worth adding that no connection between the pits and endopunctation has been recorded (Pl. 94, fig. 7).



TEXT-FIG. 1. Ventral view of a shell of *Plectospira ferita* (von Buch) showing its ornamentation. × 15. ZPAL Bp VII/663b.

EXPLANATION OF PLATE 95

Figs. 1–6. *Plectospira ferita* (von Buch). 1, view of the pitted surface of the primary layer and two tubercles. × 100. MB. B 306. 2, detailed view of a domed tubercle with an apical orifice. × 300. Same specimen as fig. 1. 3, detailed view of a trunk-like tubercle with a rosette-like pattern of arrangement of crystallites in its apical part. × 300. ZPAL Bp VII/663a. 4, view of a damaged tubercle with internal cavity. × 600. MB. B 306. 5, section through a tubercle showing the secondary shell layer penetrated by granular calcite, which is a continuation of the primary layer. × 300. MB. B 304. 6, section through a tubercle showing the succession of the primary and secondary layers. An orifice is seen in the apical part of the tubercle. × 300. Same specimen as fig. 5.



BIERNAT and BALIŃSKI, brachiopod *Plectospira*

Tubercles

These ornamental elements are developed as small trunk-like-to-domed outgrowths, on the average 200 μm in diameter and up to about 125 μm in height, arranged in a somewhat quincuncial pattern. They occur over the whole shell surface but are more densely spaced on the anterior half of adult shells (text-fig. 1). These outgrowths are made up of the primary layer with the secondary one protruding outwardly (Pl. 92, fig. 6; Pl. 95, figs. 5–6). Several types of structure are recognized, two being most common: *a*, tubercles of a slightly domed appearance with a small round orifice in the apical part (Pl. 95, figs. 2, 6); *b*, tubercles of trunk-like form possessing a wide funnel-like apical concavity; the bottom of this concavity displays a rosette-like pattern because of a radial arrangement of crystallites of the primary layer (Pl. 95, fig. 3).

The function of the tubercles still remains unclear. No doubt these elements are associated with highly specialized groups of cells of the outer epithelium of the mantle. These cells presumably acted as, for example, sensory organs, analogous to the sensory spines of some brachiopods. Considering the tubercles from that point of view, one may assume that they correspond to strongly reduced and shortened spines.

The tubercles may have an internal cavity (Pl. 95, fig. 4). In some of them the internal cavity is quite large and often filled in with granular calcite, which is a distinct continuation of the primary shell layer. This calcite may penetrate the secondary shell layer to a depth of about 100 μm (Pl. 95, fig. 5). No communication of the tubercles proper with the interior of adult shell has been indicated.

The differences observed in the structure of the tubercles may result, to some extent, from the unequal lengths of the period of their functioning during the growth of the animal. Probably the shortest was the functioning of those tubercles which show a radial arrangement of crystallites in their apical part (Pl. 95, fig. 3). Their activity must have terminated before the secretion of the fibres of the secondary layer began. The longest appears to be the functioning of the tubercles with a deep funnel-like canal filled in with the granular calcite and a protruding secondary layer (Pl. 95, fig. 5). In this case the cells of the mantle had to be retracted from the central canal of the tubercle merely within the time of the secondary-layer secretion. Outwardly deflected fibres of the secondary layer around the canal indicate that the granular calcite has been secreted much later than the fibres of the secondary layer.

The structure of tubercles suggests that they were functional near the antero-lateral valve margins only. During the growth of the shell the contact between the tubercles and the shell interior became cut off. Thus, the older and non-functional tubercles were then replaced by new ones formed continually at valve edges.

CONCLUSIONS

From the structure of the shell of *P. ferita*, we suggest the following:

1. The mineral punctate shell of *P. ferita* consisted of primary and secondary layers.
2. The outermost, thin layer recognized on the best-preserved specimens, and overlying the primary layer, is considered here as a periostracum. It is the first discovery of a preserved periostracum on fossil brachiopods.
3. The fossil periostracum of *P. ferita* consists mainly of lamellar and vesicular tissues.
4. Regular and densely distributed hemispherical thickenings of periostracum in *P. ferita* have no equivalents among known Recent brachiopod periostraca. This indicates further possibilities of structural differentiation and specialization of the cells of brachiopod mantle edges through their history.
5. The external surface of the primary layer is ornamented densely by pits which are the moulds of hemispherical thickenings of periostracum. The pits may be sometimes filled up with patches of disintegrated periostracum, resulting in a characteristic ornamentation of shell exterior.
6. The shell is covered by numerous tubercles which could have functioned as sensory organs.

Acknowledgements. The authors are grateful to Dr. Hans Jaëger (Palaeontological Museum of the Humboldt University, Berlin) for lending them the specimens of *P. ferita* and to A. Piotrowski, M.Sc. for specimens from the Holy Cross Mountains. We also thank Dr. S. Przeniosło and K. Kujawski, M.Sc., both from the Geological Institute, Warsaw, who have been helpful in supplying us with some supplementary SEM. Thanks are extended to Professor A. Williams (Glasgow University) and I. Urbanek for critical reading of the manuscript. Scanning electron micrographs were made at the Laboratory of Electron Microscopy of the Nencki Institute of Experimental Biology, Polish Academy of Sciences, Warsaw. The micrograph prints were prepared by Mrs. E. Wyrzykowska (Institute of Palaeobiology, Warsaw).

REFERENCES

BIERNAT, G. 1966. Middle Devonian brachiopods of the Bodzentyn syncline (Holy Cross Mountains, Poland). *Acta palaeont. pol.* **17,** 1-162, pls. 1-32.

—— and WILLIAMS, A. 1970. Ultrastructure of the protegulum of some acrotretide brachiopods. *Palaeontology,* **13,** 491-502, pls. 98-101.

BUCH, L. VON. 1834. Über Terebrateln, mit einem Versuch, sie zu classificiren und zu beschreiben. *Abh. Kön. Ak. Wis.* 21-144.

ERBEN, H. K., FLAJS, G. and SIEHL, A. 1969. Die frühontogenetische Entwicklung der Schalenstructur ectocochleater Cephalopoden. *Palaeontographica,* Abt. **B 132,** 1-54, pls. 1-15.

GRÉGOIRE, C. 1966. On organic remains in shells of Palaeozoic and Mesozoic Cephalopods (nautiloids and ammonoids). *Bull. Inst. r. Sci. nat. Belg.* **42,** 1-36.

—— and VOSS-FOUCART, M.-F. 1970. Proteins in shells of fossil cephalopods (nautiloids and ammonoids) and experimental simulation of their alterations. *Arch. internat. Physiol. Bioch.* **78,** 191-203, pls. 1-11.

—— and TEICHERT, C. 1965. Conchiolin membranes in shell and cameral deposits of Pennsylvanian cephalopods, Oklahoma. *Okla. Geol. Notes,* **25,** 175-201.

IVANOVA, E. A. 1971. Introduction to the study of spiriferoids. *Trudy Paleont. Inst.* **126,** 150 pp., pls. 1-12. [In Russian.]

JOPE, H. M. 1965. Composition of brachiopod shell. *In* R. C. MOORE (ed.), *Treatise on invertebrate paleontology,* Part H, Brachiopoda, 156-164. Geol. Soc. Am. and University of Kansas Press.

—— 1969. The protein of brachiopod shell, IV. Shell protein from fossil inarticulates: amino acid composition and disc electrophoresis of fossil articulate shell protein. *Comp. Biochem. Physiol.* **30,** 225-232.

MACKINNON, D. I. 1974. The shell structure of spiriferide Brachiopoda. *Bull. Br. Mus. nat. Hist.* (*Geol.*), **25,** 187-261, pls. 1-32.

MUTVEI, H. 1969. On the micro- and ultrastructure of the conchiolin in the nacreous layer of some Recent and fossil molluscs. *Acta Univ. Stockh., Stockholm Contrib. in Geology,* **20,** 1-17, pls. 1-17.

POULSEN, V. 1971. Notes on an Ordovician acrotretacean brachiopod from the Oslo region. *Bull. geol. Soc. Denmark,* **20,** 265-278, pls. 1-7.

PUGACZEWSKA, H. 1976. Trigoniidae of the Dogger of Łęczyca (Central Poland). *Acta palaeont. pol.* **21,** 79-96, pls. 16-23.

WILLIAMS, A. 1968*a*. Evolution of the shell structure of articulate brachiopods. *Spec. Pap. Palaeont.* **2,** 55 pp., 24 pls.

—— 1968*b*. Significance of the structure of the brachiopod periostracum. *Nature,* **218,** 551-554.

—— 1968*c*. A history of skeletal secretion among articulate brachiopods. *Lethaia,* **1,** 268-287.

—— and MACKAY, S. 1978. Secretion and ultrastructure of the periostracum of some terebratulide brachiopods. *Proc. R. Soc. Lond.* **B, 202,** 191-209, pls. 1-8.

—— —— 1979. Differentiation of the brachiopod periostracum. *Palaeontology,* **22,** 721-736, pls. 93-96.

G. BIERNAT and A. BALIŃSKI
Palaeobiological Institute
Polish Academy of Sciences
Al. Zwirki i Wigury 93
02-089 Warszawa
Poland

Typescript received 16 June 1981