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RYSZARD WRONA

MICROARCHITECTURE OF THE CHITINOZOAN VESICLES AND ITS PALEOBIOLOGICAL SIGNIFICANCE

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Morphology and inner structure of vesicles were studied by SEM in several chitinozoan species. Ten distinct types of vesicle surface sculpture are defined. Vesicle surface sculpture is supposed to be promising for chitinozoan taxonomy. Wall ornamentation and structure are described in various chitinozoan species. These characteristics support the idea of a planktic mode of life of some chitinozoans. Mechanic and organogenic perforation is recognized in chitinozoan vesicles. Vesicle internal structures called as "opisthosome" and "mesosome" are recognized for artifacts. The structure and position of operculum indicate that this was a rigid and fixed element separating the vesicle central cavity from the external environment, aimed to be opened for once. Variation in the mode of aggregation of vesicles and in their wall structure is suggestive of a variability in wall formation among chitinozoans. Analysis of vesicle microarchitecture permits a conclusion that Chitinozoa are a heterogenous, unnatural group.

Key words: Problematica, Chitinozoa, Lower Paleozoic, morphology, inner structure, paleobiology, Baltic region, Poland.

Ryszard Wrona, Polska Akademia Nauk, Zakład Paleobiologii, Al. Żwirki i Wigury 93, 02-089 Warszawa, Poland. *Received: June 1979.*

INTRODUCTION

Systematic position of the Chitinozoa has thus far remained unrecognized even though these fossils have been studied since over 40 years and some 500 species of 40 chitinozoan genera have been described. The Chitinozoa are known from the Ordovician to Devonian but they may have occurred already in the Precambrian (Bloeser *et al.* 1977) and may have persisted up to the Carboniferous (Wilson and Clarke 1960) and even the Permian (Tasch 1973).

The Chitinozoa were claimed to have been related to various organic groups. However, in spite of the application of electron microscope (both SEM and TEM), there are still no data permitting their unequivocal systematic attribution. With the most recent research taken into account (Eisenack 1972*b*; Laufeld 1974), the chitinozoans are to be most plausibly

interpreted as Metazoan egg capsules (Eisenack 1939, 1968; Kozłowski 1963; Laufeld 1974) or an encysted stage in the life cycle of various Protozoa (Staplin 1961; Kozłowski 1963; Obut 1973; Laufeld 1974), rather than tests of any active organisms.

This paper is aimed to present the results of morphological and inner-structural SEM analysis of vesicles belonging to some chitinozoan species, which allow to discus earlier concepts of biological nature and function of the Chitinozoa.

The investigated material makes part of the author's collection taken partly from the Upper Silurian to Lower Devonian strata found in boreholes located in SE Poland (Wrona 1980), and partly from the Ordovician to Silurian limestones found in erratic boulders of Baltic origin and in boreholes located in NE Poland. A few Ordovician to Silurian specimens derived from the erratic boulders studied by the late Professor R. Kozłowski, and some others from the Estonian collections taken by Dr. R. Männil and Dr. V. Nestor.

All the specimens described and illustrated in the present paper are housed at the Institute of Paleobiology of the Polish Academy of Sciences, Warsaw (abbreviated as ZPAL).

The methods of chemical treatment, conservation, and preparation of the specimens to SEM studies, and the applied descriptive terms are given in a preceding paper (Wrona 1980, 105, 121).

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SURFACE SCULPTURE OF VESICLE WALL

Surface sculpture of chitinozoan vesicles is usually highly variable. Most morphological elements of vesicle surface appear even under a light microscope but their shape can hardly be recognized. These characteristics of vesicle surface were most commonly called as sculpture or ornamentation. The two terms were often regarded as synonymous but vesicle surface relief was more commonly designated by the terms surface sculpture or texture, while the term ornamentation referred usually to spines and various processes scattered over vesicle surface (e.g. Jansonius 1964; Jenkins 1970). The present author restricts the range of the term surface sculpture to designate only the relief of vesicle surface and the surficial features reflecting the nature of the wall structure. The term surface sculpture in Chitinozoa is then meant in a close analogy to the surface sculpture in Acritarcha (e.g. Tappan and Loeblich 1971) and pollen and spores (e.g. Hideux and Ferguson 1976).

When studied under a light microscope, chitinozoan surface sculpture was described with use of the following terms (see Combaz *et al.* 1967): striate, punctation, granulosity, felt, ciliate thicket, spine, cone, ciliate spine. Since the time the Chitinozoa have become widely studied under a scanning microscope, the following terms are applied to describe surface sculpture of the vesicles: smooth, spinose, verrucate, granulate, rugose, porous, spongy, and rugate (Eisenack 1968; Urban 1972; Laufeld 1974). However, these terms have never been precisely defined. One may expect that well defined characteristics of chitinozoan surface sculpture will prove useful in recognition of mutual relationships between various representatives of the Chitinozoa and consequently, in determination of the natural taxonomic classification. Structural characteristics of the sculpture undergo only little (if any) change in time, which suggests that they may reflect some older phylogenetic relationships among chitinozoans than details in structure of appendices or vesicle outline (cf. Tappan and Loeblich 1971).

Descriptive terms for vesicle sculpture, used previously or introduced by the present author, are here defined as follows:

levigate (after Latin *laevigatus* — smooth) — surface smooth even under a very great enlargement (pl. 19: 1—2);

granulate (after Latin granulum — fine grain) — surface covered with densely spaced, fine (0.6 μm in diameter) grains (pl. 19: 3—5); grains are more or less uniformly but disorderly distributed; grain density at the wall surface ranges from 120—160 per 100μm² (*Linochitina* sp. B: pl. 19: 3, and Wrona 1980: pl. 33: 12) up to 140—200 per 100μm² (*Linochitina longiuscula* Wrona; pl. 19: 4, and Wrona 1980: pl. 33: 8); microgranulate variety is distinctive in finer and more densely packed grains; grains range from 0.25 to 0.35 μm in diameter, grain density attains 600—800

per 100 μm² (pl. 19: 5); granulate sculpture has been recorded in various chitionozoan species representative mostly of the genera *Ancyrochitina*, *Angochitina*, *Linochitina*, and *Lagenochitina*;

nodulate (after Latin *nodosus* — node-bearing) — surface covered with rather sparsely distributed (5 to 8 per 100 μm²) node-like swells of 2 to 3.3 μm in diameter; nodes are fused with one another in form of irregular crests arranged in a vermicular pattern (pl. 20: 4); nodulate sculpture has been recorded in vesicles of *Parachitina curvata* Eisenack (pl. 28: 1—4);

verrucate (after Latin *verrucosus* — mamillated) — surface covered with disorderly distributed or arranged in rows, nipple-like to sharp-ended tubercles that may pass here and there into spines at a single vesicle; tubercles are highly variable in size (most commonly 0.8 to 1.8μm) and density (most commonly 18 to 28 per 100 μm²) even at a single vesicle (pl. 20: 5—7); verrucate sculpture occurs most commonly in various species of the genera *Eisenackitina* and *Conochitina* (Wrona 1980: pl. 27: 14 and 16—18; pl. 28: 2; pl. 32: 13);

lanate (after Latin *lanatus* — covered with wool, fluff, hair etc.) — surface covered with very densely packed, fine, spine-like tubercles to spines fused here and there with one another in form of short irregular crests variable in height (pl. 19: 6—7); spine-like tubercles and spines attain usually 0.5—1.5 μm in diameter and up to 1.6 μm in height; lanate sculpture occurs most commonly in various species of the genera *Eisenackitina* and *Conochitina* (Wrona 1980: pl. 30: 1, 3, and 11);

rugate (after Latin *rugatus* — wrinkled, folded) — surface covered with wrinkles variable in length and width (1 to 4 μm in width), arranged more or less parallel to each other, somewhat anastomosing (pl. 20: 1); there are several varieties of rugate sculpture distinctive in wrinkle shape and arrangement; wrinkles are commonly undulate (pl. 20: 2); wrinkle density ranges between 10 and 25 per 100 μm, as measured normally to the wrinkle orientation; rugate sculpture has been recorded in representatives of the genus *Cyathochitina* (pl. 25: 1; pl. 26: 4);

reticulate (after Latin *reticulatus* — checkered) — surface covered with longitudinal and transversal costae arranged in a reticulate pattern; boxes approximate 3.5×6.0 μm in size (pl. 20: 3); reticulate sculpture occurs in various species of the genera *Cyathochitina*, *Desmochitina*, and *Margachitina* (pl. 22: 8*a*; pl. 29: 4*a*);

microporous (after Latin *porus* — opening) — surface covered with fine openings (0.2 to 0.5 μm in diameter), disorderly distributed, with average density of 90—150 or 240—400 pores per 100 μm² (pl. 21: 1—2). Pores are irregular in outline; sometimes, they are arranged in irregular clusters or more or less continuous rows (pl. 21: 1b); microporous sculpture occurs most commonly at the surface of vesicle base in *Cyathochitina*;

microspongy (after Latin *spongiosus* — spongy) — surface sculpture produced by the outer, spongy layer of vesicle wall; total area of pores

equals or little exceeds the area represented by the wall matter; pores are very small up to 0.5 μm in diameter (0.3 μm in average), and attain usually density of 270—480 per 100 μm²; they are irregular in outline because they fuse commonly with one another (pl. 21: 3—5); microspongy sculpture occurs most commonly in representatives of the genera *Desmochitina* and *Lagenochitina*;

spongy — surface sculpture produced by appearance of the inner structure of vesicle wall at the surface (pl. 21: 6—7); total area of pores considerably exceeds the area represented by the wall matter; pores are highly variable in outline, diameter (very small up to 1.6 μm or even 2.7 μm; pl. 21: 6 and 7, respectively), and density (24 to 52 pores per 100 μm²); one may recognize a more orderly variety with tightly arranged pores of more or less constant diameter; and a disorderly, spumose one (pl. 21: 7); spongy sculpture occurs at the surface of vesicles representative of *Desmochitina* (pl. 27: 1—2 and 4; pl. 36: 2—3; Wrona 1980: pl. 35: 9), and *Pterochitina*, and at some elements of vesicle ornamentation, e.g. at carina in *Anthochitina superba* Eisenack (Wrona 1980: pl. 26: 7—8).

The above described patterns of surface sculpture do not exhaust the variation recorded at the external surface of chitinozoan vesicles. The list includes only those categories that occur most commonly and under the best preservation state in the collection of the present author.

Apart from the natural sculpture of chitinozoan vesicles, one may also observe at their surface a secondary relief produced by various sedimentary grains. These are most commonly pyrite spherulites encrusting both the external (Wrona 1980: pl. 25: 9b; pl. 27: 16) and internal surface of vesicles (Wrona 1980: pl. 25: 8; pl. 26: 4; pl. 32: 8; pl. 34: 8—9 and 12a). The spherulites are pressed into vesicle wall by the compaction stress. Because of insufficient precision of a light microscope and poor preservation state of chitinozoan vesicles, such a secondary relief was in some cases considered as the basis for erection of new species. This was pointed out by Laufeld *et al.* (1975: 213). The "sculpture" recorded by Jenkins (1970: 18, pl. 8: 1; pl. 9: 1) at the surface of vesicles of *Acanthochitina barbata* Eisenack does probably also represent such a secondary relief produced by pyrite spherulites pressed into the wall; those spherulites encrusting the external surface of vesicles are actually aggregates of finer spherulites. A similar "sculpture" has been recorded at the surface of vesicles of other chitinozoans (Grahn 1978: 10, pl. 4: A—B) and in acritarchs (Martin 1972: pl. 9: 1).

VESICLE ORNAMENTATION AND ITS FUNCTION

Vesicle ornamentation includes the following elements: spines (over 3 μm in length, most commonly originally hollow inside), appendices, neck and oral processes, auricles (Wrona 1980), carina, and velum. Chiti-

nozoan vesicles show a considerable variability in ornamentation. Ornamentation elements are disorderly distributed all over a vesicle, or they are arranged into longitudinal and transversal rows. Most commonly, they are clustered at basal edge, neck, and oral margin. Ornamentation descriptions published before 1967 were reviewed and summarized up by Combaz *et al.* (1967).

The application of SEM made possible a detailed study of vesicle ornamentation and hence, permitted a less speculative interpretation of its function. Eisenack (1955*b*) and Combaz and Poumot (1962) pointed to hollow inside appendices, and Laufeld (1967) reported also hollow inside spines covering vesicle surface. Jansonius (1964) claimed that the ornamentation had been produced by the outer layer of vesicle wall, as an adaptation to either increase the hydrostatic controls of planktic chitinozoans, or permit their attachment to floating objects. Laufeld (1967) supposed that the voids inside spines and appendices had worked as floating chambers aimed to increase the chitinozoan buoyancy. He claimed also that a similar role may had been played by net-like carinae maintaining gas bubbles in their meshes.

Urban and Kline (1970), Urban (1972), Laufeld (1973, 1974), and others demonstrated that contrary to some earlier suppositions, voids inside appendices, processes, and spines had not been interconnected with vesicle central cavity. Basing upon their SEM observations, Urban and Kline (1970) and Urban (1972) claim that ornamentation elements consist exclusively of the outer layer is very thin and may be confined to ornamentation elements. Chaiffetz (1972) described bubble-like endings of appendices in *Ancyrochitina fragilis* Eisenack which are to be most plausibly interpreted as hydrostatic organs. Laufeld (1974) claims that appendices and spines were formed from outside when the main wall of a vesicle had already been developed. He supposes that their function was either to protect a vesicle against predators by increasing its size; or to increase vesicle buoyancy by acting as floating organs; or to anchor a vesicle to a substrate of floating objects. The observations made by the present author allow to support the interpretation of appendices as adapted mainly to perform the hydrostatic function.

The investigated specimens attributable to the genus *Ancyrochitina* show well preserved hollow appendices with their voids separated entirely from the central cavity. The present author is of the opinion that the wide, bulbous at the base appendices found in *Ancyrochitina bulbispina* Wrona (pl. 33: 3; and Wrona 1980: pl. 25: 15), and the wide tubular appendices recorded in *Ancyrochitina lemniscata* Wrona (pl. 33: 1; and Wrona 1980: pl: 25: 5 and 10) fit well to the Laufeld's (1974) interpretation of appendices of *Ancyrochitina* as having functioned as floating chambers rather than an anchorage. Equally plausible is the hypothesis put forth by Laufeld (1967) that porous or net-like carinae (e.g. in *Anthochitina*

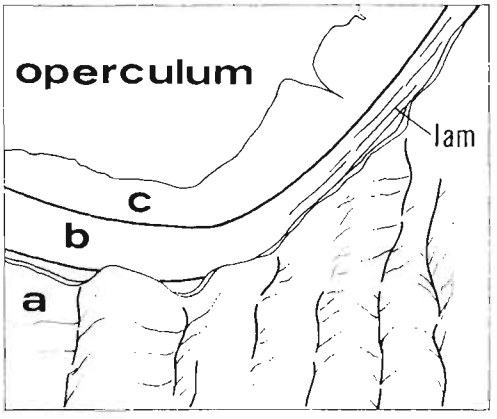

Fig. 1. *Cyathochitina kuckersiana* (Eisenack), drawing from SEM micrograph pl. 25: 1*c*: cross section through the wall of vesicle neck; note outer layer (*a*) in folds detached from mid-layer (*b*), and remains of inner layer (*c*); note also lamination (*lam*) here and there in the mid-layer.

superba Eisenack; Wrona 1980: pl. 26: 7—8) could maintain gas bubbles in their pores or meshes and hence, increase vesicle buoyancy. Some radii supporting the carina in *Anthochitina radiata* Wrona (Wrona 1980: pl. 26: 6*c*) are hollow inside and therefore light. The lacy appendices recorded in *Ancyrochitina aurita* Wrona (Wrona *l.c.*: pl. 24: 10) could maintain gas bubbles just as did the carina.

Little hollows were discovered under the screen of carina at the basal edge of *Cyathochitina campanulaeformis* (Eisenack) by Eisenack (1968: pl. 24: 3) and observed under TEM in ultrathin sections (Eisenack 1972*a*: 119, pl. 32: 1—11). They were also studied under SEM by the present author (pl. 25: 1—3; pl. 26: 3; *cf.* figs 2—3). These hollows are the largest in fully grown specimens of *C. campanulaeformis* (Eisenack) and *C. kuckersiana* (Eisenack) where they are fused with one another in form of a carinal cavity extending within the vesicle wall along the whole basal edge. A carinal cavity becomes visible only where the wall is damaged (pl. 25: 1*a*; pl. 26: 4) or the carina is broken off (pl. 25: 2*a*—*b*), or in an appropriate cross section (pl. 26: 3; *cf.* fig. 3). Specimens with poorly developed carina, resembling in outline *C. calix* (Eisenack), show merely a spongy to porous tissue of carina (pl. 25: 3; *cf.* fig. 2). No channels connecting those intercarinal hollows with vesicle central cavity have been recorded.

The position of the carinal cavity and pores in *C. campanulaeformis* and their isolation from the central cavity resemble very closely the voids found in appendices and spines. One may therefore suppose that they were also adapted to increase vesicle buoyancy. However, Kozłowski (1963) considered the vesicle chains of *C. campanulaeformis* as benthic elements attached permanently to a substrate. Laufeld (1967) pointed to another interpretation of the observations made by Kozłowski (1963): the chains could be attached to floating objects. The above presented results indicate that the planktic mode of existence of *C. campanulaeformis* could be achieved by either one or the two ways; or there were two

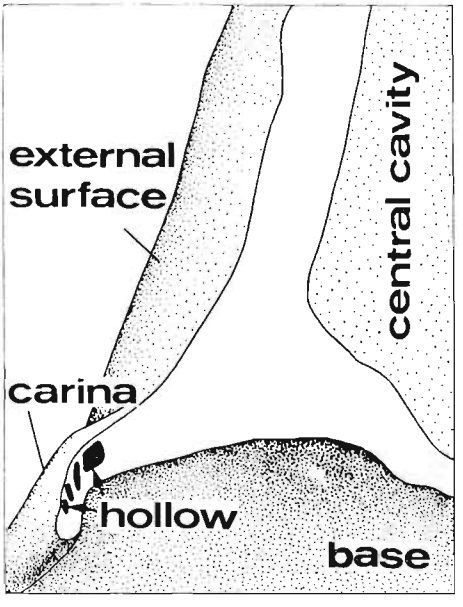

Fig. 2. *Cyathochitina* sp., drawing from SEM micrograph pl. 25: 3*b*: cross section through the wall close to vesicle basal edge; note intracarinal hollows.

successive stages: vesicles attached to floating objects at first, and drifting independently later on. The complete separation of floating chambers and central cavity of a vesicle from the external environment (Kozłowski 1963), due to the imporous wall and the operculum covering entirely the aperture, are suggestive of a passive-floating rather than an active-swimming mode of chitinozoan life.

In most cases, floating chambers occur at the aboral end of a vesicle, whole the oral end displays commonly thick and heavy spines and operculum. This distribution pattern of floating chambers may indicate that after disaggregation of a chain, the individual vesicles floated with their aboral end upwards and the oral end downwards. The same orientation could be achieved by carinate vesicles because a carina, even if devoid of gas bubbles, could hinder the vesicle from falling down.

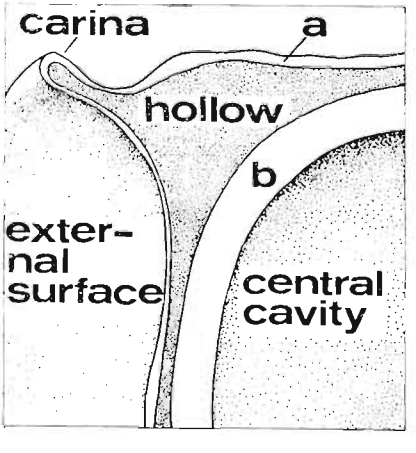

Fig. 3. *Cyathochitina companulaeformis* (Eisenack), drawing from SEM micrograph pl. 26: 3*b*: cross section through the wall close to vesicle basal edge; outer layer (*a*) builds up the carina; note large hollow between the outer layer and the mid-layer (*b*), making up intracarinal cavity.

Lagenochitina. — The space comprised within the double wall at the aboral end of vesicles in *Lagenochitina* sp. (pl. 30: 3; fig. 4) could also perform a hydrostatic function and cause a displacement of the center of buoyancy aborally. Then, the vesicles must have floated with their aperture downwards.

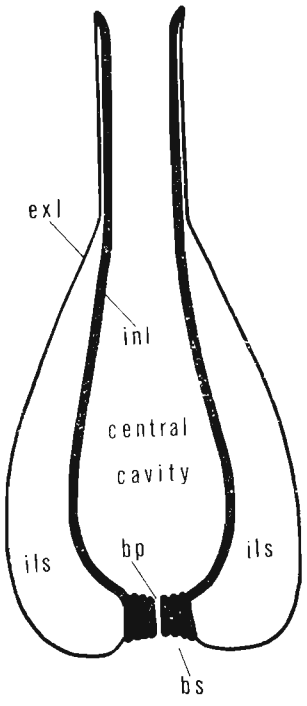

Fig. 4. Schematic longitudinal section through a vesicle of *Lagenochitina* sp.: note void (*ils*) at the aboral end of vesicle, closed between outer (*exl*) and inner (*inl*) layers of the vesicle wall. Central cavity may remain incompletely isolated from the cavity of adjacent vesicle, since basal pore (*bp*) in the basal scar (*bs*) is still open (*cf.* also pl. 30).

Acanthochitina. — Peculiar ornamentation is exhibited by *Acanthochitina barbata* Eisenack (pl. 31: 1—2; pl. 32: 1). The specimens studied prior to the present work were too poorly preserved to permit a precise recognition of the ornamentation under the light microscope (Eisenack 1931, 1976; Laufeld 1967; Jenkins 1967, 1970; Achab 1977). In a cross section (pl. 31: 2), the wall surrounding the central cavity of a vesicle of *A. barbata* is covered with densely spaced piles widening root-like at the base (pl. 31: 2*b*—*a*; pl. 32: 1*e*—*f*) and branching multiplicately at their distal end; the distal branches fuse with one another in form of a fine net surrounding the vesicle. The piles show proximal voids ranging, in form of a narrowing channel, up to their mid-height (pl. 32: 1*e*—*f*). The voids may open outside the pile wall at their proximal part (pl. 31: 2*a*—*b*; pl. 32: 1*d*), which suggests that they increased laciness of the structure without any effect on its mechanical resistance. The piles are equal in height around a vesicle, while decrease in height towards both the oral (pl. 31: 1; fig. 5) and aboral ends. The pile distal branches forming a surounding net are flattened and levelled at their outer side

(pl. 32: 1*d*) or even covered with a thin membrane here and there (pl. 31: 1*c*, 2*b*). Presumably, the membrane covered initially the whole vesicle and was supported by the net and piles (fig. 5). It was probably fused with the thick inner layer of vesicle wall close to the aperture and at the aboral end (pl. 31: 1*a*), at the edge of basal scar (pl. 32: 1*b*). Remains of the outer layer covering the piles occur also in the specimens from Shropshire (Jenkins 1967: pl. 68: 1—5, text-fig. 3*A*), preserved only at the basal

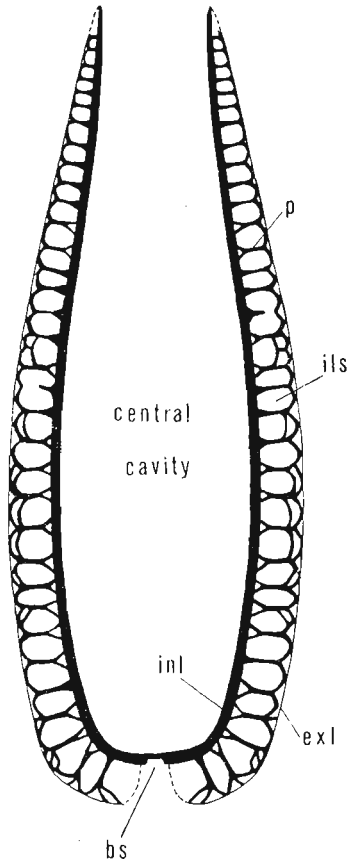

Fig. 5. Schematic longitudinal section through a vesicle of *Acanthochitina barbata* Eisenack: note void (*ils*) between thin outer layer (*exl*) and thick, compact inner layer (*inl*) supported with a net consisting of piles (*p*); central cavity was initially isolated from the exterior environment. The occurrence of basal scar is indicative of chain aggregation (*cf.* also pls. 31—32).

edge. A similarly preserved layer has also been recorded in *Acanthochitina secunda* Schallreuter (1963: 394, pl. 1: 1). The space between the two layers of vesicle wall in *A. barbata* Eisenack acted probably as a floating chamber, just as in *Lagenochitina* sp. Then, the vesicle structure in *A. barbata* Eisenack would be to be most plausibly interpreted as an adaptation to the planktic mode of existence.

VESICLE WALL STRUCTURE

The chitinozoan wall structure was initially studied in bleached, transparent vesicle under a transmitting light microscope. The results of those early investigations were summarized up by Combaz *et al.* (1967)

who concluded that a chitinozoan vesicle wall could have consisted of a single, two, or even three layers: the outer "periderm", middle "ectoderm", and inner "endoderm"; the inner layer could be confined to merely some portions of vesicle wall. Similar conclusions were commonly drawn from infrared (Jansonius 1964, 1967, 1970; Umnova 1973) and SEM studies (Urban and Kline 1970; Urban 1972; Laufeld 1973, 1974). In contrast, Eisenack (1931, 1968, 1972*b*, 1976), who applied not only all the above mentioned methods but also a transmitting electron microscope (TEM), recorded a homogenous, unilayered vesicle wall in all the Chitinozoa he studied.

Similar results are to be obtained from studies of bleached vesicles under a light microscope and infrared investigations of non-bleached vesicles. In both the cases, one is hardly able to distinguish between the true elements of wall structure and artifacts represented by foldings and fractures of the wall and mineral fills and encrustations.

The most appropriate would then be to apply a light microscope to a preliminary work aimed to choose the material adequate to studies under both transmitting and scanning electron microscopes. Spatial relationships can be observed under SEM, even though wall fractures restrict commonly the scope of the observations to small areas only. Furthermore, one can only rarely observe under SEM the ultrastructure of the organic matter constituting the chitinozoan vesicles. Observations under TEM seem to be the most appropriate to study the chitinozoan wall structure and inner structure. However, when TEM and SEM are applied separately and to a single or a few vesicles, one can hardly estimate the effects of diagenetic change of the ultrastructure of the organic matter. The results have therefore to be tested by various techniques applied to a diverse material.

The effects of early and late diagenetic factors upon the ultrastructure of the chitinozoan organic matter are unquestionable (Staplin 1969). They may appear under SEM (pl. 38: 1*b* and 3; Wrona 1980: pl. 25: 2; pl. 26: 7*b*; pl. 34: 6).

The nature of diagenetic transformations of organic matter may suggest that an initially multilayered wall can undergo a diagenetic homogenization, while an initially homogenous wall can undergo a diagenetic differentiation. Differentiation favors a secondary splitting of the wall into distinct layers due to various deformations (shrinkage) and other mechanical factors. Early and late diagenetic changes in ultrastructure result also in strains within the wall that release in displacements along sheeting planes. The position and orientation of sheeting planes depends upon variation in intensity of diagenetic transformations of the wall matter.

No doubt however that the chitinozoan wall may actually be more complex in structure than unilayered.

Conochitina. — A thin layer covering vesicle wall appears in folds and decortisation flakes at the surface of vesicles of *Conochitina* sp. (pl. 24: 1). Transversal striae and folds at the vesicle surface are also suggestive of a rhythmical formation of the wall. One may then suppose that the vesicles were growing rhythmically at their periphery rather than at the whole surface. Decortisation flakes built up by the outer thin layer occur rather infrequently at regularly developed vesicles; one may therefore regard them as suggestive of a disturbance in growth process (Eisenack 1968: 140). It seems however improbable that such a disturbance affected the mode of wall formation. The present author is of the opinion that the vesicles of *Conochitina* sp. are multilayered in their primary structure but this characteristics can be observed at the surface only under unusual conditions.

Hoegisphaera. — The multilayered structure of vesicle wall in *Hoegisphaera glabra* Staplin, *Hoegisphaera* sp., and *H. velata* Wrona appears clearly in folds produced by the outer layer at the surface of operculum and chamber itself (pl. 33: 4 and 8), and in sheeting planes at the edge of operculum and at the oral margin of vesicle (pl. 23: 9). This structure of vesicle wall in *H. glabra* was already noted by other authors and interpreted as a bilayered one (Urban 1972; Legault 1973*a*, *b*; Wood 1974).

Desmochitina. — The outer spongy layer appears very clearly at the surface of vesicles of *Desmochitina spongiloricata* Wrona (pl. 21: 7; Wrona 1980: pl. 35: 8—9). The spongy layer is separated from the underlying compact layer (or layers) by a distinct boundary apparent in form of a smooth surface close to the aperture (Wrona 1980: pl. 35: 8*a*). Similar wall structure is also shown by the vesicles of *Desmochitina minor rugosa* Eisenack (pl. 27: 1). The boundary between the layers is so sharp that décollements of the spongy layer result commonly in uncovering of almost the whole underlying compact layer (pl. 27: 2).

Aggregated vesicles of *D. minor rugosa* are attached to one another by their spongy layers (pl. 27: 4; pl. 36: 2—3) which may indicate the primary nature of the bilayered wall structure. One may also suppose that the vesicle walls were not hardened during the formation of a vesicle aggregation or cocoon (Eisenack 1968: 151). Vesicle wall was growing in *D. minor rugosa* simultaneously all over the surface.. At first, the inner, compact layer was secreted and thereafter, the spongy one. The inner layer may also show some sheeting planes in a cross section (pl. 27: 1), which are however to be interpreted as resulting from diagenetic changes in wall structure because they are confined to only a very small area. Other subspecies of *D. minor* Eisenack show a homogenous, unilayered wall accordingly to Eisenack (1968, 1976), while other authors claim that the wall is bilayered in structure (Kozłowski 1963; Jansonius 1964; Laufeld 1967).

Margachitina. — Vesicles representative of the genus *Margachitina*

show a bilayered wall in some cross sections (pl. 29: 2), and a homogenous, unilayered one in other cross sections (pl. 29: 1; pl. 34: 6—7). In spite of the study of several crushed vesicles under SEM, the author has been unable to recognize unequivocally which one of the structures was primary. The bilayered structure occurs more commonly in cross sections which may suggest that this is the true nature of vesicle wall (fig. 6). All the species attributable to *Margachitina* are here supposed to show the vesicle wall bilayered in structure. However, Laufeld (1974) claims that the Silurian vesicles of *M. margaritana* (Eisenack) from Gotland island show a bilayered wall in their aboral part and at the operculum, while the wall is unilayered in their central part.

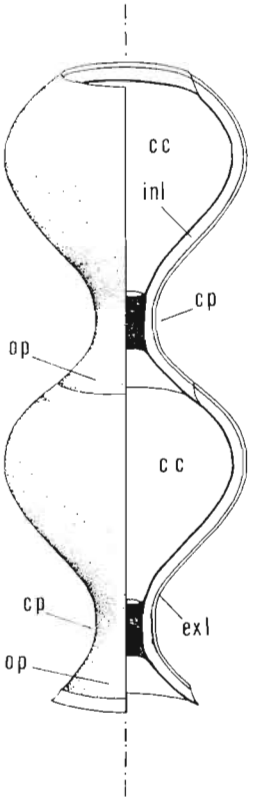

Fig. 6. Diagrammatic section through two vesicles of *Margachitina margaritania* (Eisenack) neighboring in a chain aggregate; note bilayered structure of the wall (outer layer — *exl*, inner layer — *inl*), and compact tissue filling up the weld (*cp*) and separating the central cavities (*cc*); note also the position of operculum (*op*) within the aperture.

Eisenackitina. — In *Eisenackitina lacrimabilis* Wrona, the vesicle wall is bilayered in structure in cross sections through some specimens (pl. 24: 3), and unilayered in others (pl. 34: 2). The two layers vary in thickness in a single specimen, and the boundary inbetween is far from straight; it splits and partly disappears in the thicker layer (pl. 24: 3). One can thus hardly recognize the primary structure of vesicle wall in *E. lacrimabilis*. The vesicle wall is always unilayered in structure in *E. pilose* Wrona (pl. 24: 2 and 4). The wall of *E.* cf. *urna* (Eisenack) is homogenous in structure in some parts of a vesicle (pl. 24: 5*b*), but its cross section is

suggestive of a multilayered structure here and there (pl. 24: 5c). A thin layer separated from the vesicle wall towards the oral end but fused gradually with the wall towards the aboral end appears very clearly at the inner side of the collar, beneath the operculum trace (pl. 24: 5*a*—*b*). This is most probably a detached flange of the lower margin of the operculum (pl. 35: 1). Previous authors claimed that the vesicle wall was bilayered in the genus *Eisenackitina* (see Jansonius 1964, 1967, 1970; Laufeld 1974). However, the two layers were equal in thickness in some species, while largely different in thickness in other species (Laufeld 1974). This variation, as well as that recorded in the species investigated by the present author, may be caused by diagenetic transformations of the wall structure and hence, one can hardly point to the primary nature of the wall structure in *Eisenackitina*.

Rhabdochitina. — The available data are indicative of a homogenous, unilayered wall structure in vesicles of the genus *Rhabdochitina* (pl. 33: 5).

Lagenochitina. — Jansonius (1964) and Laufeld (1967) regarded the vesicle wall in *Lagenochitina* as bilayered in structure; in turn, Eisenack (1968) recognized it for unilayered. The vesicles of *L. baltica* Eisenack investigated by the present author are very commonly coated with a mineral matter. In cross section, the mineral matter resembles an outer layer of the vesicle wall (pl. 27: 3) and may induce a misinterpretation. A bilayered wall structure occurs in vesicles of *Lagenochitina* sp. (pl. 30: 1—3). The outer layer is detached from the underlying one and forms a large-sized chamber extending from the mid-length of the neck up to the basal scar (fig. 4). At the oral part of the neck, both the layers are tightly attached to each other (pl. 30: 1). Both the layers are porous (pl. 30: 2 and 3*b*). The position and shape of the inter-layer space (pl. 30: 3) are suggestive of its hydrostatic function, analogous to that performed by voids present in appendices of some other chitinozoans. A similar chamber occurs in *L. magnifica* Umnova, as suggested by the observations in infrared light (Umnova 1973: pl. 12: 5).

Acanthochitina. — In *Acathochitina barbata* Eisenack, the vesicle wall is also bilayered in structure (pl. 31: 1—2; pl. 14: 1). The two layers are separated with a fairly large space cut across by transversal piles. One can see in cross sections that the compact inner layer is ten times thicker than the outer one (pl. 31: 2). The two layers contact each other at the margin of the basal scar and in proximity of the aperture (*cf.* fig. 5 and the description of *Acanthochitina* ornamentation).

Parachitina. — The oligolamellar structure of vesicle wall in *Parachitina curvata* Eisenack appears very clearly in cross sections (pl. 28: 5), as well as in sheeting planes apparent at both the vesicle ends (pl. 28: 1*b*). Because of the rough surface of the investigated fractures, the author has been unable to study in detail the length and thickness of particu-

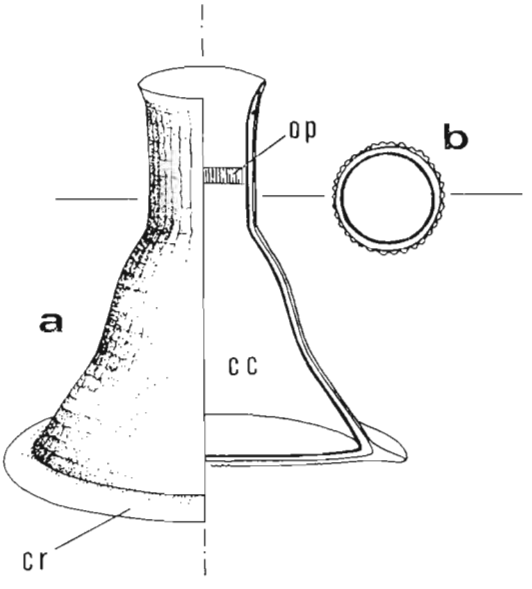

Fig. 7. Diagrammatic section (*a*) through a vesicle of *Cyathochitina campanulaeformis* (Eisenack): note the position of discoidal operculum (*op*) and reticulate sculpture at the surface of the vesicle. In cross section through the neck (*b*), note outer layer of the wall in form of folds detached from mid-layer.

lar layers. Nonetheless, there is little doubt that the wall consists of some ten layers more or less constant in thickness. A hypothesis that such a structure developed in effect of diagenetic factors seems to be implausible and hence, one may claim that the observed structure of vesicle wall in *P. curvata* is a primary structure.

Cyathochitina. — In cross section through a vesicle of *Cyathochitina kuckersiana* (Eisenack), a thin outer layer appears clearly in folds separated from the surface of the underlying mid-layer (pl. 25: 1c; fig. 1). The outer layer attains one fifth to seventh of the mid-layer in thickness. At the basal edge, the outer layer appears where the carina is broken off (pl. 25: 2) or the wall is damaged (pl. 25: 1*a*; pl. 8: 4). The mid-layer shows here and there an indistinct lamination that may reflect its true laminar structure (pl. 25: 1c; fig. 1). The inner layer can be observed in form of a thin membrane decorticated at the inner side of the neck (pl. 25: 1*b*) or in cross section through a considerably sheeted wall (pl. 25: 1c; fig. 1). The three layers are tightly attached to one another in the chamber wall (pl. 25: 1*a*) where the true structure of the wall is unrecognizeable. The above presented observations of the wall structure in *C. kuckersiana* remain still to be tested in variously located and oriented cross sections.

Separated wall layers at the basal edge and void chambers inside the carina were also observed by Eisenack (1968, 1972*b*) in *Cyathochitina campanulaeformis* (Eisenack). Basing upon TEM observations, Eisenack

(1972*b*) claims that the intracarinal voids arise from splitting of a homogenous wall at the basal edge. The present author was able to study the wall structure in *C. campanulaeformis* at the basal edge only (pl. 26: 3*b*). One can see there a large-sized chamber between the outer and middle layers (fig. 3), while the third layer, that one lining the central cavity, is invisible. In cross section through the basal edge of *Cyathochitina* sp. (?*C. campanulaeformis*), a homogenous layer appears; it builds up the carina provided with small-sized isolated voids (pl. 25: 3; fig. 2), close to those observed by Eisenack (1972*b*), instead of a single large-sized chamber. One may expect that the vesicles attributable to closely related species of the genus *Cyathochitina* resemble one another in wall structure. However, the available data do not allow to determine which one of the above described structures is the primary wall structure in *Cyathochitina*.

Linochitina. — Tiled growth layers occur at the oral end of the vesicles of *Linochitina serrata* Taugourdeau and Jekhowsky (pl. 35: 6). One may therefore suppose that the vesicle wall is multilayered in structure in that species and that it was forming rhythmically at least at the final developmental stage.

VESICLE WALL PERFORATION

The investigated chitinozoan collection includes perforated vesicles attributable to various species of variable geological age, Early Ordovician (from the erratic boulders of the Baltic origin) to Early Devonian (from SE Poland). Regular and irregular perforations can be recognized at first sight.

Irregular perforation

This perforation type is represented by openings irregular in outline, with jagged margins, variable in morphology, ranging in diameter from 0.5 (pl. 22: 1) up to some tens micrometers. Here and there, the openings form breaches in vesicle wall (pl. 22: 5; pl. 35: 3; pl. 36: 3); elsewhere, they resemble a regular perforation in morphology (pl. 22: 9). In general, there are merely a few openings of irregular perforation at a single vesicle.

No doubt that large-sized breaches with jagged margins, covering a considerable part of vesicle wall or operculum, have resulted from an external, mechanical damage. Smaller-sized openings may be due to a mechanic damage (pl. 22: 1) as well as to organic activity (pl. 22: 5). Inorganically produced openings can arise from either the stress of mineral grains and crystals (e.g. pyrite) encrusting vesicle surface and pressed from outside into the vesicle wall (Wrona 1980: pl. 25: 9*b*); or disintegration of pyrite spherulites developed inside a vesicle and their subsequ-

ent squeezing out (Martin 1971; Eisenack 1973; Laufeld 1974).

Irregular perforation may result in vesicle destruction and wall fragmentation. In well preserved, undeformed vesicles, openings of an irregular perforation can be recognized after their morphology and singular occurrence.

Regular perforation

This perforation type is represented by openings distinctive in their regular and constant morphology and size, ranging in diameter from almost one to a dozen or so micrometers. Regularly perforated vesicles occur only in a few out of several hundreds samples that were examined by the present author. Where a regular perforation does occur, it is distributed quite commonly in a sample (perforated vesicles account for 2.5% of a sample in average). Openings typical of a regular perforation do only rarely occur by ones per vesicle; most commonly there are a few up to some tens openings at a single vesicle. They are scattered disorderly and unevenly over a vesicle surface (pl. 19: 1; pl. 22: 3 and 8*a*; pl. 23: 5, 7, and 9; pl. 29: 4*a* and 5; Wrona 1980: pl. 30: 12; pl. 31: 11—12; pl. 32: 12*a*; pl. 33: 1) but in places, they form small clusters (pl. 22: 5—6) or even they contact one another (pl. 23: 4). A dense perforation results in weakening of a vesicle wall and its fragmentation up to total destruction (*cf.* Eisenack 1968). Regular perforation affects a vesicle wall and its ornamentation (pl. 33: 3; Wrona 1980: pl. 25: 15) as well as operculum (pl. 23: 5; pl. 34: 2; pl. 35: 2; Wrona 1980: pl. 32: 12). Sometimes, it occurs very closely to a basal scar (Wrona 1980: pl. 29: 10*b*) or aperture (pl. 22: 7; Wrona 1980: pl. 30: 7; pl. 35: 4). Openings located close to aperture and cutting obliquely across the operculum or collar may or may not get to the central cavity (pl. 34: 2*a*—*b*; fig. 8). Most openings break through the wall (pl. 22: 8; pl. 23: 1, 5, and 9—10); incomplete perforation occurs only sporadically (pl. 22: 4; pl. 23: 4). Regular perforation is most commonly perpendicular to vesicle surface. Only a single channel more or less parallel to vesicle surface has been recorded in the investigated material (pl. 22: 2).

The application of SEM has permitted a detailed study of perforation morphology and dimensions, and recognition of three varieties of regular perforation.

1. Cylindrical perforation: circular openings with smooth, sharp-edged margins (fig. 8*B*, *a*) and a constant diameter all over their length (pl. 22: 3 and 5—7; pl. 23: 1—10). The diameter ranges from 0.7 up to 3.3 μm but the following three size classes occur most commonly in the investigated collection:

a. — 0.7 to 1.5 μm (pl. 22: 5; pl. 23: 1 and 3);
b. — 1.8 to 2.0 μm (pl. 22: 2—3 and 7; pl. 23: 2, 5 and 7—8);
c. — 2.7 to 3.3 μm (pl. 22: 6; pl. 23: 1, 4—7 and 9—10).

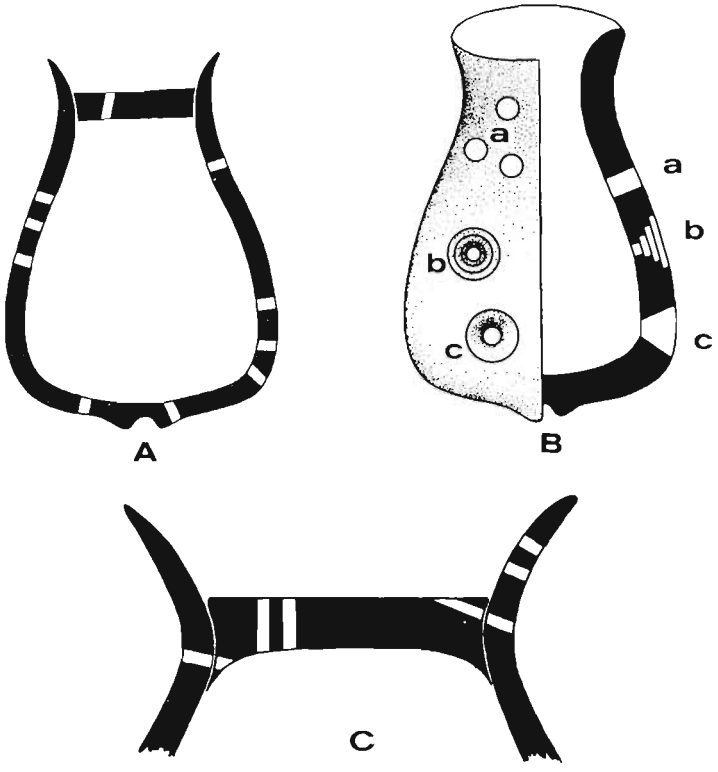

Fig. 8. *A* — Schematic section through a vesicle; note distribution of cylindrical perforation. *B* — Cylindrical (*a*), conical step-form (*b*), and conical smooth (*c*) perforations at the surface of and in a section through vesicle wall. *C* — Schematic section through the oral part of a vesicle; note distribution and orientation of regular perforation at the operculum and collar.

This is the most common variety of regular perforation.

2. Step-form conical perforation: circular openings with diameter decreasing inwards in a jerky mode (pl. 22: 4; fig. 8*B*, *b*), and with uneven to jagged outer margins. The outer diameter attains at maximum 4.4 μm, the inner diameter at maximum 2.4 μm.

3. Conical perforation: circular openings with diameter decreasing gradually inwards (pl. 22: 8; fig. 8*B*, *c*), and with smooth margins and channel surface. The outer diameter is 10—12 μm, the inner diameter is 6—8 μm.

A single variety of regular perforation occurs or at least prevails at the surface of a single vesicle. The mode of distribution of regular perforations, in particular the uneven and disorderly arrangement of the openings, their clusters resulting in destruction of vesicle wall and ornamentation, and perforation orientation leaving sometimes intact the central cavity of an affected vesicle, are indicative of the secondary nature of the perforation relative to vesicle development.

Well developed vesicles of the Chitinozoa are tightly closed capsules (Kozłowski 1963; Jenkins 1970; Laufeld 1974) with their inner space separated completely from the external surrounding. The only opening aimed to connect the central cavity of a vesicle with its external environment is the aperture, oral opening closed initially by operculum. The intercommunication onsets when the operculum is set apart. Where chain aggregations of vesicles occur, a basal scar persists usually at the aboral side of a vesicle after chain disintegration, representing a trace left by the original linkage. A basal pore occurs under exceptional conditions at the center of basal scar. It appears probably only in precariously (i.e., prior to the vesicle maturity) disintegrated chains. The initial hermeticness of vesicles appears then as an important feature of the Chitinozoa (Kozłowski 1963; Laufeld 1974), while the secondary perforation is without any functional significance (contrary to the pores in foraminiferal tests, brachiopod shells, etc.).

Regular perforation of chitinozoan vesicles was already noted in the first paper on the Chitinozoa by Eisenack (1932: 86), who supposed that it was of bacterial or fungal origin. This supposition was supported by later observations under a light microscope (Eisenack 1932: 267, pl. 12: 7; 1955*a*: pl. 4: 7; 1962: pl. 14: 9; 1972*a*: pl. 20: 6; Taugourdeau: 1965: pl. 3: 71—72; Jenkins 1967: 459, pl. 72: 9; pl. 73: 1; 1969: pl. 1: 13*b*; pl. 3: 22; pl. 5: 16; Laufeld 1967: 316; fig. 18). A rich material investigated by Eisenack (1968: 143, pl. 28: 13; pl. 30: 26—30) allowed him to present much better illustrations of regular perforation than previously. Eisenack (1968) noted also two distinct size classes among the openings (diameter range: 1 to 15 μm) and linear and cross-like clusters of the borings. Nevertheless, he assigned, even though with some reservations, the perforation to a bacterial activity in his latest paper on this topic (Eisenack 1973: 10, pl. 1: 4). The application of SEM has resulted in several new observations on the morphology of vesicle wall perforation (Eisenack 1972*b*: pl. 36: 1*c*; pl. 37: 1; Laufeld 1973: 139, figs 11—13; 1974: 119, figs 17, 24—26, 31, 36—38, 46, 57, 60, and 74; Obut 1973: pl. 18: 1; Henri *et al.* 1974: pl. 4: 3; pl. 5: 4—5 and 7—9; Grahn 1978: 10, fig. 4*A*—*B*). Laufeld (1974) concluded after the examination of his large collection of the Chitinozoa that the vesicle perforation is an effect of parasite activity.

Cylindrical perforation with opening diameter very close to that found in the Chitinozoa was also recorded in walls of various other microfossils composed of an organic matter, most commonly in pollen and spores (Elsik 1966: 515, pl. 1: 4; Eisenack 1973), acritarchs (Martin 1972: pl. 9: 4; Eisenack 1973), and scolecodonts (Taugourdeau 1971).

The striking morphological distinctness of the regular perforation, the smoothness of the surface of the openings, and their size are suggestive a chemical (e.g. by enzymatical digestion) rather than mechanical boring process. The morphology of conical perforation resembles

strikingly the traces left by some predatory gastropods on shells of their mollusk prey, in particular those achieved with use of an acid secretion by the Naticacea (see e.g. Carriker and Yochelson 1968, Taylor 1970, Hoffman *et al.* 1974). Actually, the openings recorded in chitinozoan vesicles are several tens times smaller than the gastropod boreholes but nonetheless, the mode of the boring could be essentially the same.

The observed distribution of borings and the orientation of channels may suggest that the chitinozoan vesicles were attacked at random and a single vesicle could be repeatedly bored by a single organism, just as it happens in gastropods (Taylor 1970). The actual ecological relationship of the boring organisms to the Chitinozoa cannot be unequivocally recognized at the moment. One may only suppose that the borers included predators feeding upon the alive contents of chitinozoan vesicles, as well as epiphytic organism grazing at vesicles buried in sediment. The attacks could be aimed to reach either the contents of vesicle cavity, or the organic matter of vesicle wall. The borers could also include some organisms looking for a shelter or anchorage. Microorganisms attacking organic microfossils include bacteria and fungi (Moore 1963; Elsik 1966; Eisenack 1973) but with the use of thus far applied techniques one can hardly identify the organisms responsible for the perforation recorded in chitinozoan vesicles.

The borers attacking chitinozoan vesicles may appear as an important paleoecological indicator as are the epibionts boring mollusk shells (Boekschoten 1966).

VESICLE INNER STRUCTURES

"Opistosome". — A dark-colored spindle-shaped structure was recorded at the aboral end of bleached and transparent vesicles under a transmitting light microscope (Combaz and Poumot 1962; Combaz *et al.* 1967). Such structures occur only rarely, mostly in flattened specimens. Some authors (e.g. Eisenack 1972*b*; Umnova 1973) are of the opinion that the impression of "opisthosome" is due to folds in vesicle wall and a secondary recess in vesicle bottom. Under SEM, "opisthosome" was thus far observed only by Urban (1972: 19, pl. 6: 8—9; text-fig. 6) in a single specimen of *Desmochitina parkerae* Urban. However, the structure observed by Urban differs considerably in shape from those described by earlier authors under the name of "opisthosome". Its shape, position, and sculpture identical to the vesicle surface sculpture permit a supposition that this is a fragment of the vesicle wall pressed into the vesicle central cavity.

The present author recorded an opaque structure at the aboral end of some vesicles observed in normal and infrared light. When studied un-

der SEM, these structures have appeared to be a secondary recess in vesicle bottom (Wrona 1980: pl. 30: 12*a*) or a mineral fill that is most commonly an aggregate of pyrite spherulites (pl. 35: 3). The central cavities of several hundreds of broken vesicles representative of various chitinozoan species were studied under SEM but none of them did comprise a structure resembling those described previously as "opisthosome". This supports the opinion that the "opisthosome" is an artifact.

"Mesosome". — An spherical structure located at the center of a vesicle central cavity has not been recorded by the present author in the investigated material. In turn, a mineral fill, most commonly an aggregate of pyrite spherulites, has been found in several vesicles.

"Prosome" — operculum. — The available data permit a conclusion that all the Chitinozoa were initially closed by an operculum (Eisenack 1968; Jenkins 1970; Laufeld 1974).

1. Cylindrical operculum. Vesicles with a long neck displayed a cylindrical operculum, called sometimes as "prosome", more or less compact in structure, and located deeply inside the neck. In some species, the operculum was linked with the base of another vesicle by means of a tube with thin walls. The tube had probably been filled up with a soft flesh before the interconnection between the alive contents of the two vesicles became disrupted (Eisenack 1968). The tube is more strongly attached to the operculum than to the base of the adjacent vesicle. The tube was probably detached from the base prior to the final disintegration of a chain, as it is indicated by the scarce occurrence of basal scar at the base of such vesicles. Hence, the tube protrudes commonly from a vesicle aperture and has been often called as "prosome".

2. Discoidal operculum. Vesicles with a short (if any) neck were closed by a discoidal, flat, terminally located operculum. The operculum equals or a little exceeds the vesicle wall in thickness (pl. 34: 2 and 4—7). Its lateral surface is more or less concave and attached tightly to the convex inner surface of vesicle wall. The tightness of the attachment was increased by a flange at the lower edge of the operculum. In some chitinozoan genera (e.g. *Linochitina*), the flange is in form of a long tube or sleeve (pl. 35: 1—2) which enlarges considerably the area of the contact of the operculum and vesicle wall.

Vesicles attributable to some chitinozoan species displaying typically a flat, discoidal operculum (pl. 34: 2; pl. 36: 3; Wrona 1980: pl. 29: 12) may sporadically show a convex operculum; this has been recorded in *Desmochitina minor rugosa* Eisenack (pl. 34: 3), *Eisenackitina lacrimabilis* Wrona (pl. 34: 1), and *E. cupellata* Wrona (pl. 35: 5). Similar opercula were probably observed by Eisenack (1968: 148). The significance of this variation in operculum shape remains thus far unrecognized. One may only suppose that the operculum convexity in *E. cupellata* (pl. 35: 5) is an artifact due to a partial breakage of the bottom of the adjacent vesicle.

In chitinozoan chain aggregates, the operculum of a vesicle was linked to the base of the adjacent vesicle either directly (*Desmochitina*), or through a weld (*Margachitina*, *Desmochitina*) or a basal callus (*Conochitina*, *Eisenackitina*). Such opercula show a more or less distinct scar at their oral side, so called oral scar (pl. 34: 2 and 4). The operculum is always smooth inside, without any attachment scars of a soft tissue (pl. 23: 5; pl. 34: 2 and 7; pl. 35: 4). One can see under SEM that the operculum is identical in structure to the vesicle wall in *Margachitina* (pl. 34: 6—7; pl. 29: 1—4; *cf.* Laufeld 1974). In some specimens, the operculum shows a margin accreted partially to the wall (pl. 29: 4*a*; pl. 34: 6). The wall building up such an operculum is constricted in form of a tubular weld or sleeve expanding into the wall of the base of the adjacent vesicle. At its mid-length, the weld is compact in structure and hence, it separates completely the central cavities of the two vesicles (pl. 29: 3—4; Wrona 1980: pl. 32: 5; fig. 6). In chains composed of aberrant vesicles attributable to *Margachitina margaritana* (Eisenack) or other related species (Eisenack 1968: pl. 21: 11), a vesicle wall passes directly into the adjacent vesicle, while the operculum is very weakly developed or even lacking at all; there is also no partition wall, separating the central cavities of two adjacent vesicles, in constrictions equivalent to the welds (Nestor and Wrona, in preparation). One is therefore allowed to claim that in *Margachitina*, and supposedly also in some related genera, the operculum develops coevally with the vesicle and represents actually its more specialized part. The lower edge of operculum extends laterally in form of a small flange in *Margachitina* (pl. 29: 4*a*). The inner diameter of operculum is therefore greater than the diameter of the aperture it is aimed to close (pl. 34: 6—7). Operculum of this type cannot be opened and closed repeatedly; it can be pushed or pulled up once for all only, just as it is in the case of *Desmochitina densa* Eisenack (Laufeld 1974: 77).

A similarity in structure of the wall and operculum in the genus *Hoegisphaera*, and the shape and position of the operculum indicate that this is again a more specialized part of the vesicle wall (pl. 33: 4 and 8; Wrona 1980: pl. 32: 1, 7—8, and 12). In *Parachitina curvata* Eisenack, the operculum (pl. 28: 4*b*) is in form of a thin and round partition separating two neighbouring vesicles in a chain (Kozłowski 1963); be a chain disrupted, at least a single end of the affected vesicle becomes open (pl. 28: 4*a*). Much analogy is probably shown by the operculum of *Cyathochitina campanulaeformis* (Eisenack), embedded deeply within the neck (pl. 25: 1; fig. 7). The operculum is in form of a thin and round partition, multilayered in structure (pl. 26: 1), accreted very tightly to the inner side of vesicle wall. The operculum of vesicles representative of the genus *Linochitina* was thus far described under the name of "prosome", and the whole genus was assigned to the group "prosomatiphaera" (see Jansonius 1970). However, the present SEM investigations demonstrate that the operculum

is flat and discoidal, with a more or less elongate flange (pl. 35: 2 and 4; Wrona 1980: pl. 33: 1, pl. 34: 2 and 7) in various species of the genus *Linochitina*.

The above presented observations are entirely consistent with the opinion expressed by Kozłowski (1963) that opercula attached closely to a vesicle wall perfectly separated the central cavity from the external environment and were aimed to be opened once for all only. Laufeld (1974) demonstrated also with use of SEM technique that the cylindrical operculum ("prosome") was a rigid, motionless structure adapted to the same function as the discoidal operculum. The results of the present study support also the view (see e.g. Eisenack 1968; Laufeld 1974) that the only function of the cylindrical operculum ("prosome") was to separate the central cavity from the environment; whereas they greatly undermine the hypothesis that it functioned also during the reproduction (Cramer and Diez 1970; Urban 1972).

Where the oral margin of a vesicle is attached directly to the base of another vesicle, as e.g. in *Linochitina* (pl. 35: 6; Wrona 1980: pl. 33: 3 and 8—9) and *Eisenackitina* (pl. 33: 6; Wrona 1980: pl. 31: 1—3), the operculum developed most probably within the vesicle, under the cover of its wall. A similar mode of formation can be claimed for the weld tissue in *Margachitina* and for the operculum in *Parachitina curvata*. If a chitinozoan vesicle chain does indeed develop through a budding, as it is claimed e.g. for *Ancyrochitina* and *Angochitina* (Eisenack 1968, 1972*b*, 1976; Cramer and Diez 1970, 1974), the operculum can be expected to develop along the same lines as in *Linochitina*.

Thus, one may reject, at least with regard to some chitinozoan genera, a hypothesis that the operculum (and maybe the vesicle wall, too) was formed entirely from outside.

VESICLE AGGREGATES

Chain aggregates

Most chitinozoan species show chain aggregates of vesicles (see e.g. Combaz *et al.* 1967; Eisenack 1968; Jansonius 1970; Jenkins 1970). In a chain aggregate, the oral end of one vesicle is attached to the aboral end of another one (pl. 33: 6; Wrona 1980: pl. 31: 1—4; pl. 33: 3—4, 7—12; pl. 34: 5—7; pl. 35: 1—2). Since the very moment of the discovery of the Chitinozoa (Eisenack 1931), linear chain aggregates have been repeatedly described by all but a few paleontologists working with these microfossils. Less commonly occur spirally coiled chain aggregates reported by Kozłowski (1963) and Jenkins (1970).

Central cavities of the vesicles making part of a single chain aggregate were interconnected over some time, prior to their final separation

from one another (Kozłowski 1963; Eisenack 1968). The evidence of this disrupted interconnection is a closed basal pore (pl. 30: 2; Wrona 1980: pl. 30: 6) and a basal scar (pl. 21: 2; pl. 32: 1*b*; Wrona 1980: pl. 27: 18*a*); the latter element may range from a convex to concave large area at a vesicle bottom (pl. 25: 2*a*; pl. 26: 2 and 4; Wrona 1980: pl. 28: 4*b* and 10*d*; pl. 30: 11*d*). The size of a basal scar is indicative of the diameter of the original opening (*cf.* also Eisenack 1968: 149). Mature vesicles are equal in size and external morphology in a chain; their ends, cicatrized or closed with an operculum, are completely isolated from one another as well as from the influence of the exterior environment. Chain aggregates consist thus each of vesicles indentical to each other (Wrona 1980: pl. 33: 3—4 and 7—12; pl. 35: 1—2). However, aside of such homogenous chains, chain fragments have also been recorded (pl. 33: 6; Wrona 1980: pl. 25: 7; pl. 27: 13; pl. 31: 3 and 7*a*) that include smaller-sized, immature vesicles with their central cavities interconnected through a channel variable in diameter. Such aberrant vesicles were interpreted as a juvenile developmental stage suggestive of the formation of a chain aggregate through a budding process (Eisenack 1968, 1972*b*, 1976; Cramer and Diez 1970, 1974). Eisenack (1968) found immature vesicles attached to the aboral end of a fully developed vesicle and supposed that chain aggregates had been produced by successive budding at the aboral ends of vesicles. In turn, Cramer and Diez (1970) inferred from specimens with immature vesicles attached to the oral ends of fully developed ones that the budding had to have proceeded at the oral ends of vesicles. Later on, these authors agreed that both the modes of chain aggregate formation could have occurred (Cramer and Diez 1974; Eisenack 1972*b*, 1976). However, some chain fragments have also been recorded with an immature vesicle or basal scar at the aboral end of another immature vesicle. The suggestion that an immature vesicle was able to reproduce seem to be implausible. Furthermore, immature vesicles have also been recorded in the middle of a chain composed of fully grown vesicles (Wrona 1980; pl. 31: 2*a*). The present author is of the opinion that the latter phenomenon is indicative of some disturbances inhibiting the growth process of vesicle.

In the investigated material, there are also fully grown vesicles making part of a chain aggregate but without any basal scar, which proves their terminal position in the chain (pl. 29: 5—6; pl. 33: 6—7). All these vesicles are attached to the aboral end of the penultimate vesicle in a chain.

Cluster aggregates ("cocoons")

Less commonly occur aggregates in form of a cluster of vesicles. The vesicles show walls attached to one another, the apertures pointing most commonly outwards, and the aboral ends turned towards the center of a cluster (pl. 27: 2 and 4; pl. 36: 2—3). All the cluster aggregates recorded

thus far (Kozłowski 1963; Eisenack 1968; Jenkins 1970) consists exclusively of vesicles attributable to the species *Desmochitina minor* Eisenack; this mode of aggregation may actually be specific of this chitinozoans.

In a cluster aggregate, the vesicles are fused with one another with their outer spongy layer of the wall (pl. 27: 4) that could originally be far from hardened (see remarks on wall structure in *Desmochitina minor*). The spongy layer could contact with or even pass into a mucoidal matter that accordingly to Kozłowski (1963) filled up the spaces among the vesicles. The central cavities of vesicles making part of a cluster aggregate were never interconnected with one another. Every vesicle in an aggregate was all the time independent of the others. The vesicles were jointly covered with an oversleeve (pl. 37: 1*a*) forming a closed cocoon (Kozłowski 1963; Eisenack 1968). Vesicle imprints occur at the inner surface of cocoon cover (pl. 37: 1*b*—*d*). One may therefore suppose that at the time of cocoon formation an originally soft oversleeve covered vesicles hardened already in part.

Planar unilayered aggregates ("mat-like structures")

These aggregates consist of vesicles with their apertures oriented in the same direction. The vesicles may not contact directly with one another, as they are usually united by a membranous sheet of an organic matter covering them at their "equatorial" planes. Aggregates of this type were recorded by Legault (1973*a*, *b*) in *Hoegisphaera glabra* Staplin. One may claim that this mode of aggregation is typical of the whole genus *Hoegisphaera* Staplin because an evidence for it was also found in *H.velata* Wrona (Wrona 1980: pl. 32: 1) and *H. scabiosa* Wilson and Hedlund (Jenkins 1970). Vesicles making part of a planar unilayered aggregate were mutualy independent and their central cavities were separated from one another.

Radial aggregates

Radial aggregates are spherical associations of vesicles with the basal processes interconnected through their fibrous endings (pl. 36: 1) and the oral ends oriented radially outwards. The constituent vesicle are mutually independent units with their central cavities separated permanently from one another. A dozen or so radial aggregates were discovered by the present author in thin sections of chitinozoan-bearing rocks (Wrona 1980: pl. 36: 6—8). All thus far known radial aggregates consist exclusively of vesicles attributable to *Urochitina simplex* Taugourdeau and Jekhovsky (pl. 36: 1; Wrona 1980: pl. 34: 10). One may however suppose that this mode of aggregation is typical of the whole genus *Urochitina*, as all the species assigned to *Urochitina* display basal processes branching besom-like at their end (pl. 36: 1*c*; Wrona 1980: pl. 31: 10*c*). The form of radial aggregates of *Urochitina* is as unique among the Chitinozoa as that of planar unilayered aggregates of *Hoegisphaera* (Legault 1973*b*).

The basal processes of vesicles of *Urochitina simplex* resemble closely in their structure and size the hyphae of oogonium in some fungi. Thus, oogonia of the genera *Denegardia* and *Amoebochytrchium* (the order Chytridiales) resemble in shape and dimensions the *Urochitina* vesicles. Moreover, they show also a verticil of spines (Wrona 1980) in proximity of the opening (see Batko 1977) which resemble strikingly the neck processes in *Urochitina*. To the best of the present author's knowledge, this similarity is the only evidence in support of the hypothesis that refers the Chitinozoa to fungi (Locquin 1977); however, it is so with respect to the genus *Urochitina* only.

Apart from the above described four types of vesicle aggregates, some disorderly associations of vesicles accreted of cemented together have also been recorded (pl. 33: 2; pl. 37: 2; pl. 38: 4—5); the constituent vesicles are known to form chain aggregates in nature. Presumably, these are secondary accumulations of conspecific vesicles making originally part of natural aggregates that occurred in masses. They have been cemented in diagenesis (pl. 33: 2; pl. 38: 4—5) or pressed together by compaction. The present author is of the opinion that such disorderly associations cannot be regarded as primary aggregates or colonies (Cramer and Diez 1970, 1974).

SYSTEMATIC POSITION OF THE CHITINOZOA

Systematic position of the Chitinozoa remains thus far unrecognized, in spite of many hypotheses claiming that the Chitinozoa derived from various protozoan or metazoan groups. Those hypotheses are reviewed by Taugourdeau (1966), Eisenack (1968), Jenkins (1970), Obut (1973), Tasch (1973), and others. Their weak point is that they are all based upon the characteristics of a single chitinozoan group or even genus or species, and extrapolated over all the Chitinozoa considered as a homogenous natural taxon.

The recent studies by electron microscopes have proved that aside of a morphological similarity in chitinozoan vesicles, there is also much variation in the mode of vesicle aggregation, the vesicle wall structure, and presumably the mode of wall formation, too. This variation is suggestive of biological heterogeneity of the Chitinozoa, just as it is the case with the Acritarcha (Tappan and Loeblich 1971).

The Acritarcha are also a group of organic microfossils of unknown systematic position (*cf.* Evitt 1963; Downie *et al.* 1963). Chitinozoans and acritarchs do commonly co-occur or occur in analogous facies and show a similar geographical distribution. The size ranges of chitinozoan and acritarch vesicles overlap. Processes and spines at the surface of some acritarch vesicles show hollows separated from the central cavity, just as it is in chitinozoans. Various acritarch genera display an opening called

pylome and closed with an operculum (e.g. *Asketopalla*, *Priscogalea*) resembling very closely the operculum of such chitinozoans as *Hoegispheara*, *Margachitina*, *Pterochitina*, and some others. Pylome may be surrounded with a lip or collar variable in size; while at the opposite side of an acritarch vesicle (e.g. in *Axisphaeridium*, *Polyancistrodus*) a small opening called pseudopylome may occur, most commonly closed and located at a small rise (Loeblich and Tappan 1969). The pseudopylome resembles the chitinozoan basal callus and may indicate that those acritarchs that display it did form chain aggregates. Some acritarchs (e.g. *Aremoricanum*) show a collar in form of a long neck (no operculum has been recorded in it) similar to the chitinozoan neck; while a structure suggestive of a connection with another acritarch vesicle occurs at the opposite side (Loeblich and MacAdam 1971).

Some microfossils assigned previously to the Acritarcha have been eventually recognized for dinoflagellate cysts (Evitt 1961, 1963) or algae *Tasmanites* (Wall 1962; Jux 1977). One may claim that the Acritarcha, as they are meant at the moment, are actually a heterogenous group. Some authors (e.g. Loeblich and Tappan 1969; Tappan and Loeblich 1971) suppose that these are encystment stages of extinct algae.

The distinction between the chitinozoans and acritarchs is far from unequivocal. Organic microfossils attributable to the Chitinozoa have been recently found in the Upper Precambrian of the Grand Canyon, Arizona (Bloeser *et al.* 1977), where they co-occur with abundant acritarchs. Prior to this discovery, the oldest known chitinozoans were those reported from the Ordovician (Tremadocian). The Precambrian Chitinozoa from the Grand Canyon are very poorly preserved. These are isolated vesicles resembling in their simple structure and shape some Silurian forms.

With the structural resemblance of some chitinozoans to acritarchs taken into account, the discovery in the Upper Precambrian of the Grand Canyon may suggest a phylogenetic relationship between some chitinozoan and acritarch vesicles. On the other hand, mutual phylogenetic relationships among some chitinozoan genera may now appear to be questionable.

It is quite plausible to suppose that given a sufficiently long span of geological time, evolution in various organisms living under the same environmental conditions (marine planktic macrohabitat) could produce morphologically close forms adapted to the same biological function, that of egg or encystment capsules.

CONCLUSIONS

1. Fine elements of the chitinozoan vesicle surface sculpture were persistent through geological time. One may therefore claim that the surface sculpture can be applied to recognize the phylogenetic relations-

hips among various representatives of the Chitinozoa and by implication, to establish the natural taxonomy of this microfossil group. This is indeed supported by the observed distribution of particular types of surface sculpture among various chitinozoan genera and species. In order to understand the significance of surface sculpture for taxonomy of the Chitinozoa, further studies of well preserved material variable in geological age and taxonomical composition are needed.

2. The morphological and structural analysis of vesicles attributed to some species of *Ancyrochitina*, *Acanthochitina* and of other genera, as well as some previous investigation (Laufeld 1967, 1974; Chaiffetz 1972) permit a conclusion that the ornamentation elements and their structure were of adaptive value for floating and maintenance of a proper spatial orientation. The observed distribution of chitinozoans in sedimentary rocks (Wrona 1980) does also support the hypothesis (Laufeld 1967, 1974; Chaiffetz 1972; Obut 1973, and others) that many species or even genera of the Chitinozoa were planktic forms.

3. The analysis of the usefulness of various techniques to a study of the chitinozoan inner structure and wall structure suggests that the most appropriate is the electronic microscopy with application of both TEM and SEM. Special attention must be paid to the role of early and late diagenetic factors in the process of organic matter decomposition, which may considerably obscure the true structure of chitinozoan vesicles. The present author applied to the study normal and infrared light microscopes and a scanning microscope (SEM) but nontheless, artifacts have been only tentatively distinguished from the primary characteristics of the chitinozoan wall structure. All the above presented interpretations are therefore merely working hypotheses.

4. The following varieties of wall structure have been recognized after SEM investigations of spatially oriented cross sections through vesicles and their morphological details: (i) unilayered in *Rhabdochitina gracilis* Eisenack, *Eisenackitina pilosa* Wrona; (ii) bilayered or at least bilayered in *Acanthochitina barbata* Eisenack, *Conochitina* sp., *Desmochitina minor rugosa* Eisenack, *D. spongiloricata* Wrona, *Hoegisphaera glabra* Staplin, *H. velata* Wrona, *Lagenochitina* sp.; (iii) presumably trilayered in *Cyathochitina campanulaeformis* (Eisenack); and (iv) multilayered in *Parachitina curvata* Eisenack and supposedly in *Linochitina serrata* Taugourdeau and Jekhowsky.

5. Growth lines discovered at the vesicle surface in *Linochitina serrata* Taugourdeau and Jekhowsky and *Conochitina* sp. suggest that the vesicle wall was produced rhythmically in the "equatorial" plane in some chitinozoan species. This mode of wall development was probably confined to those Chitinozoa only where the vesicle formed chain aggregates. In contrast, the wall structure and vesicle interconnections observed in cluster aggregates (cocoons recorded in *Desmochitina minor rugosa*) are

suggestive of a simultaneous growth at the whole vesicle surface, proceeding successively from the central cavity outwards; furthermore, the wall was probably soft for some time after its formation. Thus, a different mode of wall formation seems to be characteristic of chain and cluster aggregates. The variation in the mode of vesicle aggregation and wall formation may be indicative of some basic divergences within the Chitinozoa, that is of a heterogeneity of this microfossil group.

6. The detailed study of perforation of the chitinozoan vesicles (see also Laufeld 1974) and the recognition of a previously unknown perforation type, the conical smooth perforation, have offered good evidence for the secondary nature of these phenomena. A comparison to borings produced by various organisms suggests that the regular perforation recorded in the Chitinozoa resulted from a chemical (e.g. enzymatical digestion) rather than mechanical action exerted by some unknown organisms.

7. The analysis of the vesicle inner structure permits a conclusion that various structures described thuse far under the names of "opisthosome" and "mesosome" are artifacts.

8. The analysis of various discoidal and cylindrical opercula (*cf.* also Laufeld 1974) makes possible an inference that these were rigid and motionless structures adapted to perform the isolation function only. The operculum structure and position in the neck allow to conclude that in some chitinozoan genera (*Margachitina* and *Hoegisphaera*) the operculum was a more specialized part of vesicle wall aimed to open a vesicle once for all (Kozłowski 1963, Laufeld 1974).

9. The observations under SEM do not undermine the Kozłowski hypothesis (Kozłowski 1963) that vesicles of *Desmochitina minor* Eisenack forming cocoons were the metazoan egg capsules, but it is improbable that this was the nature of all the chitinozoan genera.

10. The recent observations of the Chitinozoa and Acritarcha under electron microscopes have permitted a comparison of the two microfossil groups. One may conclude that the taxonomic limits set inbetween are far from unequivocal. The comparison of the Chitinozoa to Acritarcha and the structural analysis of the Chitinozoa indicate that the chitinozoans make up a heteregenous group, just as it is the case with the Acritarcha.

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RYSZARD WRONA

MIKROARCHITEKTURA CHITINOZOA I JEJ ZNACZENIE PALEOBIOLOGICZNE

Streszczenie

Przedstawiono wyniki wykonanej za pomocą SEM analizy morfologicznej i strukturalnej vesicul następujących Chitinozoa: *Acanthochitina barbata*, *Anthochitina superba*, *Ancyrochitina aurita*, *A. lemniscata*, *A. bulbispina*, *Cyathochitina campanulaeformis*, *C. kuckersiana*, *C. stentor*, *Desmochitina minor rugosa*, *D. spongiloricata*, *Eisenackitina cupellata*, *E. lacrimabilis*, *E. pilosa*, *E.* cf. *urna*, *Hoegisphaera glabra*, *H. velata*, *Linochitina serrata*, *L. longiuscula*, *Lagenochitina esthonica*, *L.* sp., *Margachitina margaritana*, *M. gratiosa*, *Urochitina simplex*. Zdefiniowano 10 typów rzeźby powierzchni vesicul: gładką, granularną, nodularną, brodawkowaną, lanarną, pomarszczoną, retikularną, mikroporowatą, mikrogąbczastą i gąbczastą. Wysunięto przypuszczenie, że rzeźba znajdzie zastosowanie do określenia pokrewieństwa między rozmaitymi przedstawicielami Chitinozoa i w taksonomii tej grupy. Szczegółowo scharakteryzowano ornamentację i budowę ściany wielu gatunków Chitinozoa. Na tej podstawie potwierdzono koncepcję planktonicznego sposobu życia licznych gatunków i rodzajów Chitinozoa. Opisano perforację vesicul o genezie mechanicznej i organogenicznej, w której wyróżniono kilka klas perforacji cylindrycznej, stożkowej gładkiej i stożkowej schodkowej. Struktury wewnętrzne vesicul znane jako „opistosoma" i „mezosoma" uznano za artefakty. Analiza budowy i położenia w vesiculi wieczka dyskoidalnego i cylindrycznego zwanego także „prosomą", pozwoliła stwierdzić, że były to sztywne i nieruchome elementy doskonale izolujące wewnętrzną jamę vesiculi od środowiska zewnętrznego i służyły do jednokrotnego otwarcia. Na podstawie analizy 4 rodzajów zespołów vesicul i budowy ich ścian stwierdzono, że wielu gatunkom Chitinozoa odpowiadały różne sposoby tworzenia ścian. Przedyskutowano przydatność dotychczasowych metod badania wewnętrznej budowy Chitinozoa i ich ścian oraz zwrócono uwagę na udział czynników wczesno- i późnodiagenetycznych w procesie dekompozycji substancji organicznej, fałszujących obraz budowy ściany. Najnowsze obserwacje w SEM umożliwiły porównanie vesicul z rodzaju *Urochitina* z lęgniami niektórych grzybów, oraz na ogólne porównanie Chitinozoa i Acritarcha. Przedstawione w pracy porównania i analiza mikroarchitektury vesicul pozwalają stwierdzić, że Chitinozoa nie są jednorodną, naturalną grupą.

Praca została wykonana w ramach problemu międzyresortowego Mr II/3, finansowanego przez Polską Akademię Nauk.

EXPLANATION OF THE PLATES 19—38

Plate 19

Vesicle surface sculpture in the Chitinozoa
Levigate sculpture

1. *Eisenackitina cupellata* Wrona, ZPAL Ch. II/4S30, ×720.
2. *Anthochitina superba* Eisenack, ZPAL Ch. II/2S06, ×2000.

Granulate sculpture

3. *Linochitina* sp. B, ZPAL Ch. II/2S119, ×1133.
4. *Linochitina longiuscula* Wrona, ZPAL Ch. II/2S111, ×2000.
5. *Lagenochitina* sp., ZPAL Ch. V/7S4, ×4000.

Lanate sculpture

6. *Eisenackitina lacrimabilis* Wrona, ZPAL Ch. II/2S5, ×2000.
7. *a Eisenackitina* sp., ZPAL Ch. II/2S3, ×2000; *b* fragment of the same vesicle surface, ×6666.

Plate 20

Vesicle surface sculpture in the Chitinozoa
Rugate sculpture

1. *Cyathochitina stentor* (Eisenack), ZPAL Ch. IV/5S3, ×400.
2. *Cyathochitina* aff. *stentor* (Eisenack), ZPAL Ch. IV/5S8, ×600.

Reticulate sculpture

3. *Cyathochitina* sp., ZPAL Ch. IV/7S5, ×533.

Nodular sculpture

4. *Parachitina curvata* Eisenack, ZPAL Ch. III/8S2, ×1000 (see also pl. 28: 1—4).

Verrucate sculpture

5. *Eisenackitina pilosa* Wrona, ZPAL Ch. II/4S26, ×720.
6. *Conochitina* sp., ZPAL Ch. II/15S9, ×1333.
7. *a Eisenackitina* sp., ZPAL Ch. II/15S4, ×1333; *b* fragment of the same vesicle surface, ×4000.

Plate 21

Vesicle surface sculpture in the Chitinozoa
Microporous sculpture

1. *a Cyathochitina campanulaeformis* (Eisenack), ZPAL Ch. IV/5S9, ×2000; *b* fragment of the same vesicle surface, ×4000.
2. *Cyathochitina campanulaeformis* (Eisenack), ZPAL Ch. IV/3S2, ×2400.

Microspongy sculpture

3. *a Lagenochitina* sp. A, ZPAL Ch. V/8S11, ×2133; *b* fragment of the same vesicle surface, ×4267.
4. *Lagenochitina* sp. B, ZPAL Ch. V/8S31, ×4000.
5. *Lagenochitina* sp. C, ZPAL Ch. V/8S14, ×6667.

Spongy sculpture (spumose variety)

6. *Anthochitina superba* Eisenack, ZPAL Ch. II/3S63, ×2400.
7. *Desmochitina spongiloricata* Wrona, ZPAL Ch. II/4S13, ×2400.

Plate 22

Vesicle wall perforation in the Chitinozoa
Irregular perforation

1. Mechanically produced hole in vesicle wall in *Linochitina* sp., ZPAL Ch. II/ /2S233, ×3333.
9. Supposedly mechanically produced hole in vesicle wall in *Eisenackitina pilosa* Wrona, ZPAL Ch. II/2S127, ×2000.

Regular perforation

2. Cross section through vesicle wall in *Cyathochitina kuckersiana* (Eisenack); note opening of a channel more or les parallel to the vesicle surface; ZPAL Ch. IV/3S3, ×1200.
3. Cylindrical perforation at the lateral surface of a vesicle of *Eisenackitina lacrimabilis* Wrona; note perforation density; ZPAL Ch. II/2S190, ×1333.
4. Conical step-form perforation in chamber wall in *Eisenackitina cupellata* Wrona, ZPAL Ch. II/4S30, ×8000.
5. Cylindrical perforation at the base of a vesicle of *Cyathochitina campanulaeformis* (Eisenack); note distribution of the perforation and degree of the wall destruction; ZPAL Ch. V/8S19, ×4000.
6. Cylindrical perforation in chamber wall in *Cyathochitina stentor* (Eisenack), ZPAL Ch. III/5S12, ×2000.
7. Cylindrical perforation in apertural lip in *Margachitina gratiosa* Wrona, ZPAL Ch. II/2S18, ×2333.
8. *a* Distribution of conical smooth perforation at vesicle surface in *Cyathochitina* sp., ZPAL Ch. IV/7S5, ×267; *b* fragment of the base of the same specimen; note conical outline of the perforation; ×667.

Plate 23

Vesicle wall perforation in the Chitinozoa
Regular perforation

1. Cylindrical perforation variable in diameter in vesicle wall in *Eisenackitina* sp., ZPAL Ch. II/2S175, ×2000.
2. Cylindrical perforation in vesicle wall in *Eisenackitina lacrimabilis* Wrona, ZPAL Ch. II/2S146, ×3333.
3. Cylindrical perforation in vesicle wall in *Margachitina gratiosa* Wrona, ZPAL Ch. II/2S17, ×8000.

4. Cylindrical perforation in chamber wall in *Eisenackitina cupellata* Wrona; note two incomplete, fused openings; ZPAL Ch. II/4S30, ×1600.
5. Distribution of cylindrical perforation at the surface and operculum of a vesicle of *Margachitina gratiosa* Wrona, ZPAL Ch. II/2S19, ×1000.
6. Cylindrical perforation at the base of a vesicle of *Eisenackitina lacrimabilis* Wrona, ZPAL Ch. II/4S21, ×2400.
7. *a* Distribution of regular perforation at the surface of a vesicle of *Eisenackitina* sp., ZPAL Ch. II/2S12, ×533; *b* fragment of the same vesicle surface, note distribution and outline of the openings, ×2000.
8. Cylindrical perforation in vesicle wall in *Eisenackitina cupellata* Wrona, ZPAL Ch. II/3S15, ×8000.
9. *a* Distribution of cylindrical perforation at the surface of vesicle of *Hoegisphaera glabra* Staplin, ZPAL Ch. II/1S2, ×1800; *b* a single opening in the same specimen, ×6666.
10. Cylindrical perforation in chamber wall in *Ancyrochitina aurita* Wrona, ZPAL Ch. II/4S39, ×1600.

Plate 24

Vesicle wall structure in the Chitinozoa

1. *a Conochitina* sp., ZPAL Ch. IV/5S2, ×87; *b* fragment of the same vesicle surface, note outer layer in folds detached from the underlying layer, ×433.
2. *Eisenackitina pilosa* Wrona, section through the wall in the oral part of a vesicle; note unilayered structure; ZPAL Ch. II/2S33, ×6666.
3. *Eisenackitina lacrimabilis* Wrona, section through the wall; note irregular boundary between two constituent layers; ZPAL Ch. II/1S1, ×4000.
4. *a Eisenackitina pilosa* Wrona, vesicle with the bottom broken off, note central cavity in aboral view, ZPAL Ch. II/2S67, ×500; *b* fragment of a section through the vesicle wall, note unilayered structure, ×6666.
5. *a Eisenackitina* cf. *urna* (Eisenack), inside view of the oral part of a broken vesicle, ZPAL Ch. II/14S16, ×400; *b* fragment of the inner surface of the collar, note inner layer (? flange) of a section through the vesicle wall, note heterogenous, (?) multilayered structure, ×4000.

Plate 25

Vesicle wall structure in the Chitinozoa

1. *a Cyathochitina kuckersiana* (Eisenack), broken vesicle, ZPAL Ch. IV/3S3, ×173; *b* fragment of the same vesicle in oral view, note neck partly broken off, section through the wall, and operculum; ×1280; *c* fragment of a section through the vesicle wall, note trilayered structure with outer layer apparent in folds detached from mid-layer, ×2400 (*cf.* also fig. 1).
2. *a Cyathochitina* sp., vesicle in aboral view, note carina broken off, and base partly pressed into the vesicle, ZPAL Ch. IV/5S4, ×300; *b* fragment of the basal edge, note that where carina is broken off, outer layer appears in folds detached from the underlying layer, ×1333.
3. *a Cythochitina* sp., crushed vesicle in lateral view, ZPAL Ch. IV/3S27, ×160; *b* fragment of a section through the wall close to the basal edge, note intracarinal voids (arrowed), ×2400 (*cf.* also fig. 2).

Plate 26

Vesicle morphology and inner structure in the Chitinozoa

Cyathochitina campanulaeformis (Eisenack)

1. Operculum extracted from a vesicle in aboral view, note multilayered structure, ZPAL Ch. III/8S28, ×1000.
2. *a* Vesicle in aboral view, ZPAL Ch. IV/3S26, ×260; *b* central part of the base of the same specimen, note basal callus and basal scar, ×1280.
3. *a* Longitudinal section through a vesicle, note central cavity and wall section, ZPAL Ch. III/8S27, ×200; *b* fragment of a section through the wall close to the basal edge of the same specimen, note void space between the wall inner layer and the outer layer contributing to carina, ×2000 (*cf.* also fig. 3).

Cyathochitina kuckersiana (Eisenack)

4. Vesicle in aboral view, note basal depression and basal scar, ZPAL Ch. IV/ /8S15, ×133.

Plate 27

Vesicle morphology and wall structure in the Chitinozoa

Desmochitina minor rugosa Eisenack

1. *a* Oral part of a longitudinally broken vesicle, ZPAL Ch. III/8S23, ×666; *b* fragment of a section through the wall of the same vesicle, note bilayered structure, ×4000.
2. Fragment of a cluster aggregate (cocoon) including three vesicles, note that the central vesicle is partly stripped of outer (spongy) layer, ZPAL Ch. IV/7S3, ×200.
4. *a* Fragment of a cluster aggregate (cocoon) including three vesicles, note scars after connections with other vesicles in the outer layer of the vesicles, ZPAL Ch. III/8S24, ×300; *b* fusion of the outer (spongy) layers of the neighbouring vesicles is the same aggregate, ×1333.

Lagenochitina esthonica Eisenack

3. Fragment of a section through vesicle wall; note seemingly bilayered structure, the "outer" layer is a secondary mineral cover of the vesicle, ZPAL Ch. III/6S7, ×1333.

Plate 28

Vesicle morphology, inner structures, and wall structure in

Parachitina curvata Eisenack

1. *a* Aberrant vesicle, ZPAL Ch. III/8S2, ×100; *b* pole of the same vesicle, note sheeting planes revealing multilayered wall structure, ×1000.
2. Vesicle typical of the species; note nodular surface sculpture, ZPAL Ch. III/ /8S9, ×133 (*cf.* also pl. 20: 4).
3. Contorted vesicle making originally part of a spirally coiled chain aggregate, note nodular surface sculpture, ZPAL Ch. III/8S1, ×166.

4. *a* A little soiled vesicle in lateral view, ZPAL Ch. III/8S3, ×200; *b* oral part of the same vesicle, note operculum, ×1000.
5. Fragment of a section through vesicle wall, note multilayered structure, ZPAL Ch. III/8S4, ×2000.

Plate 29

Vesicle inner structure and wall structure in *Margachitina margaritana* (Eisenack)

1. Broken operculum in lateral view, its bilayered structure is invisible in the section, ZPAL Ch. IV/3S55, ×1600.
2. *a* Broken vesicle, note weld and damaged base wall in inside view, ZPAL Ch. IV/3S58, ×880; *b* section through the wall of the same vesicle, note bilayered structure, ×1600.
3. Section through a weld; note compact structure of the matter separating two neighboring central cavities, and section through the weld wall, ZPAL Ch. IV/3S47, ×2000.
4. *a* A little deformed vesicle, note distribution of cylindrical perforation and a trace after weld at the operculum, ZPAL Ch. IV/3S43, ×560; *b* center of the operculum, note wall section and trace after the broken off weld, ×1600.
5. Vesicle terminal in a chain aggregate in lateral view, note its operculum interconnected through a weld with the base of adjacent vesicle, and its base lacking any evidence for interconnection with another vesicle, ZPAL Ch. IV/3S45, ×640.
6. Vesicle terminal in a chain aggregate in aboral view, note two mechanical damages at the base lacking any evidence for interconnection with another vesicle, ZPAL Ch. IV/3S60, ×506.

Plate 30

Vesicle structure in *Lagenochitina* sp.

1. *a* Vesicle in oblique lateral view, note aboral part stripped of the wall outer layer, ZPAL Ch. VI/688, ×100; *b* flange formed by a detached portion of outer layer, preserved at the oral part of the vesicle, ×666.
2. *a* Incomplete vesicle in lateral view, note removed outer layer of the wall, ZPAL Ch. V/8S14, ×200; *b* the same vesicle in aboral view, note basal pore, ×1000.
3. *a* Vesicle in lateral view, note outer layer party damaged, removed, and separated from the underlying layer, ZPAL Ch. V/8S31, ×100; *b* aboral part of the same vesicle, note partly damaged outer layer, ×400 (*cf.* also fig. 4).

Plate 31

Vesicle and wall structure in *Acanthochitina barbata Eisenack*

1. *a* Vesicle in lateral view, note removed outer layer and exposed, party damaged piles, ZPAL Ch. III/9S2, ×133; *b* fragment of the same vesicle surface, note partly damaged piles (one pile is incompletely developed), ×1333; *c* another fragment of the same vesicle surface, note piles and remains of their cover built up by outer layer, ×1333.

2. *a* Transversally broken vesicle in aboral view, ZPAL Ch. III/9S3, ×400; *b* fragment of the same specimen in lateral view, note piles and remains of their cover built up by outer layer, ×1333; *c* another fragment of the same specimen, note section through the wall, and piles and remains of their cover, ×1333 (*cf.* also fig. 5).

Plate 32

Vesicle and wall structure in *Acanthochitina barbata* Eisenack

1. *a* Vesicle in oblique lateral view, note partly damaged piles and outer layer, ZPAL Ch. III/9S1, ×133; *b* the same vesicle in aboral view, note basal scar and traces after broken piles, ×666; *c* fragment of the same vesicle surface, note piles with their distal ends forming a net, ×666; *d* fragment of the surface shown in 1*c*, note naturally onen inside hollows of some piles (arrowed), ×2000; *e* fragment of the surface shown in 1*c*, note channels of inside hollows in sections through the pile bases, ×2000; *f* fragment of the surface shown in 1*c*, note inside hollow in section through a pile, ×4000.

Plate 33

Vesicle ornamentation and mode of aggregation in the Chitinozoa

1. *Ancyrochitina lemniscata* Wrona, note wide, hollow inside appendices, ZPAL Ch. II/14S6, ×466.
2. *Linochitina* sp., secondary accumulation of vesicles formed by chance after a chain disintegration, note disorderly arrangement of the vesicles and the cementing matter, ZPAL Ch. II/15S7, ×200.
3. *Ancyrochitina bulbispina* Wrona, aboral part of a vesicle, note bullate, hollow inside appendices, ZPAL Ch. II/4S38, ×2000.
4. *Hoegisphaera velata* Wrona, note folded outer layer at vesicle surface, ZPAL Ch. II/4S37, ×480.
5. *Rhabdochitina gracilis* Eisenack, section through the wall of a vesicle base, note unilayered structure, ZPAL Ch. VI/1S11, ×1133.
6. *Eisenackitina* cf. *urna* (Eisenack), terminal part of a chain aggregate; note the lack of any trace of interconnection with another vesicle at the base of the ultimate vesicle, ZPAL Ch. II/15S19, ×133.
7. *Eisenackitina* cf. *urna* (Eisenack), terminal vesicle in a chain aggregate, note the lack of any trace of interconnection with another vesicle at the vesicle base, ZPAL Ch. II/15S18, ×400.
8. *Hoegisphaera* cf. *glabra* Staplin, note pyrite spherulites filling up the vesicle and imprinted at its surface, ZPAL Ch. II/2S217, ×933.

Plate 34

Operculum morphology and position in the vesicles

1. *Eisenackitina lacrimabilis* Wrona, note convex operculum within the aperture, ZPAL Ch. II/4S35, ×1200.
2. *a Eisenackitina lacrimabilis* Wrona, longitudinally broken vesicle, note unilayered structure of the wall and operculum in oblique aboral view, ZPAL Ch. II/4S25, ×1200; *b* the same operculum in oral view, note indistinct oral scar, ×1200.

3. *Desmochitina minor rugosa* Eisenack, note convex operculum within the aperture, ZPAL Ch. VI/7S9, ×2000.
4. *Eisenackitina pilosa* Wrona, note operculum standing ajar in the aperture and well developed oral scar, ZPAL Ch. II/4S28, ×1200.
5. *Eisenackitina* sp., note vesicle base and basal callus attached to operculum of adjacent vesicle in a chain aggregate, ZPAL Ch. II/15S15, ×1000.
6. *Margachitina gratiosa* Wrona, fragment of a chain aggregate, note operculum and its lower margin within the aperture, ZPAL Ch. II/2S22, ×1733.
7. *Margachitina gratiosa* Wrona, fragment of a chain aggregate, note operculum in aboral view and its lower margin (arrowed) within a broken vesicle, ZPAL Ch. II/2S18, ×1466.

Plate 35

Operculum morphology and vesicle interconnection in the Chitinozoa

1. *Eisenackitina* cf. *urna* (Eisenack), fragment of a chain aggregate, note operculum protruding from the aperture of a vesicle and attached to the base of adjacent vesicle, ZPAL Ch. II/15S13, ×666.
2. *Linochitina serrata* Taugourdeau and Jekhowsky, vesicle base attached to the operculum of adjacent vesicle, note wide flange at the inner side of the perculum, ZPAL Ch. II/4S9, ×1200.
3. *Eisenackitina cupellata* Wrona, note mineral fill visible through a breach in vesicle wall, ZPAL Ch. II/2S194, ×1066.
4. *Linochitina* sp., operculum in aboral view, note its smooth inner surface, ZPAL Ch. II/4S22, ×1600.
5. *Eisenackitina cupellata* Wrona, oral part of a vesicle, note convex operculum within the aperture, ZPAL Ch. II/4S30, ×1600.
6. *Linochitina serrata* Taugourdeau and Jekhowsky, vesicle interconnection, note basal edge of a vesicle attached to the collar of adjacent vesicle, note also growth lines and lamellae at the collar surface, ZPAL Ch. II/4S9, ×1600.

Plate 36

Vesicle aggregates in the Chitinozoa
Urochitina simples Taugourdeau and Jekhowsky

1. *a* Part of a larger aggregate including three vesicles, ZPAL Ch. II/14S11, ×146; *b* vesicle interconnection, note vesicle bases and interconnected basal processes, and basal processes of other vesicles removed from the aggregate, ×400; *c* a single basal process, note fibrous branching at the distal end, ×4000.
4. Fragment of a vesicle base along with a basal process, note fibrous branching of the process reaching almost the vesicle base, ZPAL Ch. II/14S14, ×3000.

Desmochitina minor rugosa Eisenack

2. Fragment of a cluster aggregate (cocoon) including five vesicles, note arrangement and orientation of the vesicles, ZPAL Ch. III/7S7, ×200.
3. Fragment of the surface of a cluster aggregate (cocoon), note arrangement and orientation of the vesicles, ZPAL Ch. III/8S29, ×400.

Plate 37

Vesicle aggregates in the Chitinozoa

Desmochitina minor rugosa Eisenack

1. *a* Fragment of a damaged cluster aggregate (cocoon), note vesicle arrangement and remains of the oversleeve, ZPAL Ch. VI/1S4, ×166; *b* fragment of the oversleeve of the same aggregate, note its inner surface with vesicle imprints, ×333; *c* fragment of the inner surface of the same oversleeve, note imprint of a single vesicle ×1133; *d* imprint of surface sculpture of a vesicle at the inner surface of the oversleeve, ×6666.

Cyathochitina aff. *campanulaeformis* (Eisenack)

2. *a* Two vesicles attached by chance to each other, note neck of one vesicle inserted into the other vesicle, ZPAL Ch. IV/9S20, ×133; *b* interconnection of two vesicles, note their tight fitting to each other, ×666.

Plate 38

Vesicle aggregates in the Chitinozoa

Eisenackitina cf. *urna* (Eisenack)

1. *a* Vesicle along with operculum of adjacent vesicle, ZPAL Ch. II/14S5, ×300; *b* fragment of the same vesicle base attached to the operculum of adjacent vesicle, note considerable transformation of the operculum, its obscured original form and structure, ×1333.

Linochitina sp.

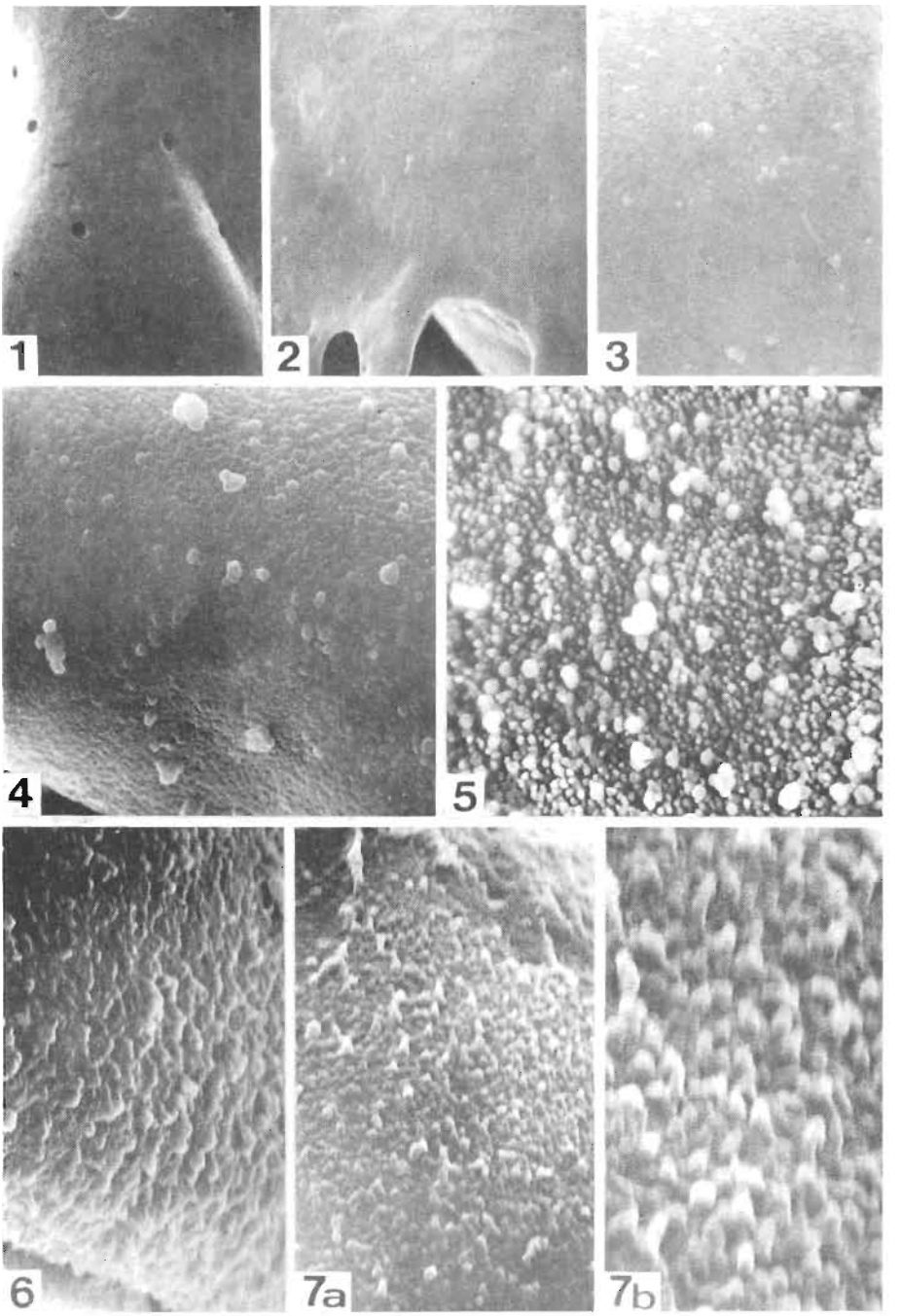
2. *a* Fragment of a chain aggregate, note two unseparated vesicles, ZPAL Ch. II/2S40, ×266; *b* interconnection of two vesicles making part of the same aggregate, note continuous transition of the collar of one vesicle into the base of the other one, ×1333.
3. Vesicle attached to operculum of another vesicle, note considerable transformation of the vesicle wall, ZPAL Ch. II/2S37, ×400.

Cyathochitina aff. *stentor* Eisenack

4. Two vesicles attached by chance to each other, note their position and mineral cement (?), ZPAL Ch. IV/3S20, ×36.
5. Secondary accumulation including three vesicles attached by chance to one another, note position of the vesicles and their mineral cement (?), ZPAL Ch. IV/3S19, ×64.

Margachitina margaritana (Eisenack)

6. A little damaged vesicle, note remains of operculum of another vesicle within the aperture, and remains of still another vesicle accreted to operculum attached to the vesicle base, ZPAL Ch. III/5S11, ×400.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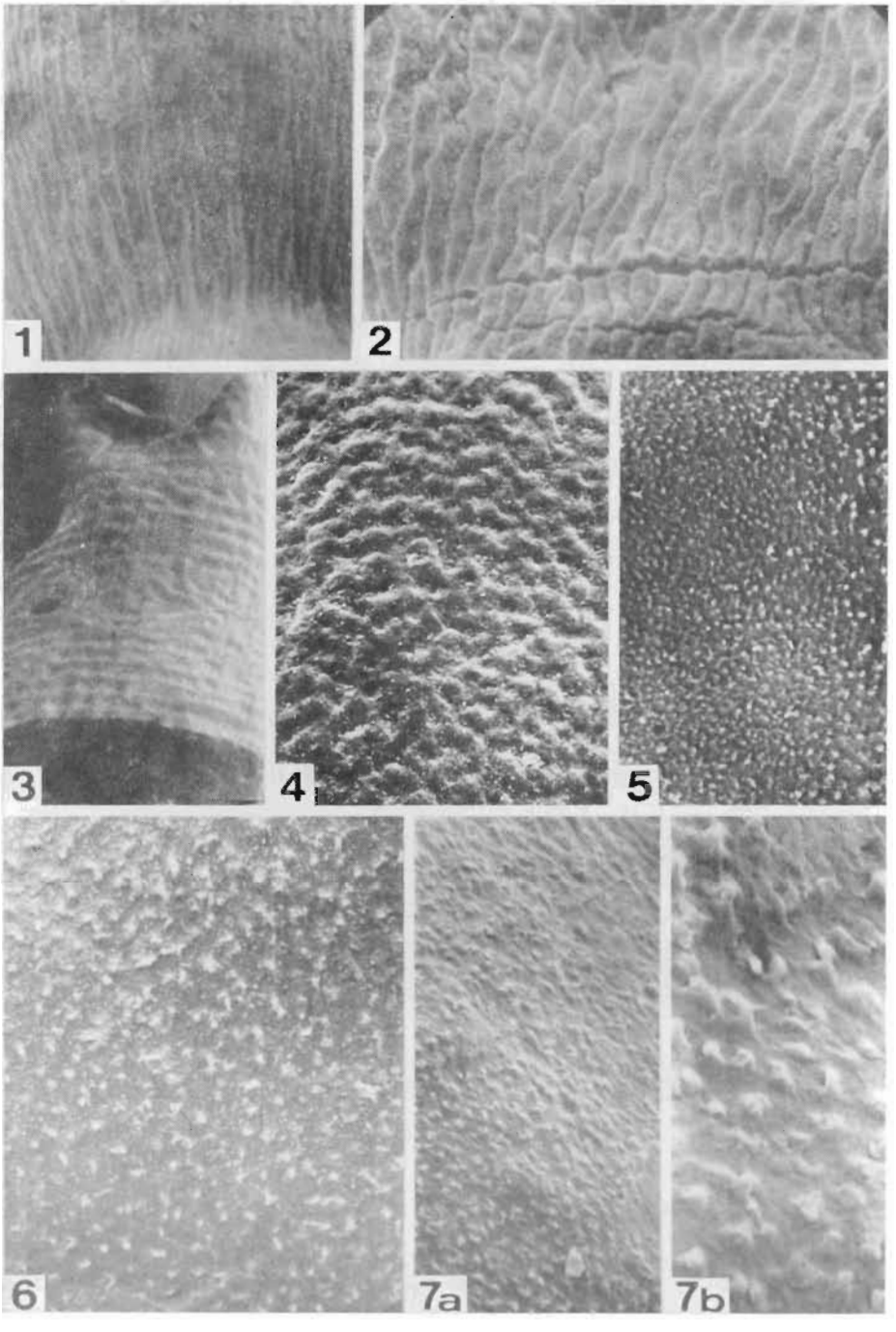
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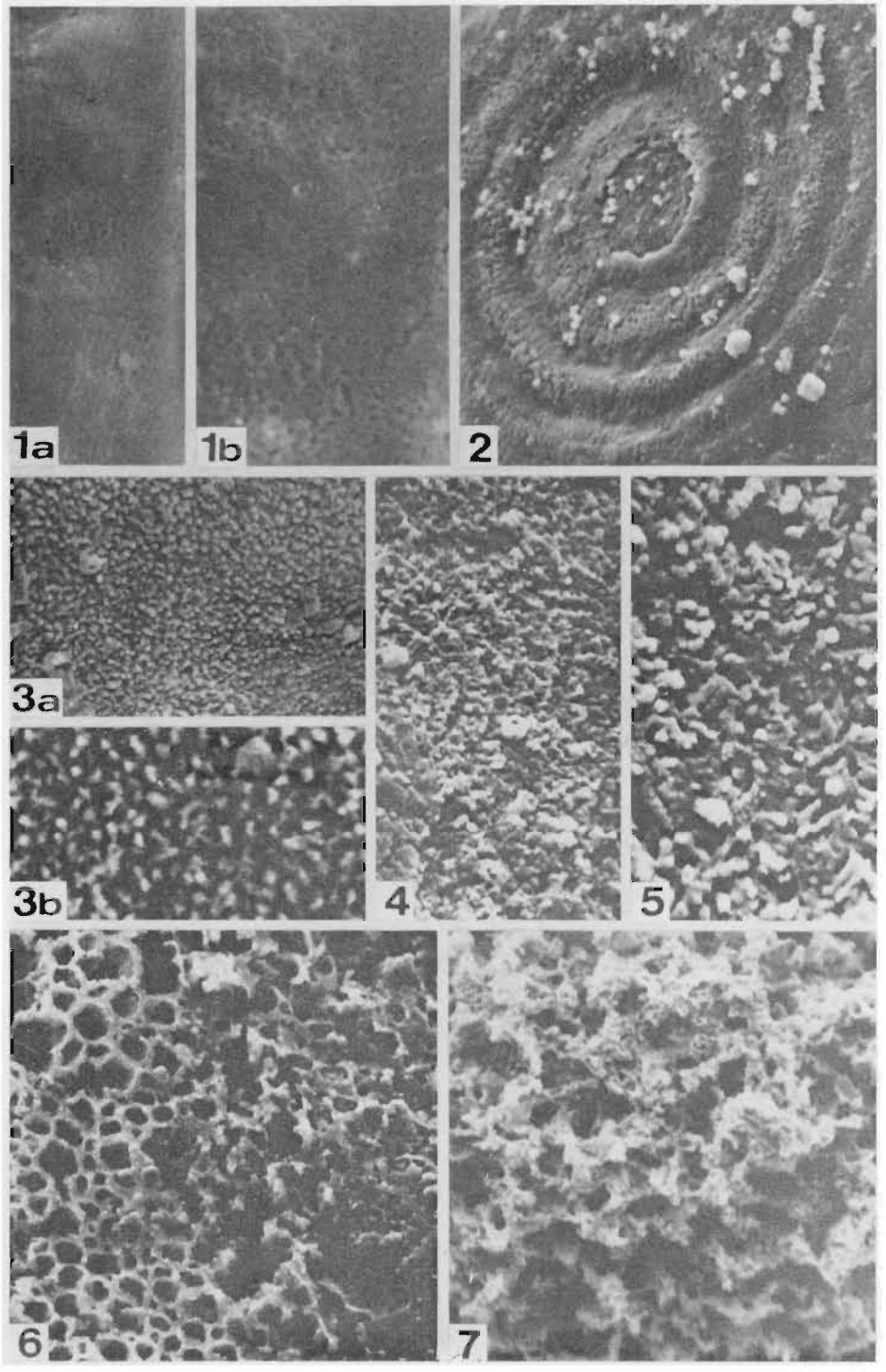
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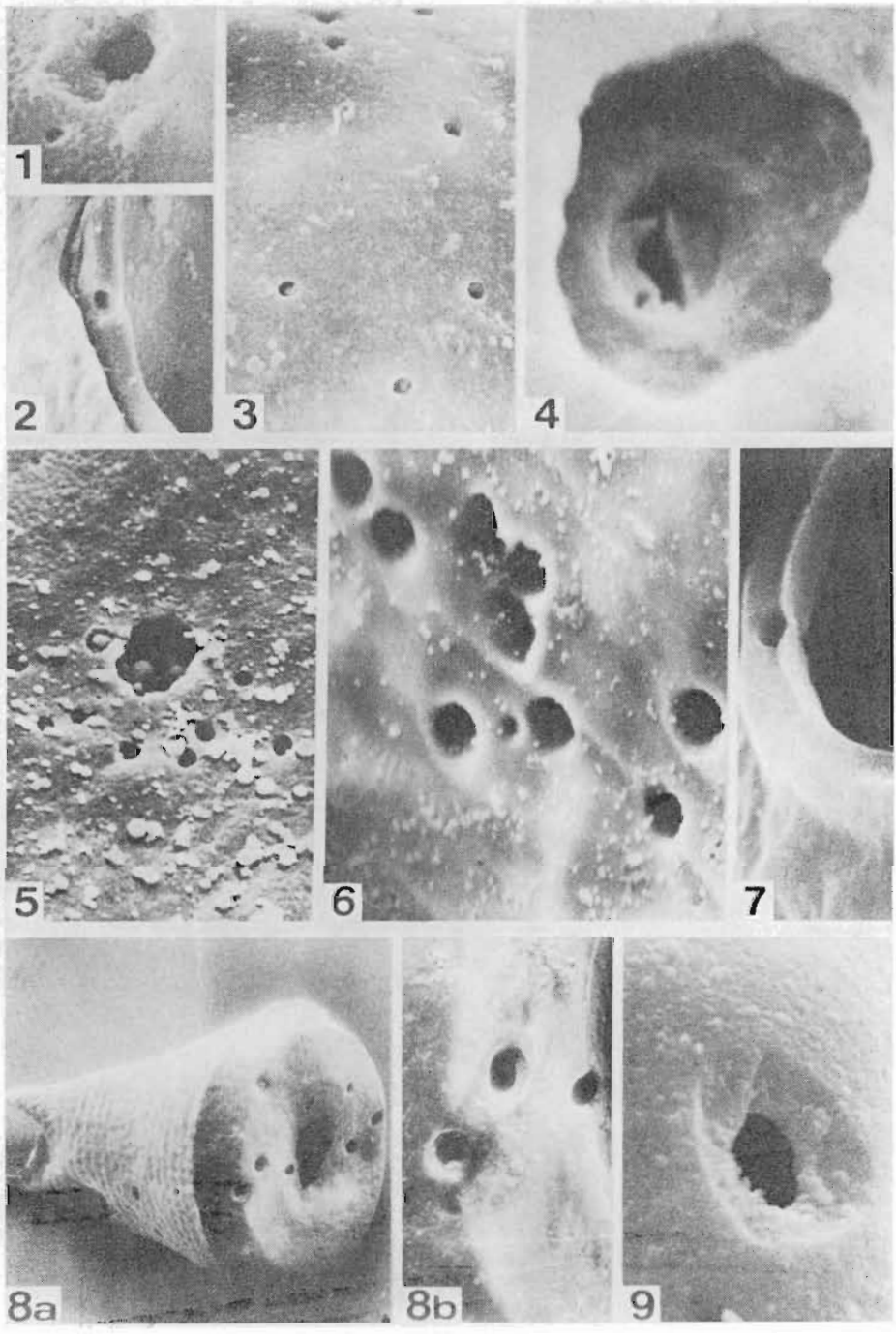
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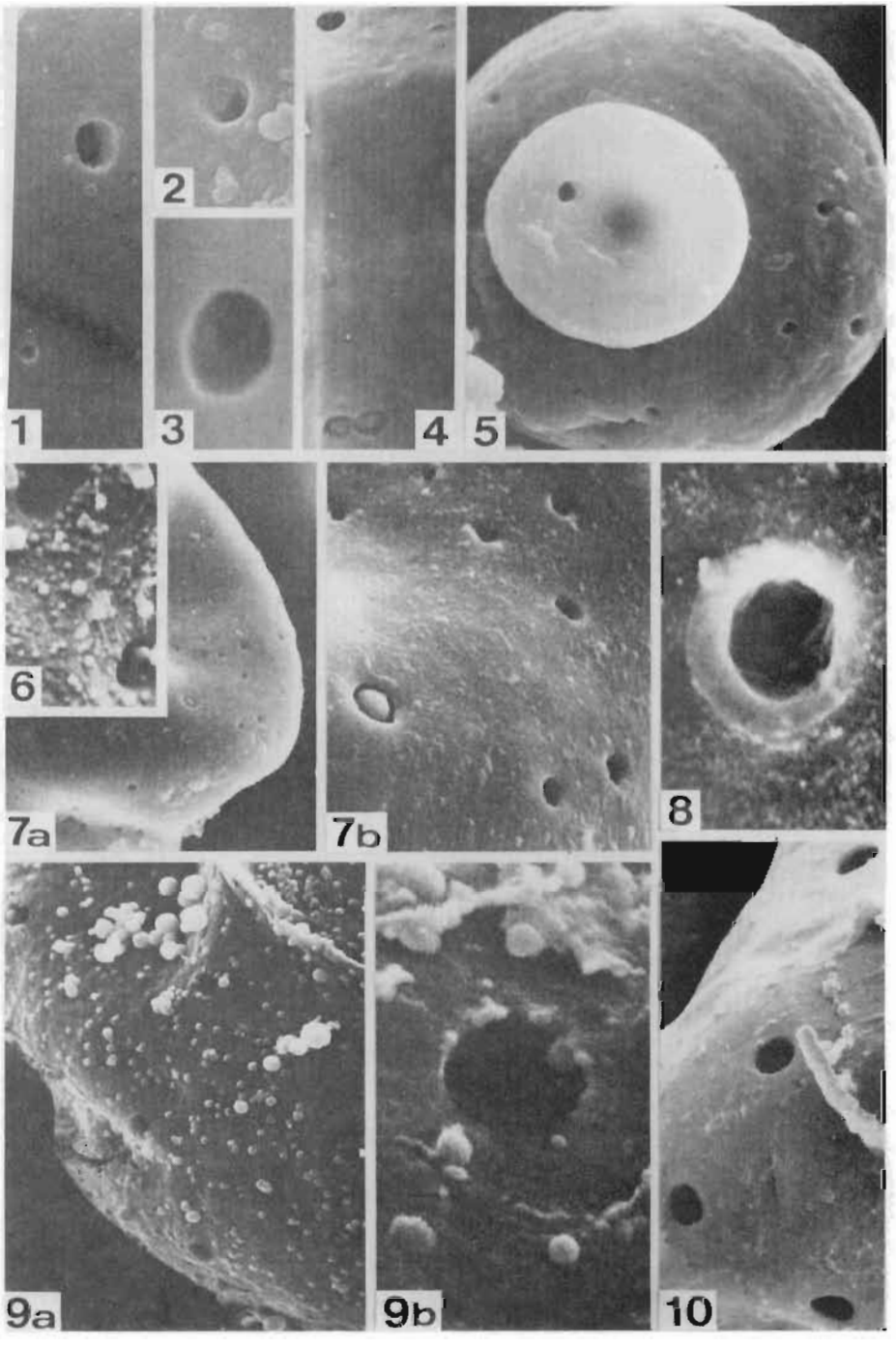
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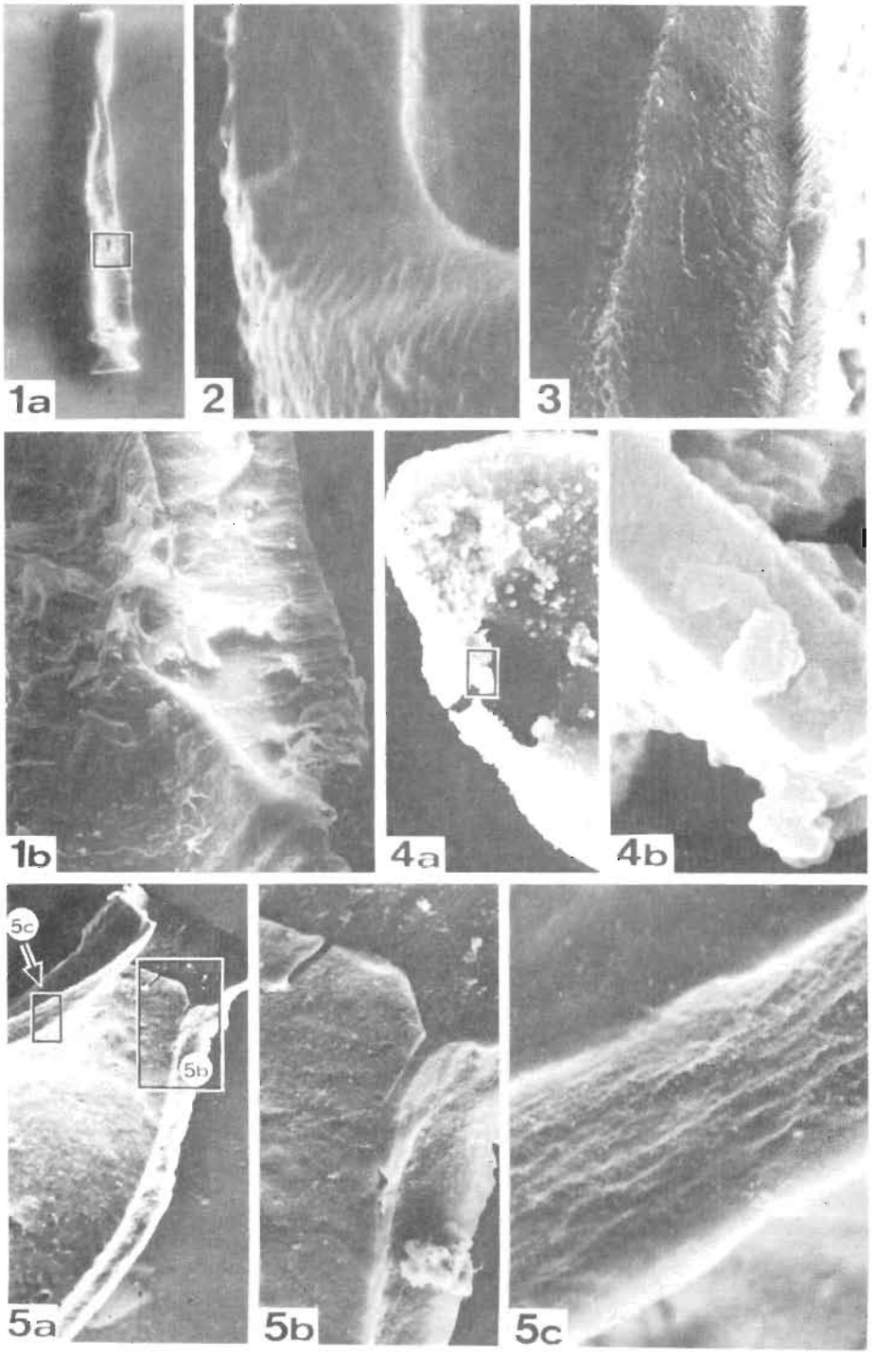
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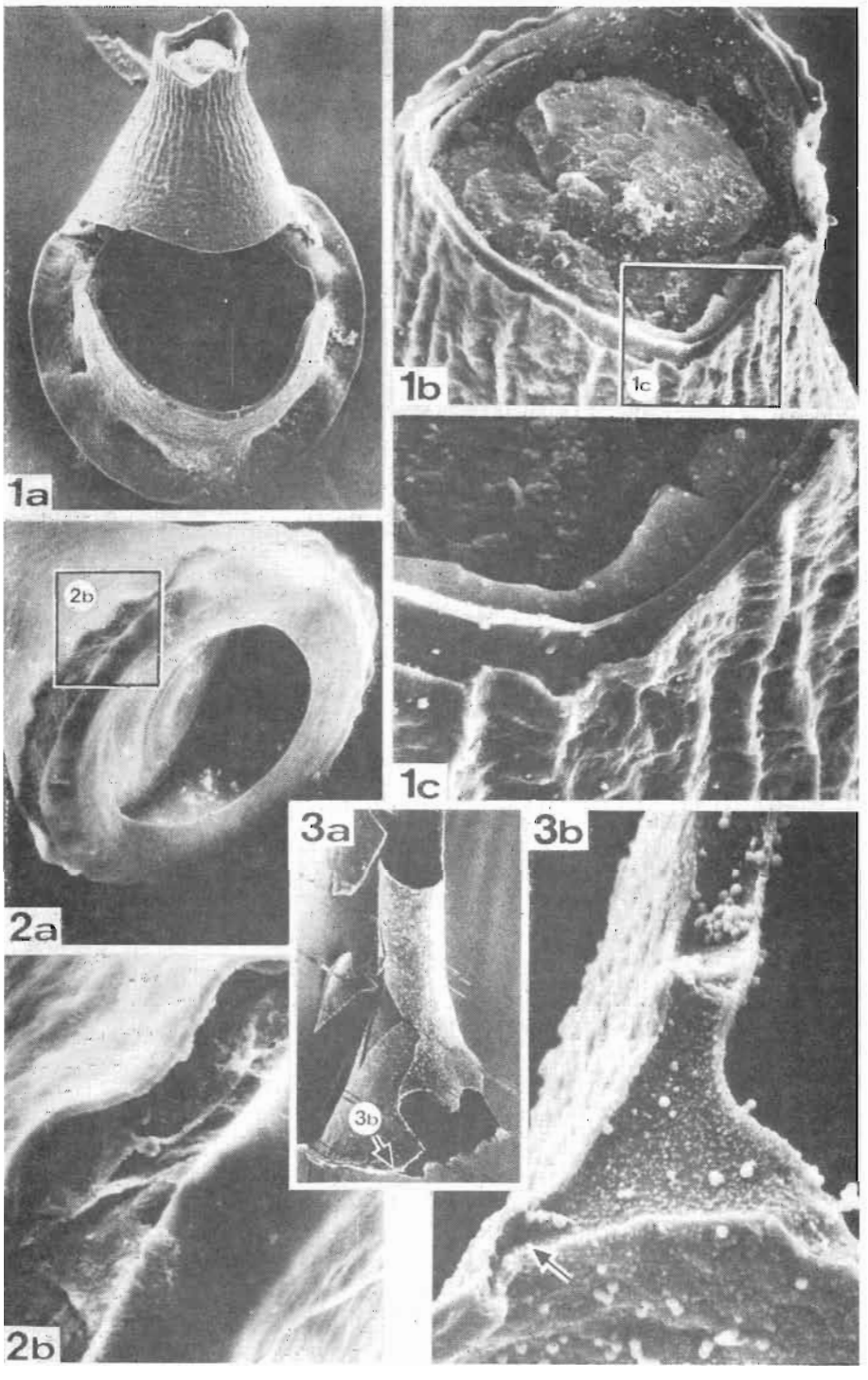
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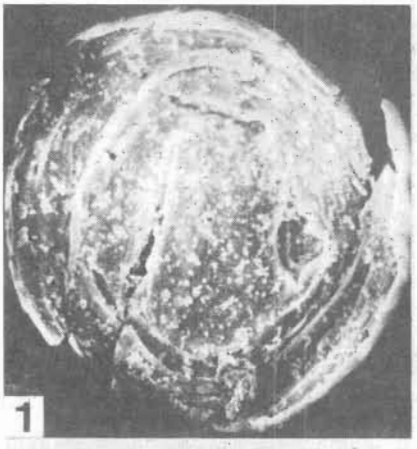
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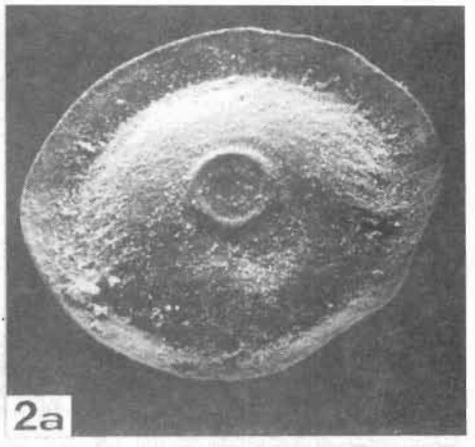
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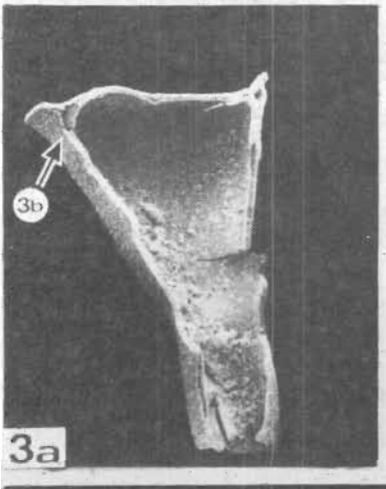
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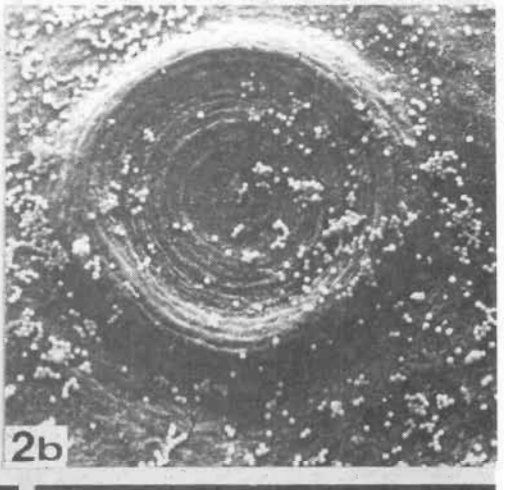
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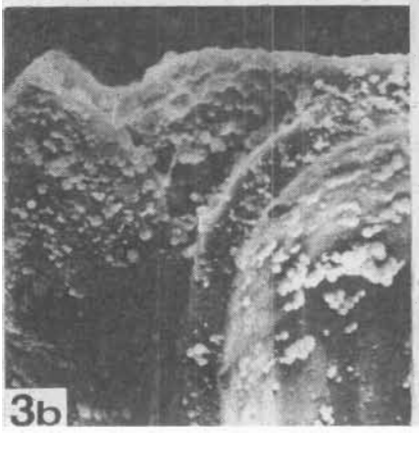
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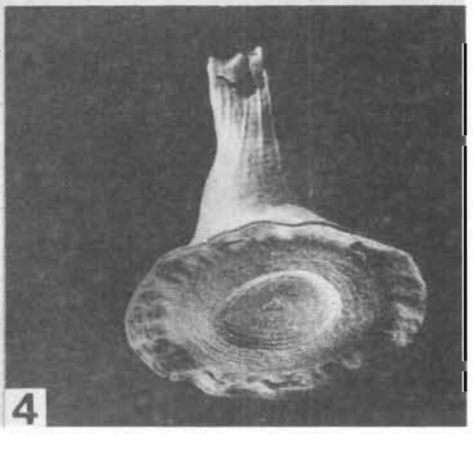
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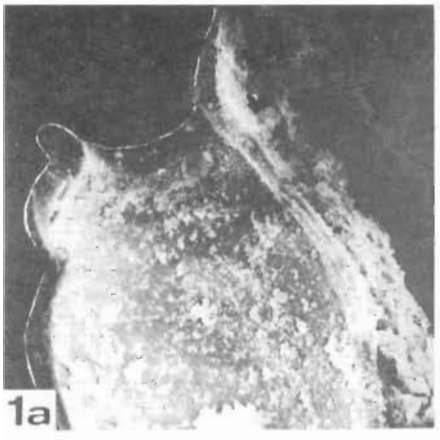
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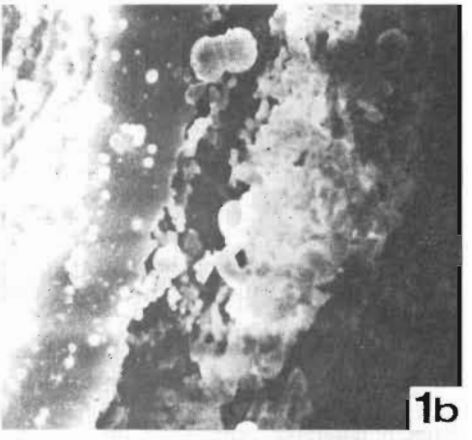
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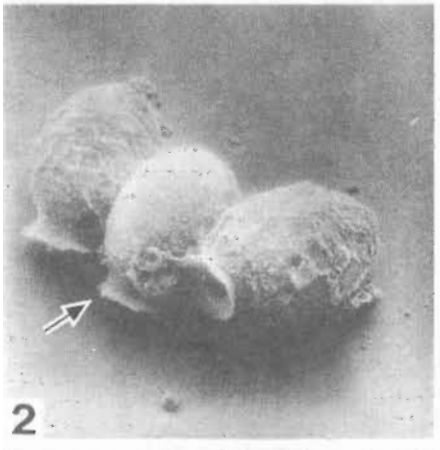
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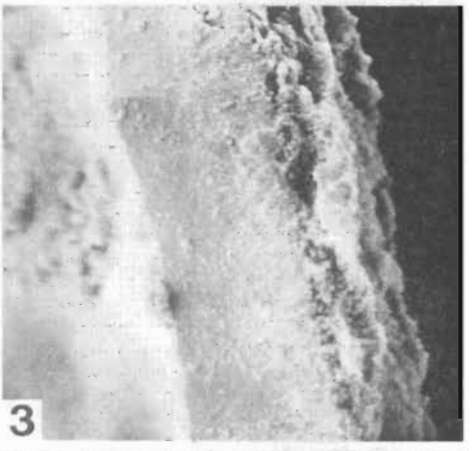
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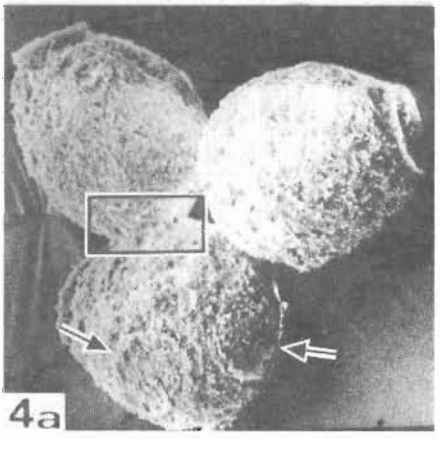
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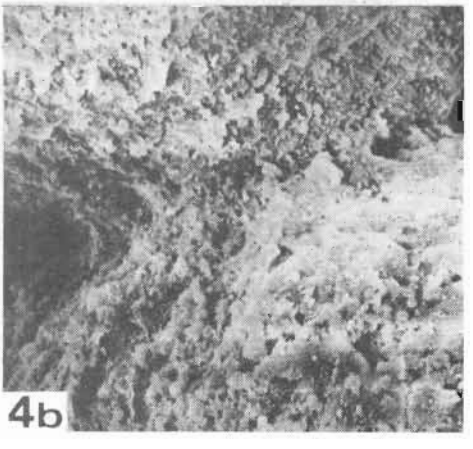
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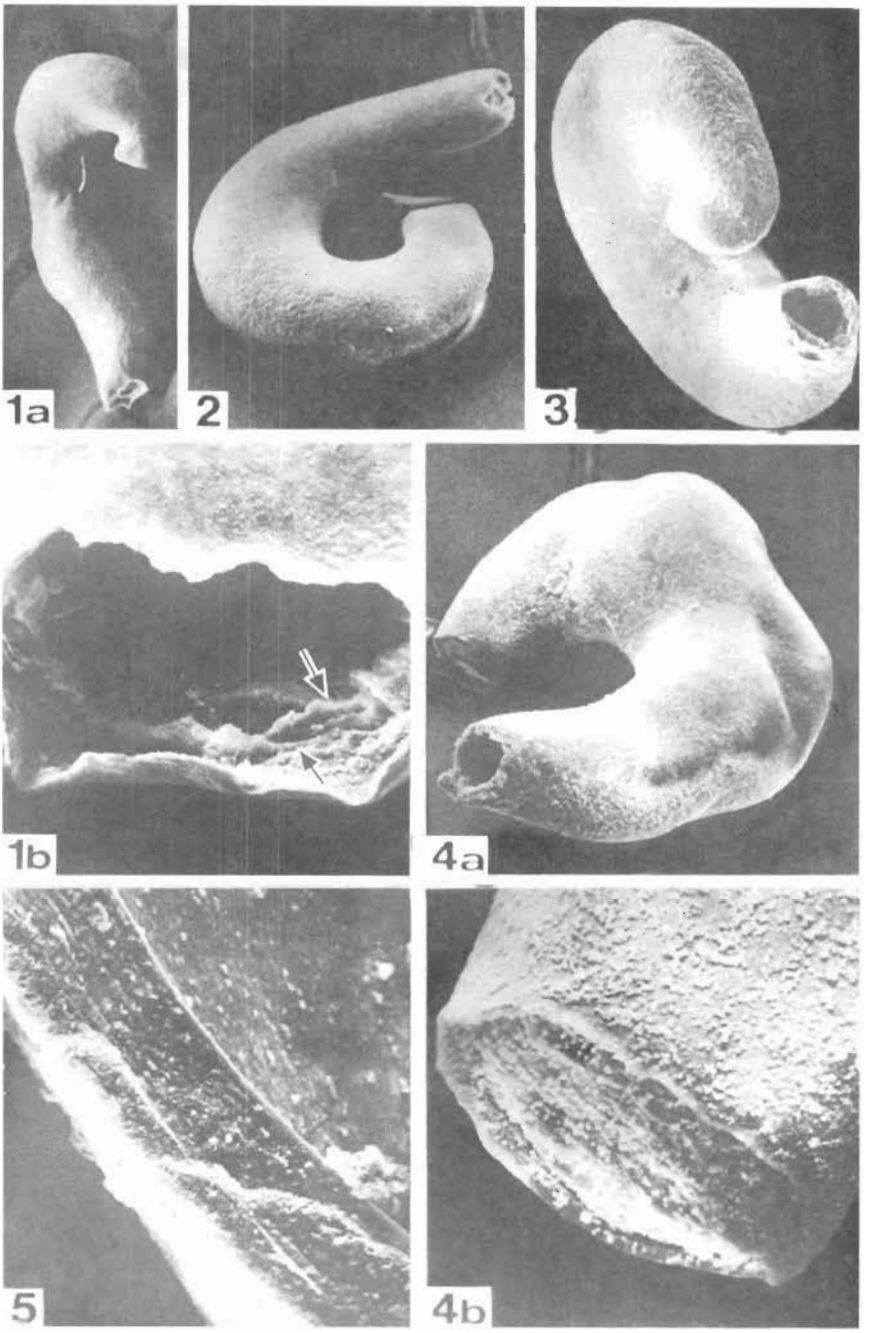
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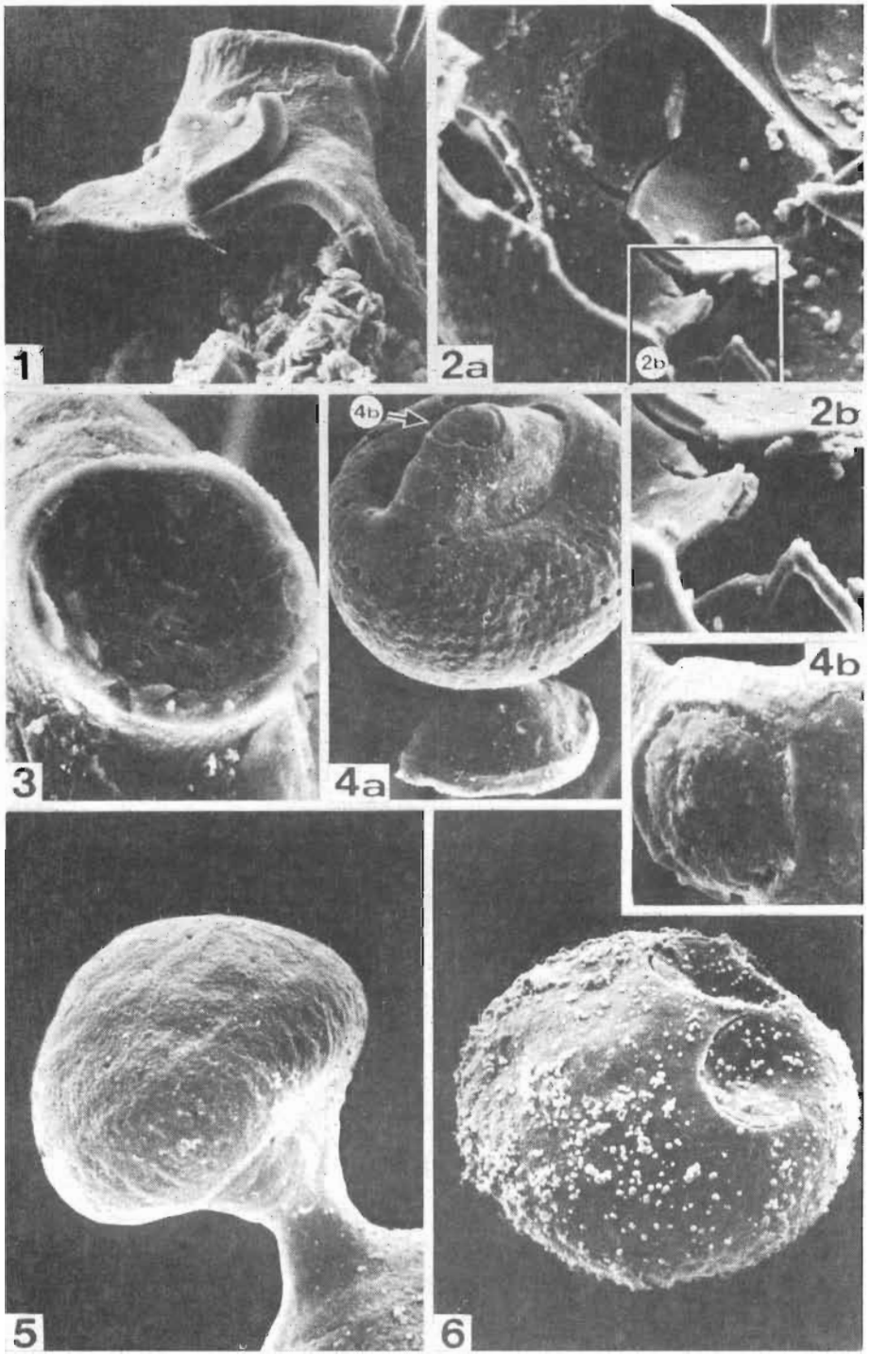
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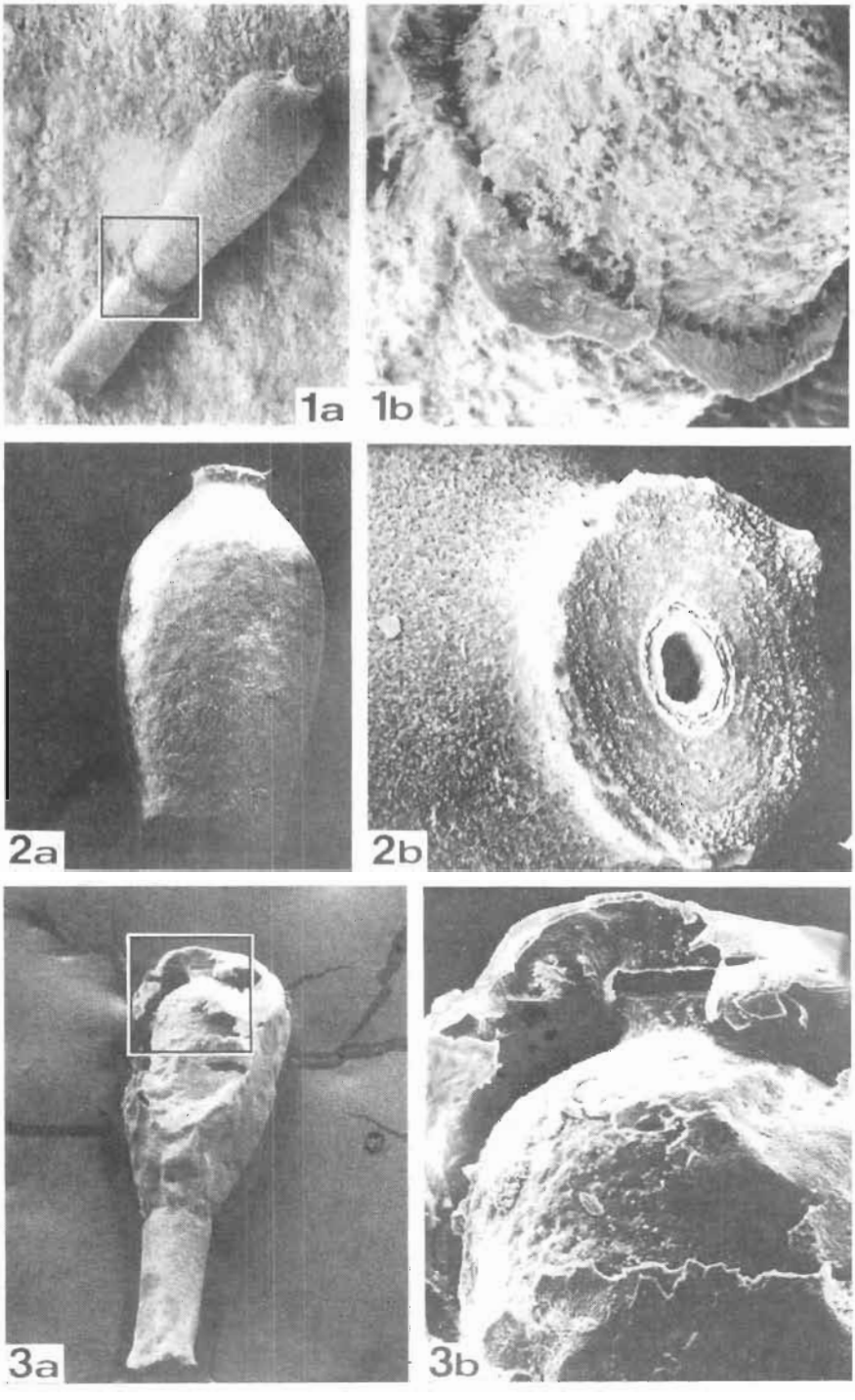
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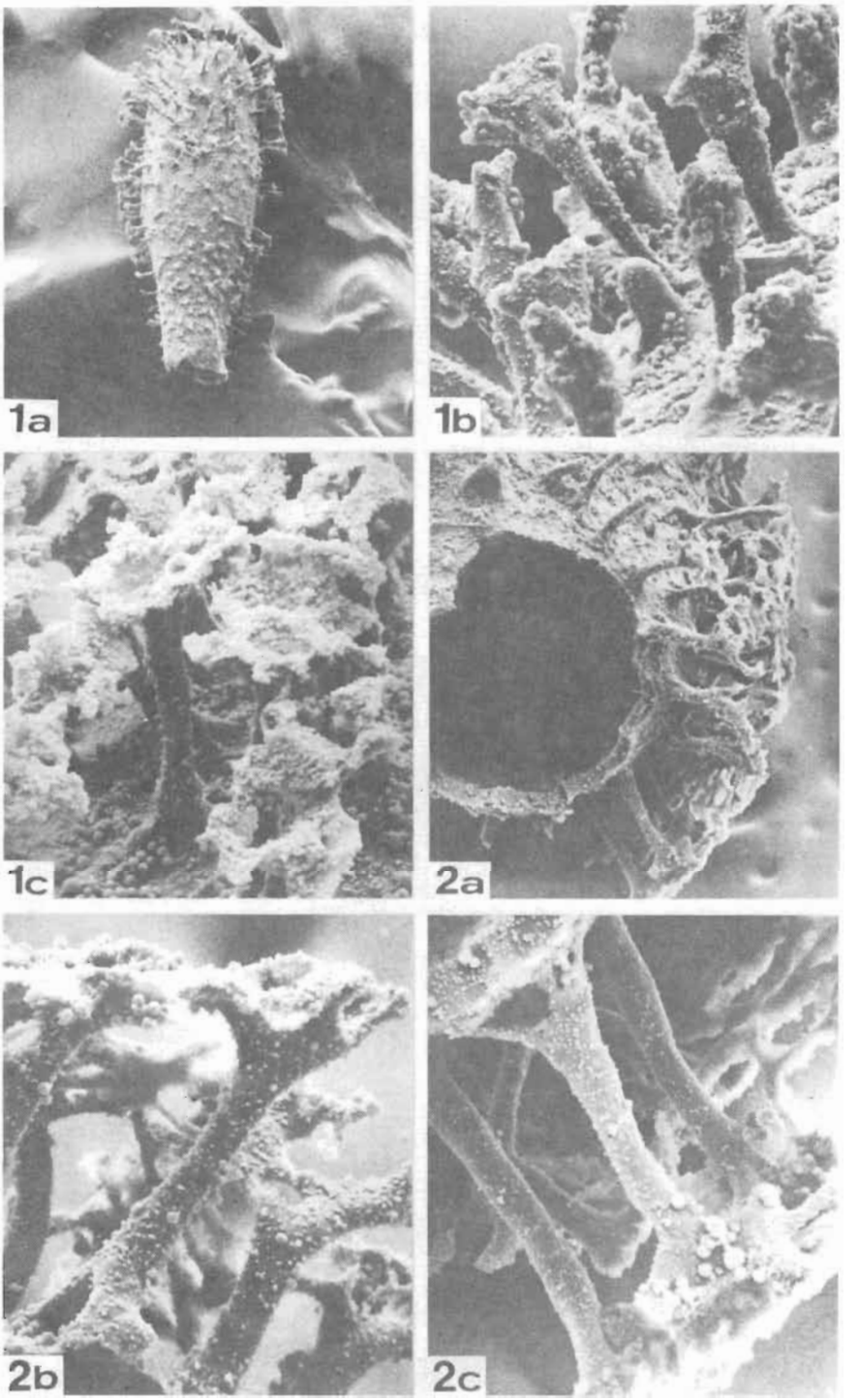
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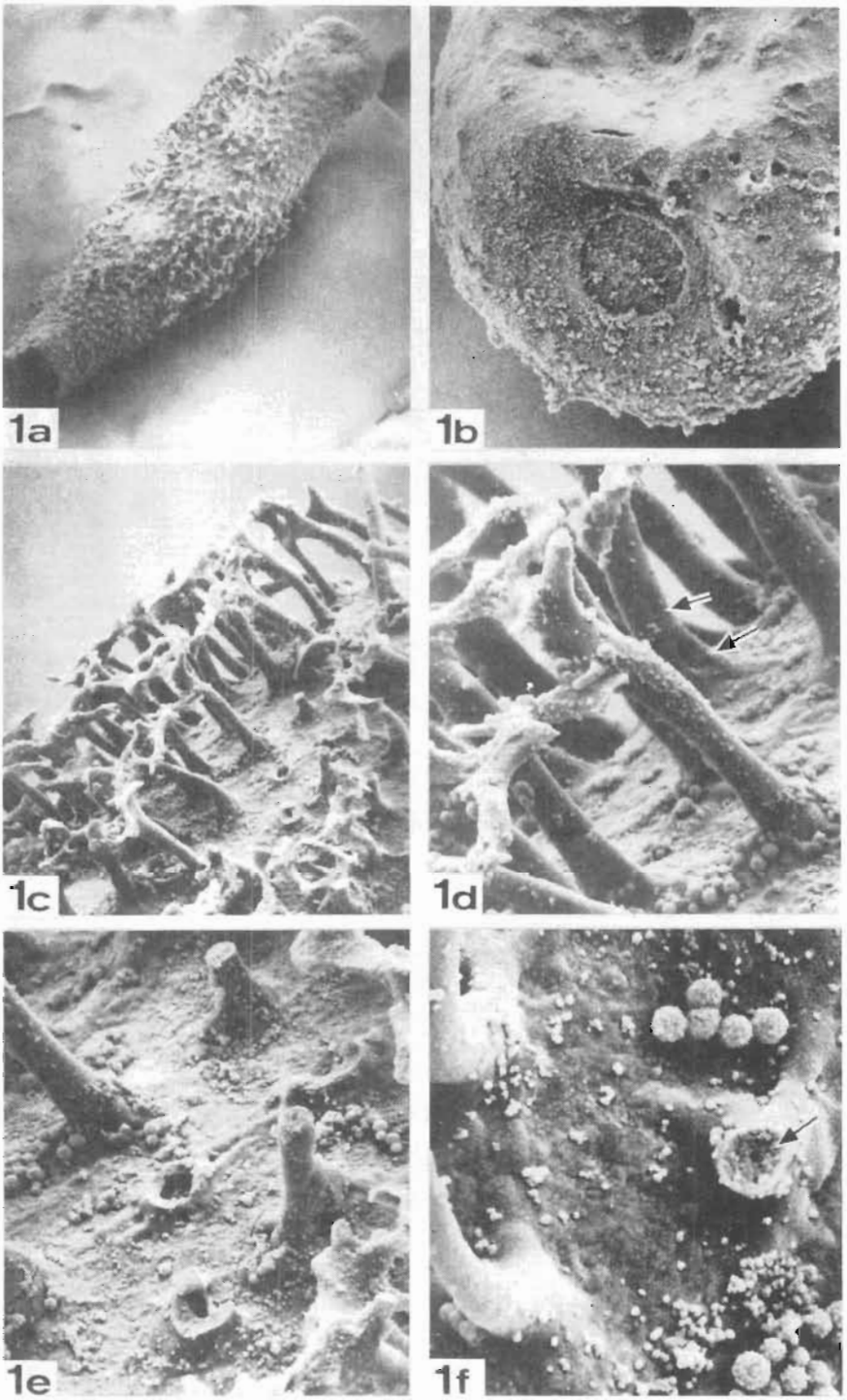
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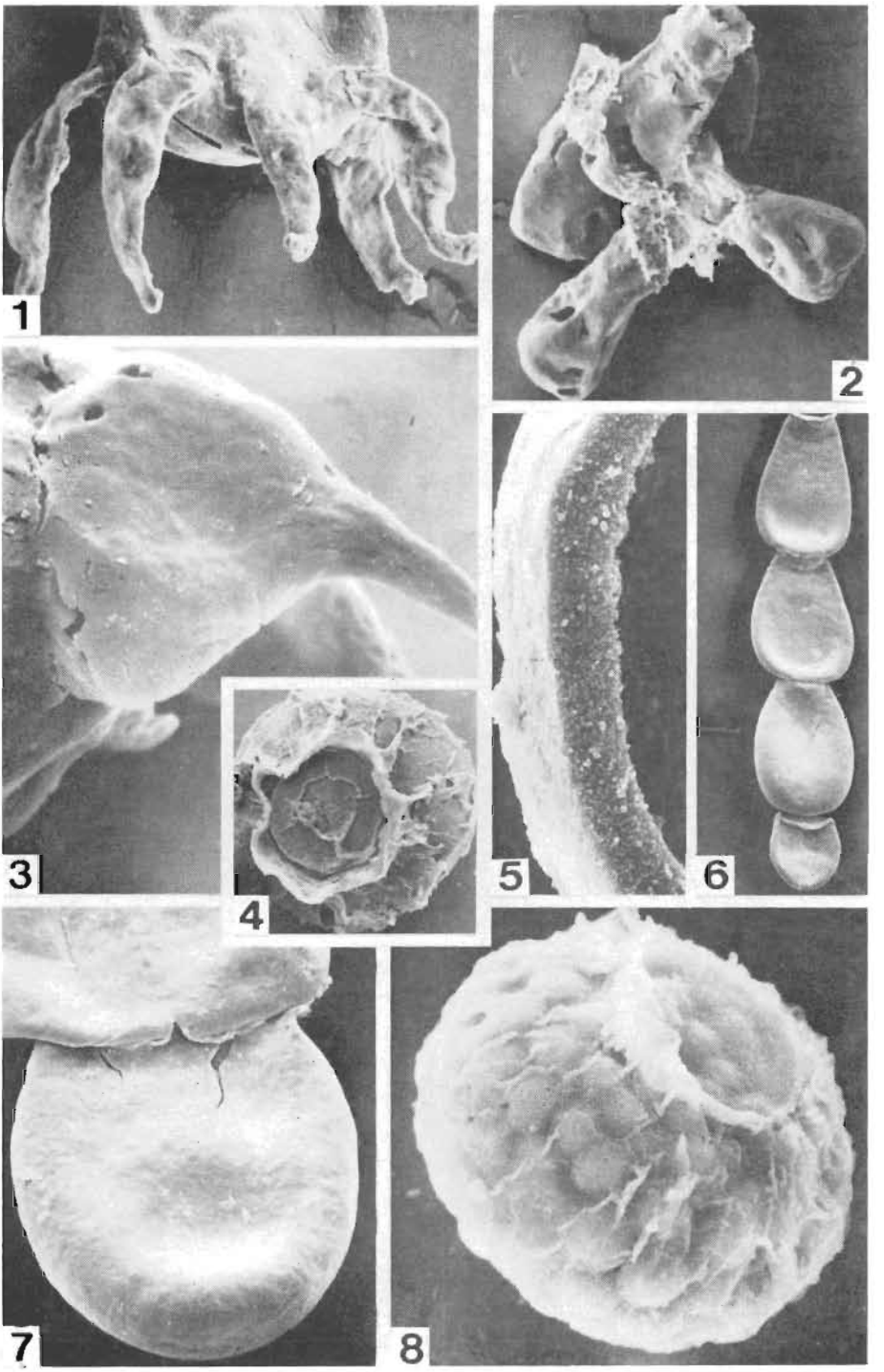
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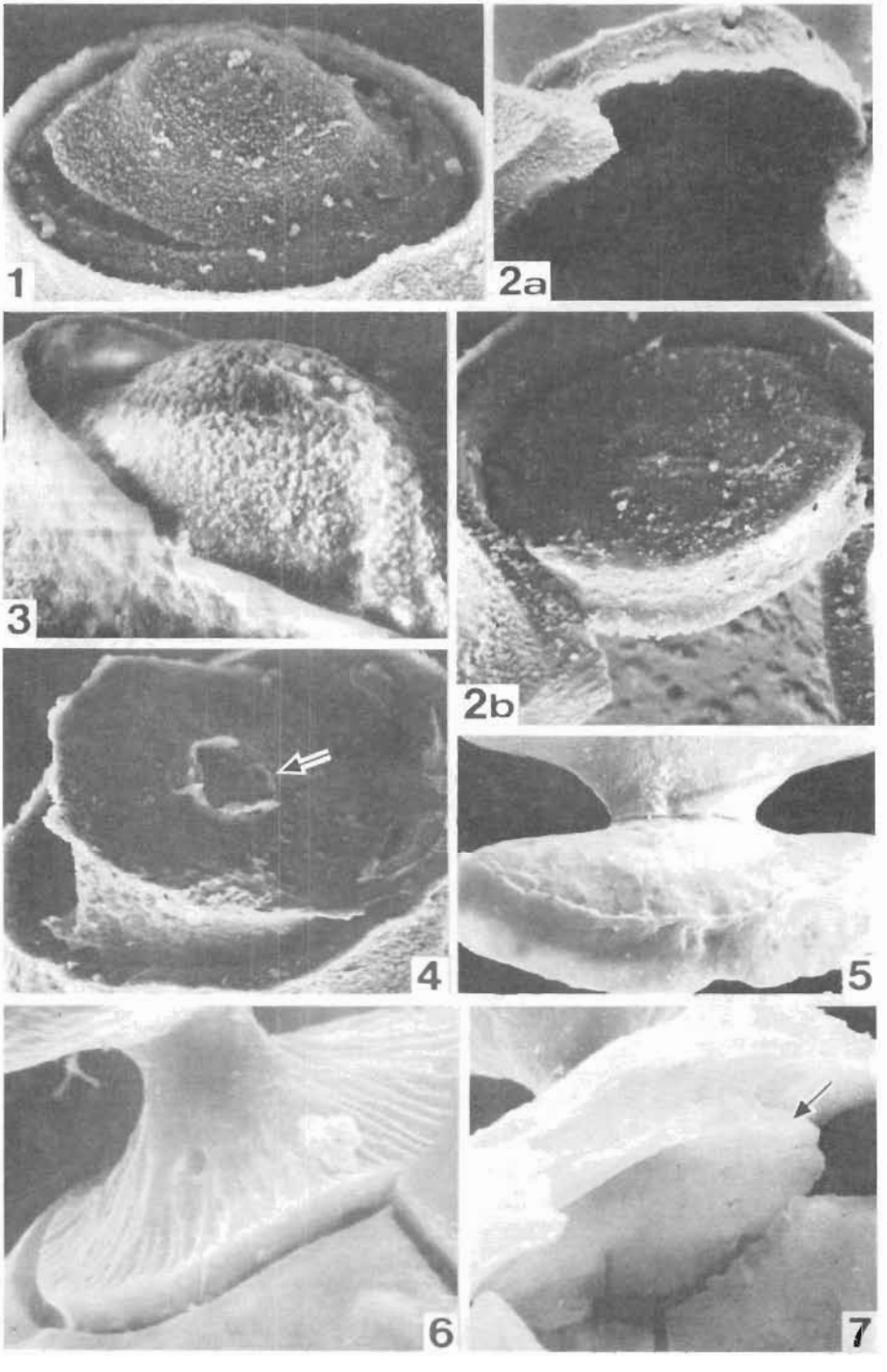
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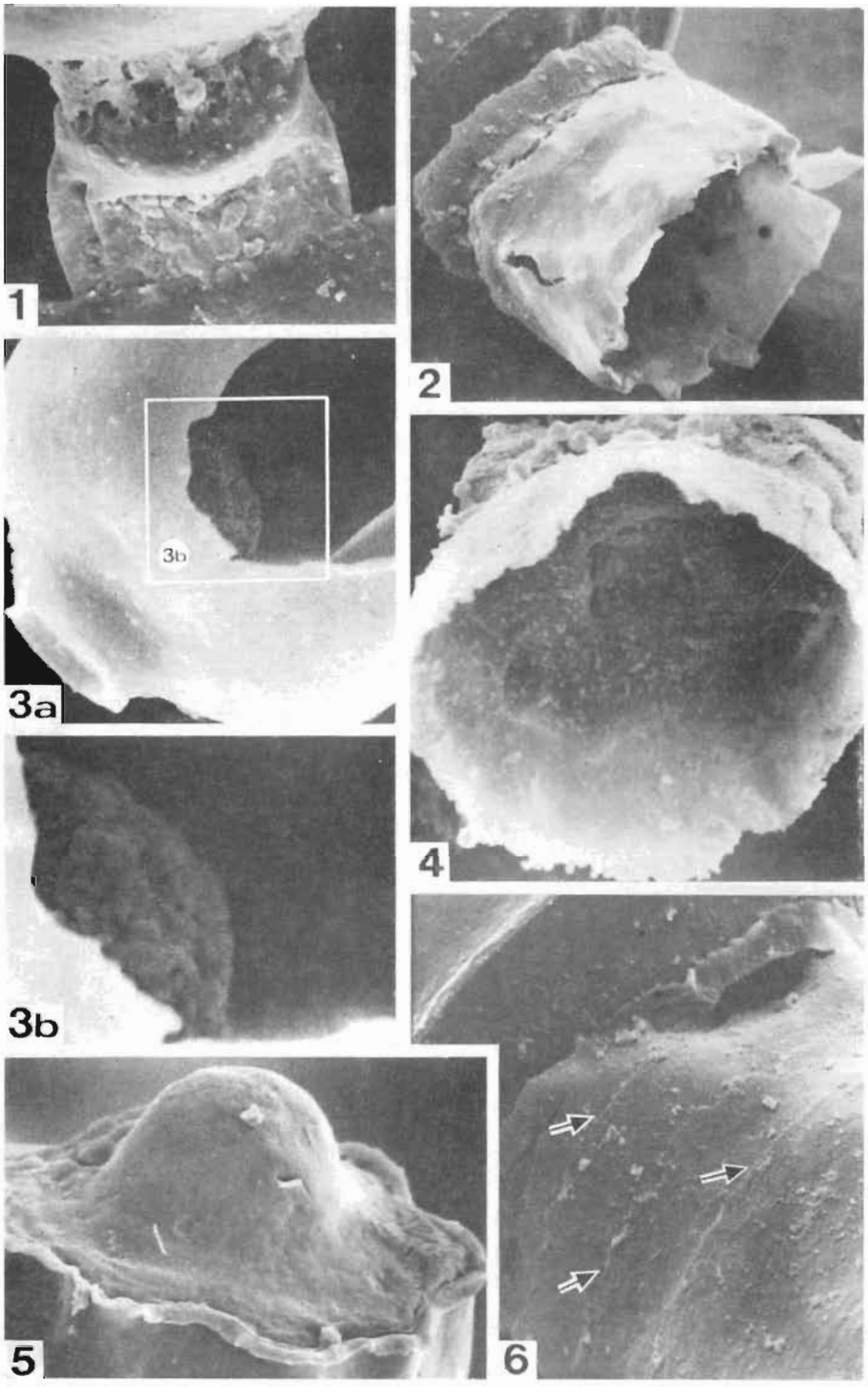
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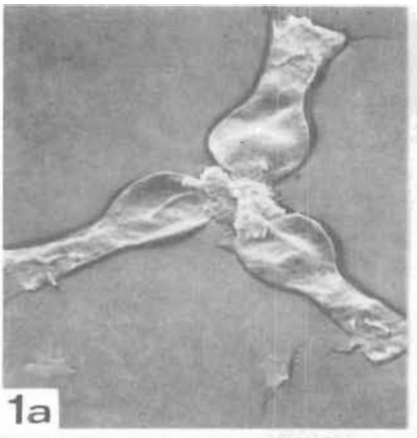
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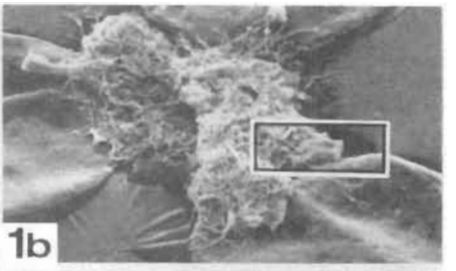
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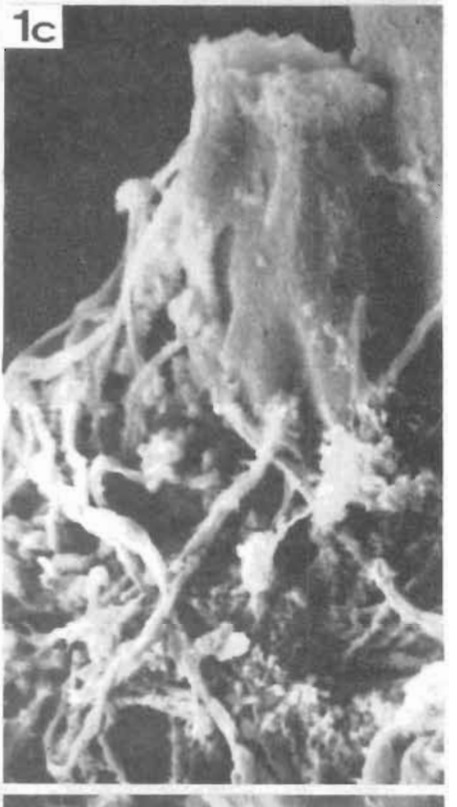
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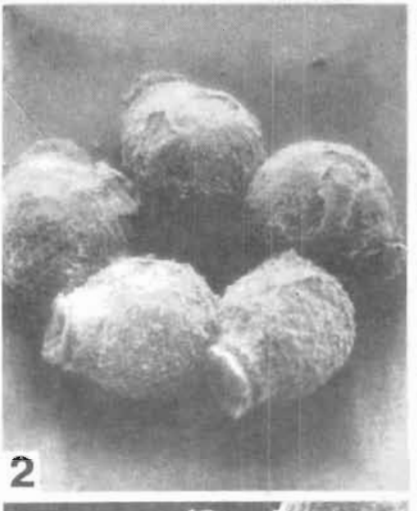
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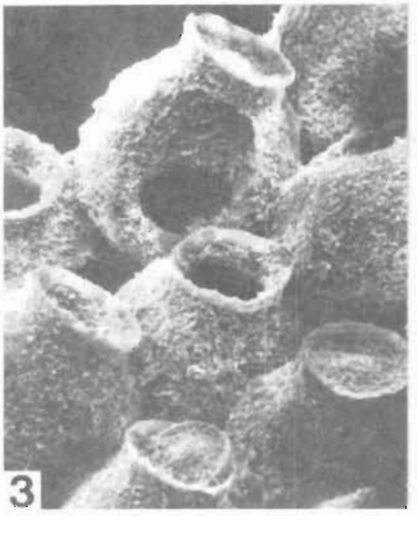
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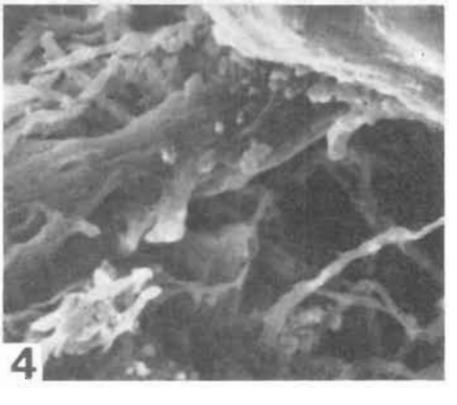
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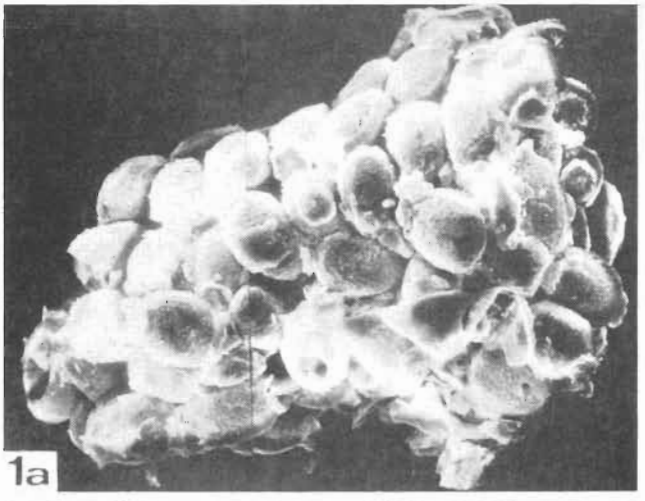
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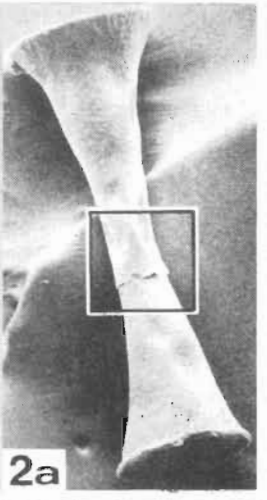
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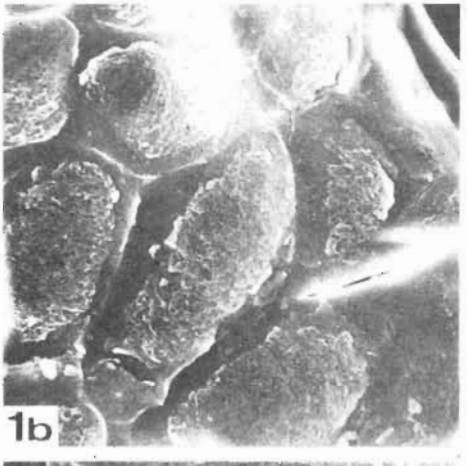
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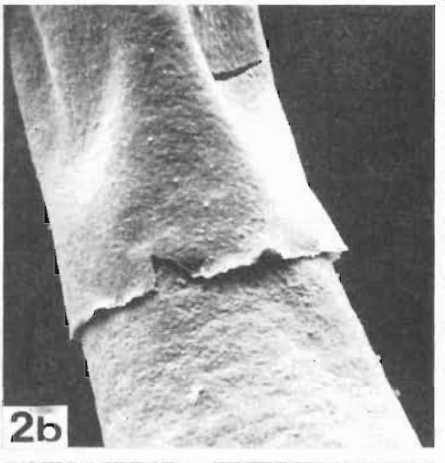
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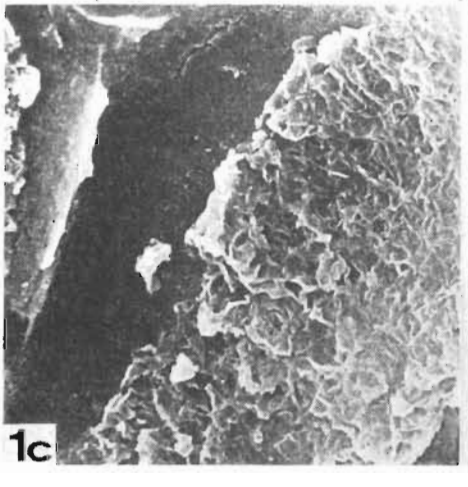
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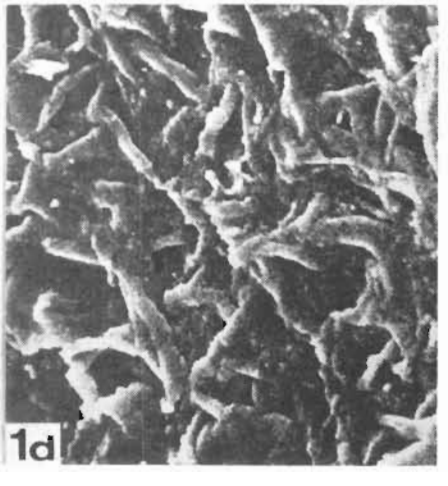
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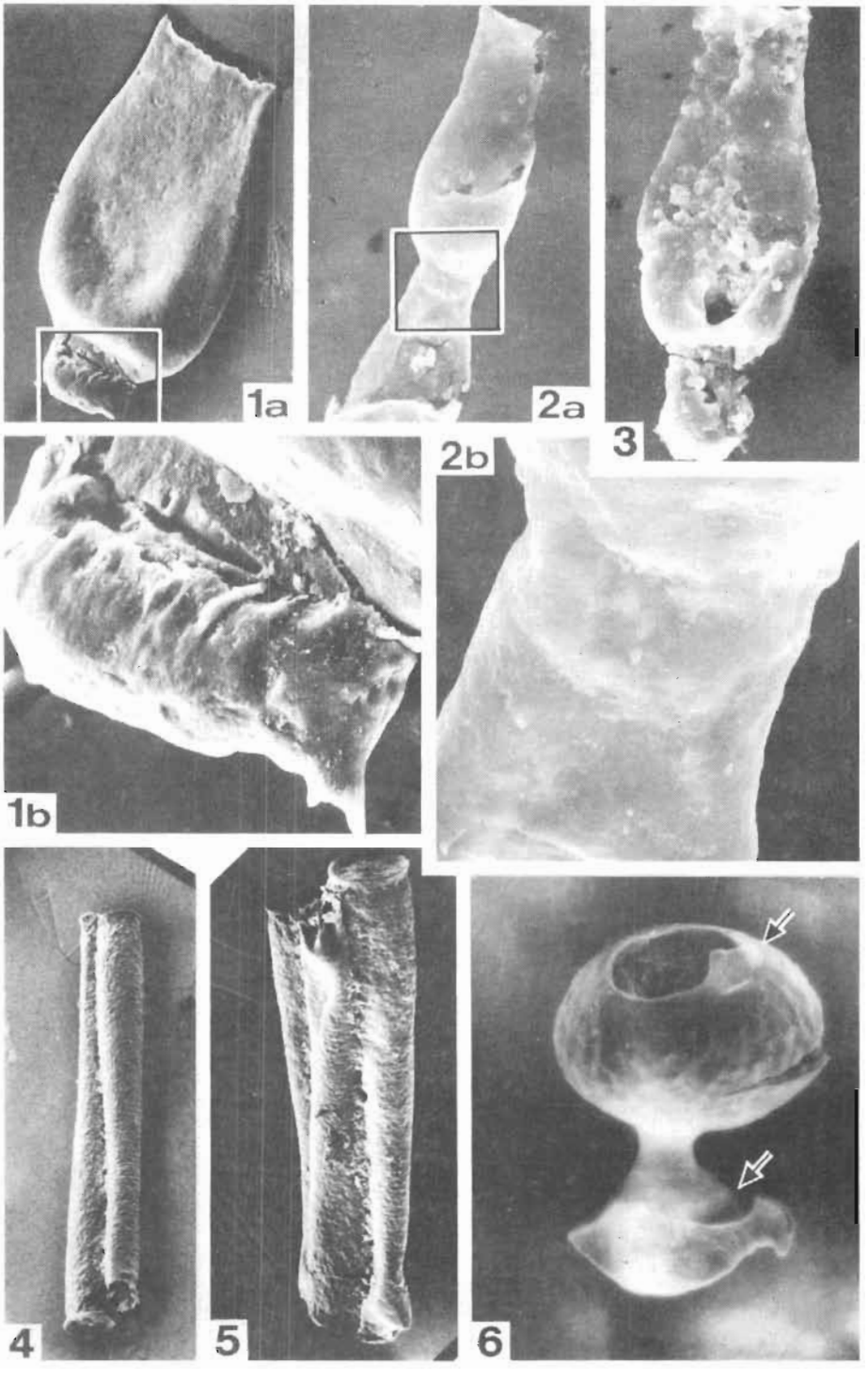
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