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SHELL MORPHOLOGY AND STRUCTURE IN *LINGULIPORA* GIRTY

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The Devonian *Lingulipora* Girty is the only genus among the Recent and fossil Lingulidae with a punctate shell; its shell structure, however, has been very poorly known. Micro-ornamentation and internal structure of the shell as well as the structure of its endopuncta are here studied on specimens isolated chemically from various horizons of the Upper Devonian. The material includes specimens with strong radial ornamentation in the form of sharp ridges as well as specimens with strong concentric ornamentation. The internal structure of both the valves was examined. The endopuncta are in the form of simple cylindrical canals 4 to 15 µm in diameter, distally covered by canopy 1.5 to 2.6 µm thick. Canopy is perforated by one opening, usually 1 to 2 µm in diameter but sporadically wider. The hypothetical function of caeca in *Lingulipora* is discussed in comparison to those in living and fossil Brachiopoda

Key words: *Lingulipora*, Upper Devonian, shell micro-ornamentation, shell interior, punctation, function of puncta

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INTRODUCTION

Shell punctation occurs in twelve different stocks of the fossil and living Brachiopoda. There is no doubt that endopuncta must have evolved several times and quite independently during the evolution of the phyllum. The Devonian genus *Lingulipora* Girty is the only known stock with punctate shell among the fossil and Recent Lingulidae.

Shell punctation in *Lingulipora* is regarded as its important, or even the most diagnostic, feature. Although the genus is known since the end of the nineteenth century (Girty 1898), its shell structure has not been studied in detail. The present study of specimens isolated chemically from the rock allowed for an investigation of the variation in shell micro-ornamentation and its internal structure as well as of the structure of puncta in shells derived from various horizons of the Upper Devonian.

The investigated material is housed in the Institute of Paleobiology, Polish Academy of Sciences, Warsaw (ZPAL).

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MATERIAL AND METHODS

All the specimens studied come from limestone samples dissolved in 10% acetic acid. The phosphatic valves of linguliporids obtained by this method usually are fragmentary and unsuited for taxonomical study, but they are unusually valuable for analysis of the shell structure.

Table 1

Stratigraphic distribution of samples with *Lingulipora* used in this study

SERIES	STAGE	Standard conodont zone	Dębnik						Jabłonna		Łagów
			RD 3,6 7	Z-6	Z-2 1. 39 101	Z-8	PG	Z.orb 13	J-57 J-60 J-62	J-8 J-3D J-7	Ł-20
UPPER DEVONIAN	FAMENNIAN	praesulcata									
		expansa									
		postera									
		trachytera									
		marginifera									■
		rhomboidea									
		crepida					■	■		■	
		triangularis			■	■			■		
	FRASNIAN	gigas		■							
		A. triangularis									
		asymmetricus	■								

The material studied herein comes from 16 samples representative of several conodont zones of the Frasnian and lower Famennian (Table 1). The samples were taken in the Holy Cross Mts. (Łagów and Jabłonna sections) and Cracow region (Dębnik anticline). Totally, 116 specimens, including 44 fractures and sections, have been investigated under SEM.

TAXONOMIC REMARKS

As noted above, the material is fragmentary and of little use for taxonomic study. Therefore, all the specimens with shell punctation are here determined as *Lingulipora* sp. The present study contributes, however, a variety of new data on shell micro-ornamentation and internal structure in this group of inarticulate brachiopods. These data, though, are not comparable with the species diagnostic features in the genus *Lingulipora*. All the species of this genus, the type species *L. williamsiana* (Girty) including, were defined on the basis of specimens embedded in a rock and studied at low magnification, which did not allow for recognition of more subtle features than the presence of puncta and concentric growth lines on valve exteriors.

The present study, in turn, reveals that forms sharply different in micro-ornamentation and internal shell structure occur among the punctate lingulids grouped thus far together in the genus *Lingulipora*. Moreover, specimens from different stratigraphic horizons differ also in structure of the distal part of their puncta. There can be no doubt that the material under study contains forms displaying morphological differences of at least the species level.

MICRO-ORNAMENTATION

Linguliporids usually have rather small dimensions; hence nothing but a more or less pronounced concentric ornamentation can be detected under an ordinary optical microscope. The present study reveals, however, that linguliporid valves often are ornamented also with distinct radial elements, which become visible only under a greater magnification. These radial elements are very distinct in the specimens from the lower Frasnian of Dębnik (pl. 11: 1—2) and the Famennian of Jabłonna (pl. 11: 3; pl. 12: 1). They are formed by sharp, radial ridges situated on concentric wrinkles, and therefore their length equals the thickness of particular wrinkles and ranges from 3 to 13 μm. Frequently, however, the ridges from adjoining wrinkles are aligned and form longer, slightly undulating ridges (pl. 11: 2) These radial elements of micro-ornamentation are distributed every 3 to 10 μm, sometimes less densely; there are about 140 radial ridges per millimeter.

The radial ornamentation is best developed in the median sector of the valve. Laterally, the ridges become weaker and fewer and finally vanish completely (pl. 11: 5). The lateral parts of the valve (flanks) have no radial ornamentation but only a stronger concentric one (pl. 11: 4). Thus, the radially ornamented linguliporid valves can be divided into three sectors: the median one, bearing both concentric ornamentation and pronounced radial elements, and two lateral ones, without radial elements but with stronger concentric ornamentation. Radial ornamentation can sometimes be disturbed by weaker and irregular oblique elements. In these cases, the external surface of the valve is irregularly wrinkled, although the radial ridges still dominate (pl. 12: 2).

This radial ornamentation was not previously detected in linguliporids. It may be of taxonomic importance at the species level, but one must remember that it can be confined to the median sector of the valve. Suprisingly, a similar radial ornamentation occurs in the Ordovician *Lingulasma* Ulrich (see e.g. Cooper 1956, pl. 12: 9, 12, 17, 21; pl. 13: 17), in which, however, radial elements are considerably larger-sized and more sparsely distributed than in *Lingulipora*.

Specimens from the lowermost Famennian of Dębnik (samples Z-2, l. 39 and 101) show another type of micro-ornamentation. They have no radial ridges at all, and the valve exterior is ornamented solely with strong, concentric, slightly irregular wrinkles or ridges, usually 7 to 27 μm thick. These wrinkles bear peculiar swellings or tubercles, each with a centrally located, external opening of a punctum (pl. 12: 5). Valves with ornamentation of this type unquestionably represent a different species from those described above. Unfortunately, the studied specimens are so fragmentary that nothing but their ornamentation could be examined.

VALVE INTERIOR

There is no significant variation in internal structure among the investigated brachial valves from different zones of the Frasnian and Famennian. The structure of the posterior part of the valve is very simple in the illustrated specimens (pl. 12: 3—4) which show only a thickened posterior margin with a slight median flattening or depression.

The considered pedicle valves have a large, well defined, flat to slightly concave pseudointerarea (pl. 13: 1—5; pl. 14: 1—3). The postero-lateral margins of pseudointerarea are sharp, straight or, more frequently, laterally expanded in an earlike form (pl. 13: 1; pl. 14: 2—3) and thus enlarging the surface of propareas. The pseudointerarea bears distinct wrinkles, sometimes slightly irregular, parallel to its anterior margin. The propareas are divided medially by a triangular pedicle opening and a concave pedicle groove in the apical part (e.g., pl. 13: 2; pl. 14: 2—3).

A longitudinal median trough, which slightly widens anteriorly, occurs at the bottom of the posterior, thickened part of the valve and anteriorly to pedicle groove. It can be very shallow, barely visible (pl. 14: 1—3), or deeply incised into the valve and thus considerably decreasing its thickness. The valve becomes so thin in the apical part of the trough (down to just a few μm) that prepared specimens usually undergo damage in the form of perforation with irregular edges, 30 to 150 μm in diameter (pl. 13: 1—5; pl. 14: 1, 3).

The form of the median trough is rather uniform in all the studied linguliporids except for those from the sample Dębnik Z-6 (uppermost Frasnian). In the latter specimens, the median trough is delimited laterally by two distinct and high ridges. The bottom of the trough gently raises anteriorly of the apical part, and falls again past the midlength, thus resulting in a transverse ledge (pl. 13: 3, 5). In two specimens, the trough assumes the form of a platform hanging above the valve bottom and supported laterally with two blades. An unusual structure originates by this way, resembling in its complexity the spondylium of some Articulata (pl. 13: 1, 4).

The median trough may have acted like the pedicle groove, i.e. as the canal through which the pedicle was pulled out between the valves. It seems more likely, however, that it was the attachment site of the pedicle adjustors.

On both the sides of the trough, genital markings occur in the form of pits (ca. 10 μm in diameter) in the valve bottom (pl. 13: 5).

SHELL PUNCTATION

Puncta are nonuniformly distributed in the shell of linguliporids. They are very rare in, or even absent from, the most posterior region of either valve (pl. 12: 3—4; pl. 13: 1—5; pl. 14: 1—3). Anteriorly, the density of punctation gradually increases and, at a distance of 2 to 3 mm from the umbo, it may even exceed 500 per mm^2 (pl. 14: 4). More frequently, however, this density is smaller and often reaches only ca. 140 per mm^2. Generally, there is no regularity in distribution of puncta, but sometimes a hexagonal close-packing pattern appears nevertheless.

The puncta of *Lingulipora* are simple, unbranched cylindrical canals permeating the valve more or less normally to its outer surface. From inside a broad funnel-like hollow leads into the canal of each punctum. This hollow is subsequently repeated by the following shell layers (pl. 15: 3) thus forming a "funnel-in-funnel" structure. In valves which are exfoliated from inside, a deflected fragment of the removed layer breaks off and encircles the punctum with a peculiar ring (pl. 15: 1).

The internal openings of puncta usually range from 8 to 12 μm, but with extremes of 4 and 15 μm. The diameter of each punctum is more or less constant although the proximal end of punctum may be a bit wider in thick valves. The distal end of each punctum is covered with an external layer 1.5 to 2.6 μm thick (pl. 15: 4; pl. 16: 3, 5) which forms a structure analogous to the canopy of some punctate Articulata. As opposed to the canopy of Spiriferida and Terebratulida, however, which is densely perforated by very small canals, the punctum of *Lingulipora* opens to the exterior with only one, more or less centrally located perforation. In the majority of specimens, the exterior opening ranges from 1 to 2 μm in diameter. The widest openings, reaching 2 to 4 μm and sometimes even up to 7 μm in diameter, occur in the specimens from the lower part of the Famennian of Dębnik (samples Z-2 l. 39 and 101) (pl. 12: 5). Some of the primarily wide openings (4 to 7 μm) can be secondarily narrowed as much as down to 1 μm (pl. 16: 2).

The external openings of puncta are generally subcircular, sometimes transversely elliptical in outline (pl. 16: 4). In specimens with strong radial ornamentation, they are situated on poorly defined elevations. Specimens strongly ornamented concentrically have openings placed on much more distinct elevations or tubercles (pl. 12: 5).

Because of the difference between the proximal and distal openings, the punctation is much better visible at the valve interior. Under an ordinary optical microscope, the punctation is practically invisible from outside, unless the valve under study is slightly translucent. The punctation can only be seen from the outside in specimens lacking the external layer forming a canopy (pl. 16: 1).

DISCUSSION

The last twenty years of the study on brachiopod shell structure, and especially the application of electron microscopy, has markedly increased our knowledge about the structure and function of puncta in fossil and living brachiopods. As generally accepted, the endopuncta in fossil brachiopods, like those in Recent terebratulids and craniaceans, must have accomodated caeca, or tubular, multicellular outgrowth of the outer lobe of the mantle [1].

Two kinds of caeca occur in Recent brachiopods. In the Craniacea, the caeca are branched or arborescent with very fine distal tubules which do not reach the periostracum (Williams and Wright 1970). Similar branched caeca have also been recorded in the Silurian enteletacean *Dicoelosia* King (Wright 1966). In Recent terebratulids, the caeca are tubular, occasionally bifurcating, with their distal ends covered with a thin canopy of calcite built up by the primary shell layer (Owen and Williams 1969). The canopy is perforated by very numerous and fine canals through which extensions of the caecum reach the periostracum. Such endopuncta have also been

[1] In some Recent and fossil lingulids and discinds, very fine (ca. 60 nm wide) extensions of the mantle epithelium have been observed to penetrate the shell (Chapman 1914). These extensions, however, are strands of endoplasm rather than true caeca (Williams and Wright 1965: H78; Williams 1984: 743, fig. 23).

recognized in fossil terebratellaceans and spiriferinaceans (Mackinnon 1971).

When comparing the puncta of *Lingulipora* with the analogous structures of inarticulate and articulate brachiopods, it is evident that the former are quite different from the branched puncta of the Craniacea and *Dicoelosia*. When compared to terebratulids and spiriferinaceans, on the other hand, the general morphology of the puncta of *Lingulipora* displays several astonishing, though superficial, analogies. In *Lingulipora*, as also in spiriferinaceans and terebratulids, the puncta are in the form of simple, cylindrical canals covered at the distal end with a perforate canopy. The canals of *Lingulipora* are only distinctive in that they lack the slightly expanded head region which is so characteristic of the articulates mentioned above; in the latter, the puncta can also occasionally branch (e.g., Thompson 1927; Cloud 1942; Muir-Wood 1955; Owen and Williams 1969; Mackinnon 1974), a phenomenon which has not been observed in the specimens under study herein.

The puncta in *Lingulipora* are only slightly smaller in diameter (4 to 15 μm) than those in spiriferinaceans (10 to 40 μm) and almost equal to those in terebratulids (5 to 20 μm, but sometimes even up to 100 μm). The canopy thickness in *Lingulipora* (1.5 to 2.6 μm) also comes very close to that in spiriferinaceans and terebratulids (1 to 5 μm).

The main difference in structure of the endopuncta between *Lingulipora* on the one hand, and spiriferinaceans and terebratulids, on the other, consists in the canopy perforation. The canopy is perforated by numerous (at least 1200) and fine canals (100 nm wide) in these articulates, whereas it is pierced by a single larger canal (usually 1 to 2 μm wide, sometimes even wider) in *Lingulipora*. The thin canals permeating the canopy in Recent terebratulids contain tubular extensions of the caecum, or brush, which do not communicate directly with the environment because they are covered, as is also the whole shell, with an external, thin layer of periostracum. Consequently, there is no indication that the caecal secretion passes regularly to the shell exterior (Owen and Williams 1969: 199—200). The studies of these authors have revealed that the principal function of caecal cells in these articulates consists in synthesis, storage and secretion of certain chemical components circulating within the mantle.

Although the endopuncta of *Lingulipora* differ in details of their structure from those in spiriferinaceans and terebratulids, it is not unlikely that they could perform analogous functions. Thus, the cells of the caecum in *Lingulipora* could store materials, which could be mobilized during periods of their deprivation and used for metabolic purposes.

It is a separate question whether the distal end of the caecum in *Lingulipora* was covered with periostracum, as in articulate brachiopods, or whether it could directly communicate with the shell exterior. In principle, either possibility is likely, but the wide external opening of the punctum in *Lingulipora* may suggest that it was not covered with periostracum. In this case, the caecum could act as an excretory or secretory organ. It could, for example, secrete a mucous substance consolidating the wall of the burrows, which were probably — judging after their modern relatives — made by linguliporids in sediment.

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ANDRZEJ BALIŃSKI

MORFOLOGIA I STRUKTURA MUSZLI *LINGULIPORA* GIRTY

Streszczenie

W pracy przedstawiono rezultaty badań lingulipor z franu i dolnego famenu Gór Świętokrzyskich i regionu krakowskiego. Materiały otrzymano z prób konodontowych rozpuszczonych w kwasie octowym. Uzyskane tą drogą fosforanowe skorupki są fragmentaryczne i nie nadają się do badań taksonomicznych, stanowią jednak niezwykle cenny materiał do badań ornamentacji, budowy wewnętrznej i mikrostruktury muszli, tym bardziej, że aspekty te nie były dotąd zupełnie badane.

Badania mikroornamentacji wykazały, że skorupki najczęściej ornamentowane są silnie wyrażonymi, charakterystycznymi, radialnymi, ostrymi grzbiecikami (pl. 11: 1—3; pl. 12: 1). Te radialne elementy mikroornamentacji rozmieszczone są zwykle co 3—10 μm; średnio w 1 mm mieści się ok. 140 grzbiecików. Tego rodzaju radialna ornamentacja najlepiej rozwinięta jest w sektorze środkowym skorupki (pl. 11: 3). Ku bokom skorupki radialne grzbieciki stopniowo zanikają, tak że części marginalne skorupki są jedynie ornamentowane koncentrycznymi wałeczkami (pl. 11: 4—5).

Inny typ ornamentacji wykazują okazy z najniższego famenu Dębnika, u których radialne grzbieciki nie występują zupełnie. Powierzchnia skorupek ornamentowana jest jedynie silnymi koncentrycznymi wałeczkami i brodawkowatymi nabrzmieniami, na których usytuowane są ujścia porów (pl. 12: 5).

Budowa wewnętrzna skorupek ramieniowych lingulipor pochodzących z różnych poziomów franu i famenu nie wykazuje większych różnic (pl. 12: 3—4). Natomiast skorupki nóżkowe wykazują zmienne wykształcenie rowka na nóżkę (pedicle groove), który może być zagłębiony w dno skorupki (pl. 13: 2; pl. 14: 1—3) lub wykształcony w formie platformy uniesionej nad dno skorupki a czasami nawet podpartej po bokach dwiema listwami (p. 13: 1, 3—4).

Skorupki lingulipor przebite są licznymi (do 500 na 1 mm^2) prostymi kanalikami (porami) o średnicy najczęściej 8—12 μm (pl. 14: 4—5). W części dystalnej pory przykryte są przez zewnętrzną, ornamentowaną warstewkę muszli o grubości 1,5—2,6 μm stanowiącą „canopy" (pl. 15: 2, 4; pl. 16: 1, 3, 5). „Canopy" przebita jest centralnie jednym okrągławym lub eliptycznym otworkiem mierzącym najczęściej 1—2 μm (pl. 16: 2—5) a dochodzącym na niektórych okazach z famenu Dębnika do 7 μm średnicy.

Chociaż endopory lingulipor różnią się w szczegółach budowy od endoporów u niektórych Articulata (Spiriferida, Terebratulida), to nie można wykluczyć, że wypustki płaszcza mieszczące się w tych porach (caeca) mogły pełnić anaogiczne funkcje. Tak więc komórki caecum lingulipor, podobnie jak u współczesnych terebratul, mogły służyć do magazynowania substancji, które następnie, w razie okresowego wzrostu zapotrzebowania na nie, mogły być ponownie użyte do celów metabolicznych. Jeżeli jednak ujścia porów u lingulipor, w przeciwieństwie do porów u współczesnych terebratul, nie były przykryte periostrakum, a komunikowały się swobodnie ze środowiskiem zewnętrznym, wówczas caeca mogły pełnić funkcje wydalnicze lub wydziel-

nicze. Mogły one, na przykład wydzielać śluzowatą substancję wzmacniającą ścianki nor, które zapewne lingulipory drążyły w osadach dennych, analogicznie jak współcześni reprezentanci tej grupy ramienionogów.

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EXPLANATION OF PLATES 11—16

All specimens represent *Lingulipora* sp.

Plate 11

1. Specimen with strong radial micro-ornamentation; at this magnification the external openings of puncta are practically unrecognizable. Lower Frasnian (Dębnik RD-3), ×300. ZPAL Bp MsI/3-8.
2. Details of radial (sharp ridges) and concentric (wrinkles) shell micro-ornamentation; arrows point to the openings of two puncta. Lower Frasnian (Dębnik RD-6), ×1000. ZPAL Bp MsI/9-3.

3—4. Two views of a single specimen with different micro-ornamentation in *3* — median sector and *4* — lateral sector (flank) of the valve; arrows indicate the openings of puncta. Famennian (Jabłonna J-30), ×1000 and ×300. ZPAL Bp MsI/24-6.

5. Gradual change of micro-ornamentation in the transitional zone from the median (lower right corner) to the lateral (upper left corner) sector of valve. Famennian (Jabłonna J-7), ×300. ZPAL Bp MsI/21-7.

Plate 12

1. Micro-ornamentation in the form of a combination of radial sharp ridges and concentric wrinkles. Minute openings of puncta (ca. 1 μm in diameter) are visible (two of them indicated by arrows). Famennian (Jabłonna J-3D), ×600. ZPAL Bp MsI/21-5.
2. Micro-ornamentation consisting of concentric wrinkles and radial and oblique ridges; two openings of puncta indicated by arrows. Loc. as above, ×600. ZPAL Bp MsI/11-16.

3—4. Interior of two brachial valves (posterior parts) from *3* — Upper Frasnian (Dębnik Z-6) and *4* — Lower Frasnian (Dębnik RD-4), ×100 and ×150. ZPAL Bp MsI/1-7 and 2-2.

5. Micro-ornamentation consisting of strong concentric wrinkles and low tubercles each with opening of a punctum. Lower Famennian (Dębnik Z-2, l. 101), ×300. ZPAL Bp MsI/10-12.

Plate 13

1—5. Interior of five pedicle valves (posterior parts). *1*, *3—5* — Upper Frasnian (Dębnik Z-6); *2* — Lower Frasnian (Dębnik RD-3), 1—3 ×200, 4—5 ×100. ZPAL Bp MsI/1-4, 4-6, 20-4, 1-5 and 20-2.

Plate 14

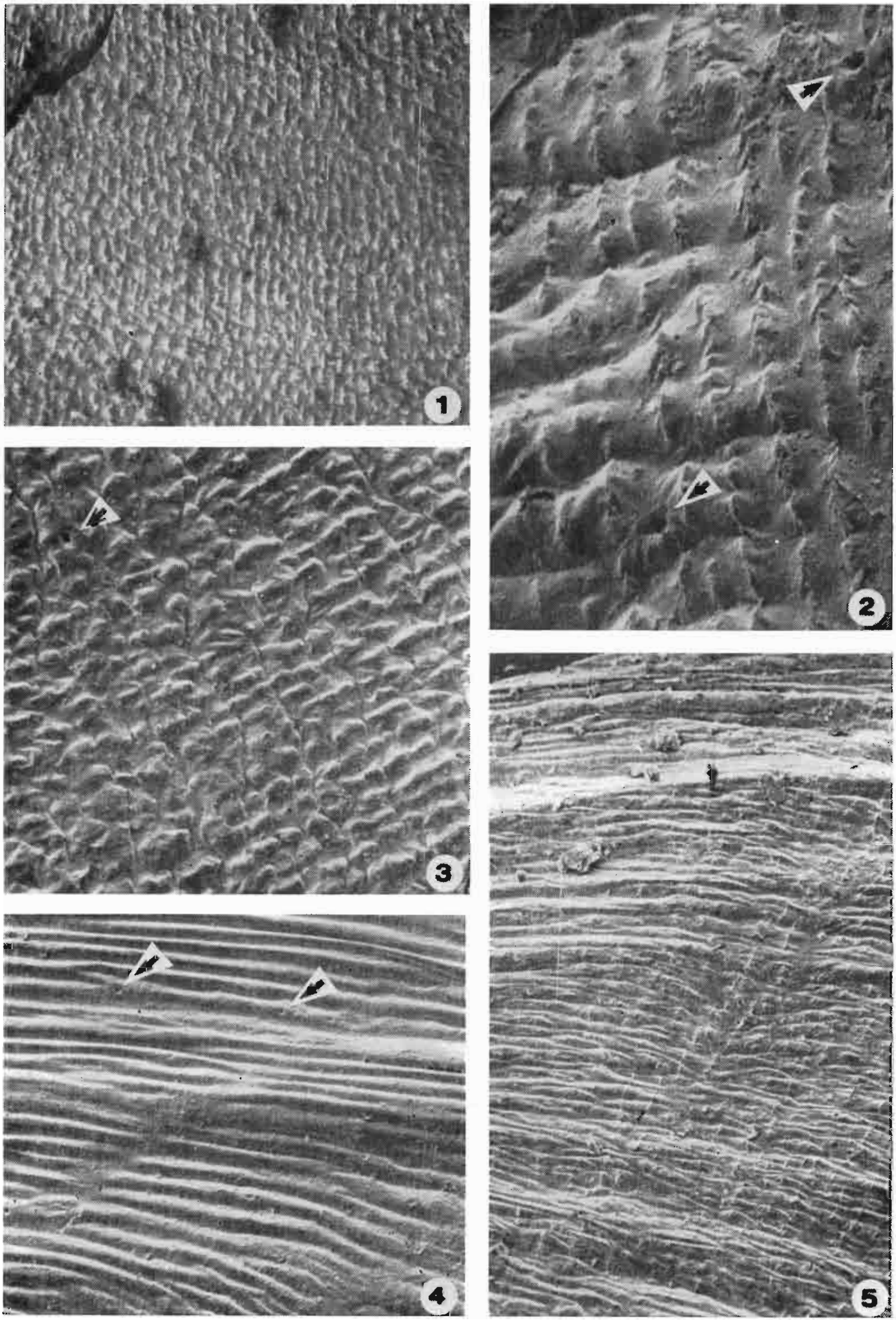
1—3. Interior of three pedicle valves (posterior parts). Famennian (Łagów K-20, Jabłonna J-3D), Jabłonna J-60), all ×100. ZPAL Bp MsI/21-1, 23-1 and 21-4.
4. Internal view of a densely punctated valve. Famennian (Łagów Ł-20), ×100. ZPAL Bp MsI/21-1.
5. Details of internal openings of puncta. Famennian (Dębnik Z. orb.-13), ×300. ZPAL Bp MsI/15-23.

Plate 15

1. Internal view of an exfoliated specimen with broken rings of the exfoliated layer around puncta (explanation in text). Upper Frasnian (Dębnik Z-6), ×1000. ZPAL Bp MsI/1-9.
2. Formation of puncta at the valve margin (top): *cp* — canopy. Famennian (Łagów Ł-20), ×600. ZPAL Bp MsI/21-1.
3. Fracture through the proximal end of a punctum; note the outwardly deflected layers forming the cylindrical canal of a punctum; valve interior (in) at the top. Upper Frasnian (Dębnik Z-6), ×3000. ZPAL Bp MsI/3-4.
4. Fracture through a valve showing a punctum; *a* — general view, *b* — detailed view of the distal end of the punctum: *cp* — canopy, *ex* — external surface of valve. Lower Frasnian (Dębnik RD-7), ×1000 and ×3000. ZPAL Bp MsI/6-4.

Plate 16

1. External view of a valve with partially exfoliated external, ornamented layer which forms the canopy and covers the puncta. Famennian (Łagów Ł-20), ×300. ZPAL Bp MsI/21-2.
2. External view of a punctum; note its secondarily narrowed opening. Upper Frasnian (Dębnik Z-6), ×3000. ZPAL Bp MsI/1-8.
3, 5. Two puncta as seen from inside: note the perforated canopy (cp). Famennian (Łagów Ł-20 and Jabłonna J-60), ×3000 and ×2000. ZPAL Bp MsI/21-1 and 23-1.
4. External view of a punctum showing the presumable outline of perforated canopy. Lower Frasnian (Dębnik RD-7), ×6000. ZPAL Bp MsI/8-9.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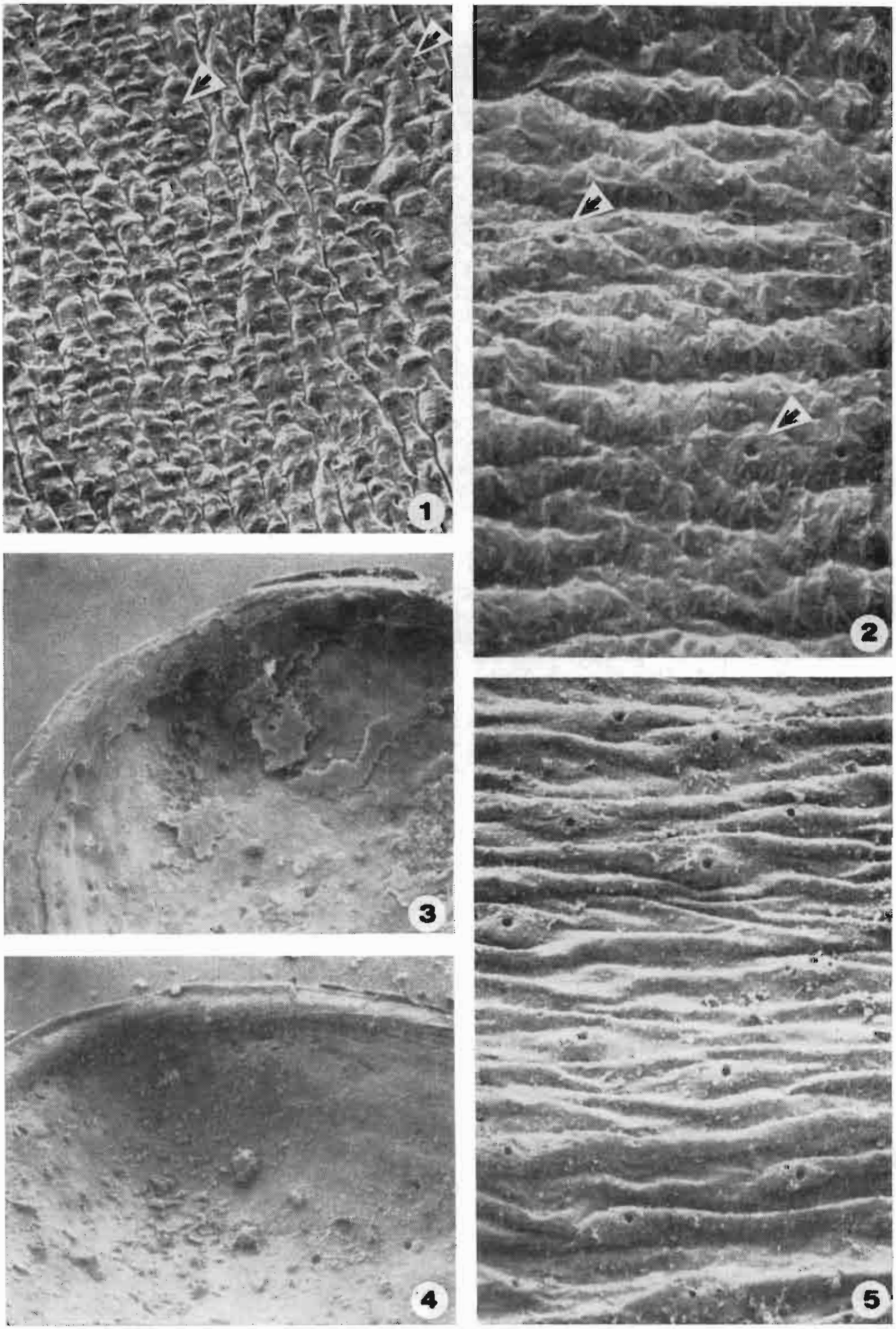
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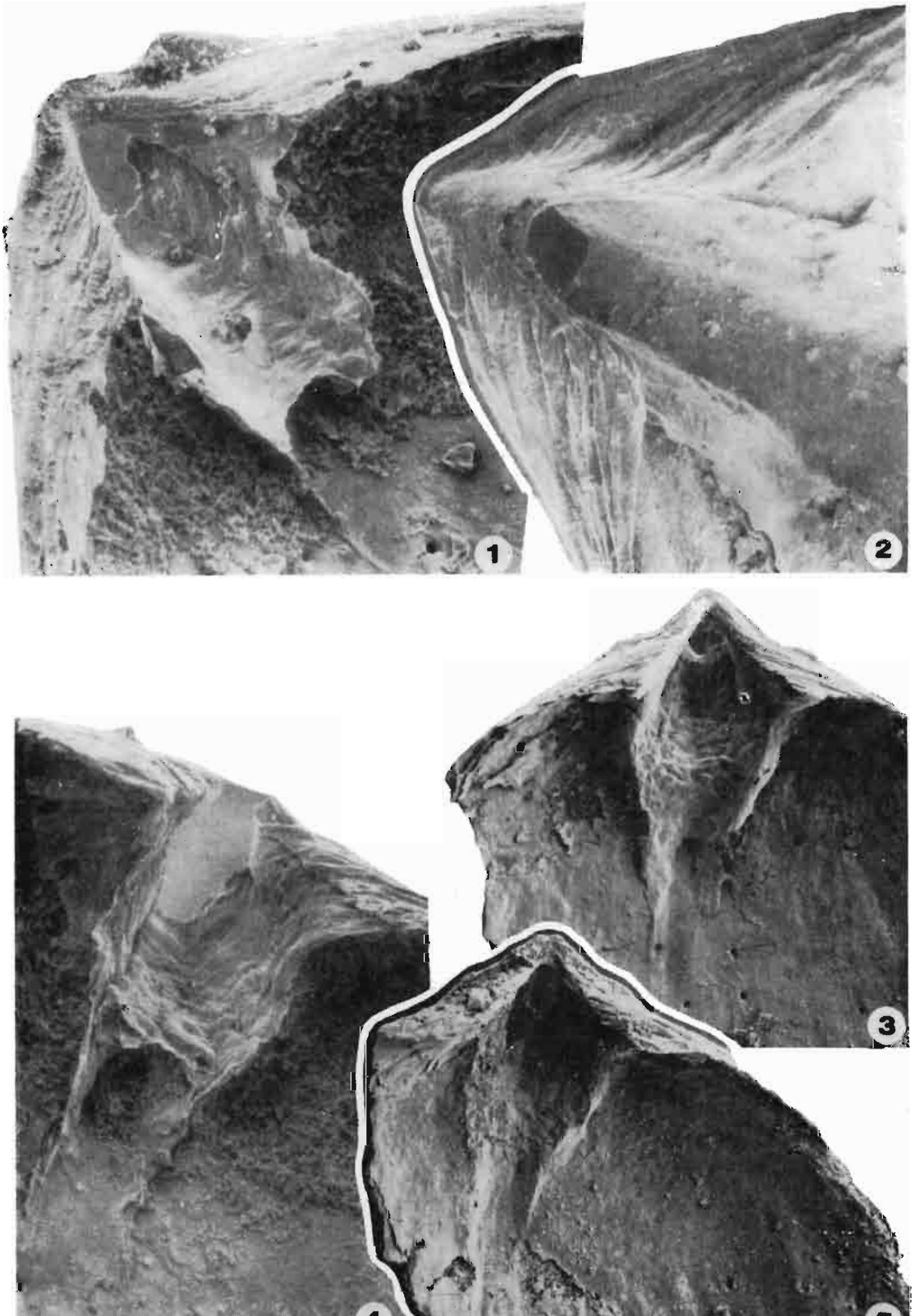
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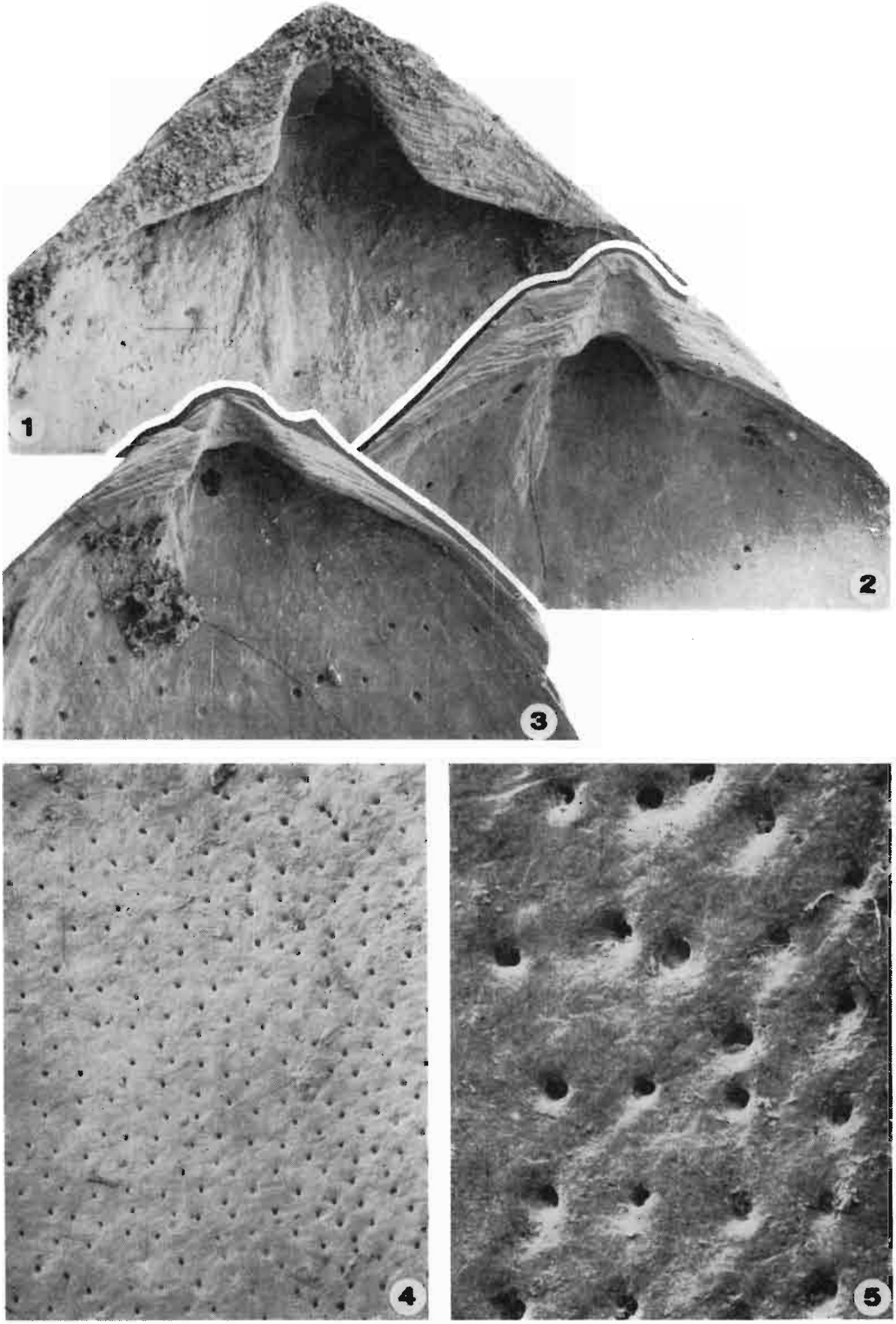

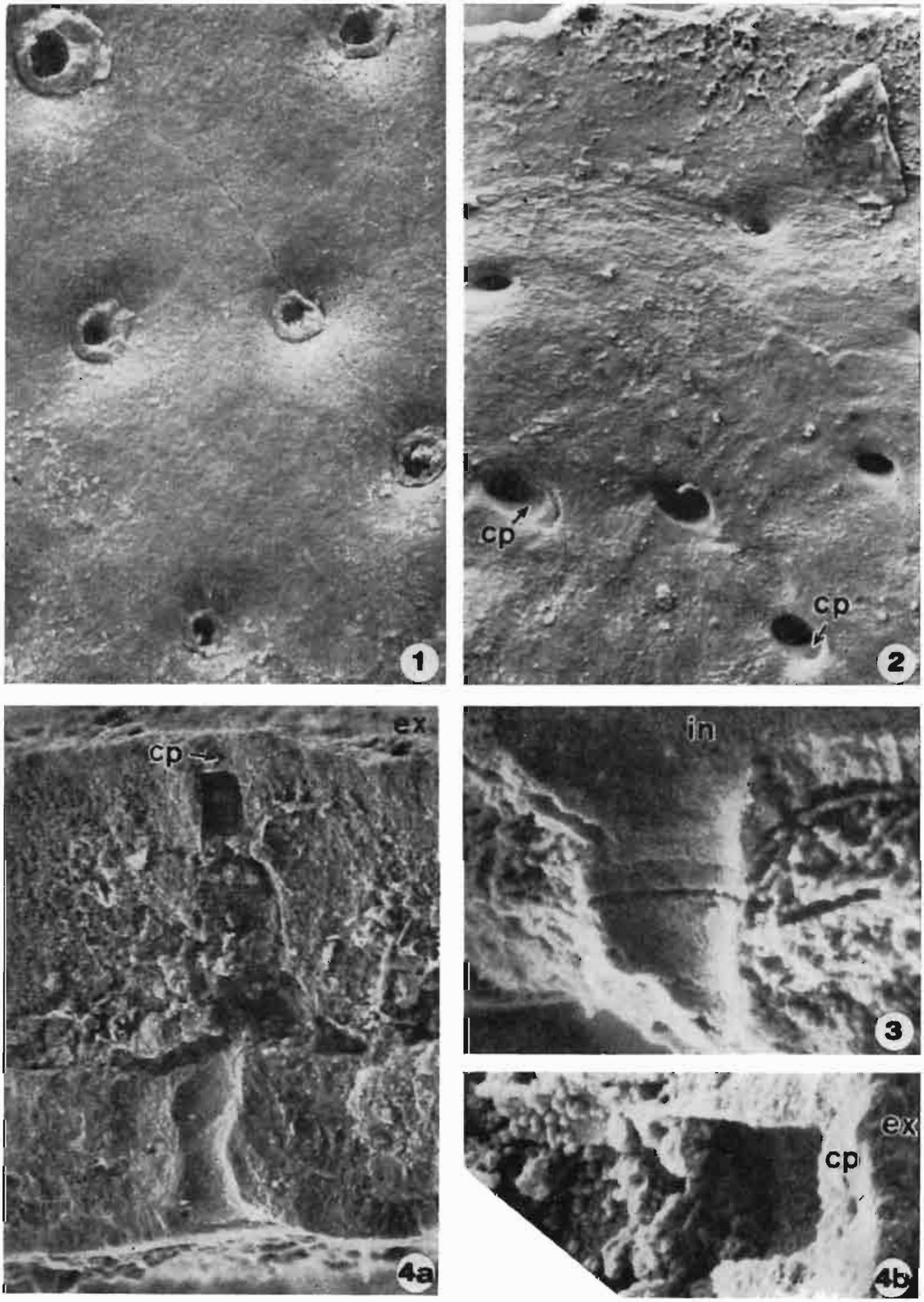
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cp
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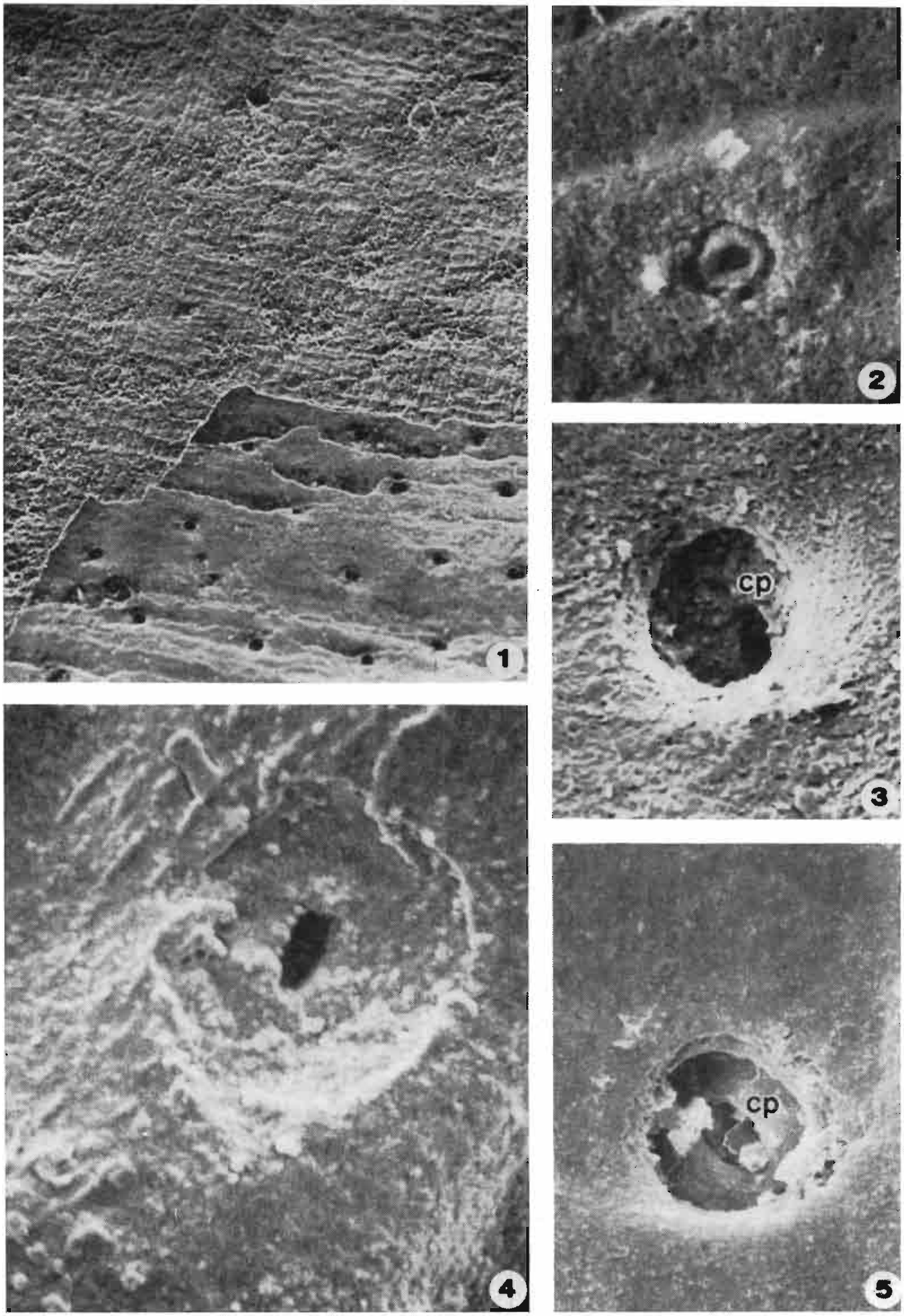
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