THE STRUCTURE AND ARRANGEMENT OF ECHINOID TUBERCLES

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[Plates 1–22]

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Tubercles and spines of 33 species of extant irregular echinoids were studied to provide data for interpreting tubercle structure and arrangement in fossil echinoids. Tubercle morphology is analysed functionally. It is possible to infer much about the posture, movement and function of the associated spine from tubercle morphology. The development and direction of areole enlargement and the structure of the platform are the most important features in this respect. Surface stereom porosity is used to differentiate tubercles and miliaries, which bear either spines or pedicellariae, from granules, which have no such appendages.

Tubercles of regular echinoids are usually radially symmetrical and can be broadly separated into fixed-pivot and sliding-pivot systems. In irregular echinoids, spines are usually modified for a particular function and tubercle morphology is correspondingly varied. The power stroke of the oral spines is radial in pygasteroids and holectypoids, whereas, in clypeasteroids and cassiduloids, it is posterior. This is reflected in their different burial and locomotory behaviour. Oral spine and tubercle arrangement in *Cassidulus* resembles that found in spatangoids and this again is reflected in its behaviour. Spine and tubercle differentiation becomes quite pronounced in certain clypeasteroids. It is argued that lunules and notches are modifications which allow sand dollars to feed on the organic-rich surface layer of sediment while remaining infaunal.

Tubercle and spine diversity is most pronounced in the spatangoids and is described in detail for *Echinocardium*. Each group of spines with a particular function is associated with morphologically distinct tubercles. Tufts of spines are readily recognizable from the tubercle arrangement. The considerable variation in the arrangement of spines and tubercles within the anterior ambulacrum is thought to reflect the varying emphasis placed on adoral transportation of sediment.

Fasciole arrangement shows no correlation with depth of burial or grain size of the substratum. Aboral tubercle density is correlated with sediment grain size. To maintain a water-filled space between the tip of the spines and the test surface, echinoids increase spine density and develop a uniform covering of spines with either distally swollen or spatulate tips. In spatangoids, a more effective coverage is achieved by development of curved or oblique aboral spines, and the aboral mucous coat prevents fine particles from falling between spines and clogging the burrow.

The structure and arrangement of tubercles can be extremely useful in palaeobiological studies.

I. General introduction

All Recent echinoids possess calcareous spines which may be employed in locomotion, defence, protection against sediment abrasion, excavating, feeding, burrowing and funnel building. Spines articulate with tubercles that reflect in their structure the form and function of the spine supported. In irregular echinoids, and especially in spatangoids, spine diversity is often pronounced. Unfortunately, fossil echinoids are rarely preserved with their spines in position and, even then, such preservation can provide little information on spine posture and movement prior to fossilization. Valuable data, otherwise lost to the palaeontologist, can, however, be recovered from studying the microarchitecture of the tubercles. In this way, it is relatively easy to determine the posture and movement of the associated spine and to identify its probable shape and function. A great deal can be learnt about the life style of a species by analysis of the variation in tubercle morphology across the test.

Surprisingly little is known about the details and variety of structure of echinoid tubercles. Although the variation in structure and function of spatangoid spines has been clearly demonstrated by Nichols (1959), Chesher (1963) and Buchanan (1966), there is no comparable description of the concomitant variation of tubercles. Only Hoffman (1914) has attempted to correlate spine function with tubercle construction in both Recent and fossil echinoids. The lack of information concerning the fine structure of tubercles has obscured the importance of tubercle morphology in palaeobiological studies.

Methods and materials

The tubercles and spines of a large number of regular and irregular echinoids were examined, both at the light microscope level and with a scanning electron microscope. Most emphasis was given to Recent irregular echinoids, and table 1 lists those studied in detail. In most instances, the histology of the associated soft tissue was also examined by means of the technique outlined by Smith (1978*b*).

TABLE 1. SPECIES OF IRREGULAR ECHINOID IN WHICH TUBERCLE STRUCTURE AND ARRANGEMENT WERE EXAMINED

PYGASTEROIDA
  Plesiechinus ornatus (Buckman) [Jurassic]

HOLECTYPOIDA
  Conulus albogalerus Klein [Cretaceous]
  Echinoneus cyclostomus Clark
  Holectypus depressus (Leske) [Jurassic]

CASSIDULOIDA
  Apatopygus recens (Milne-Edwards)
  Cassidulus cariboearum Lamarck
  Clypeus ploti Klein [Jurassic]
  Conolampas sigsbei Agassiz
  Echinolampas crassa (Bell)
  Galeropygus agariciformis (Forbes) [Jurassic]
  Nucleolites scutatus Lamarck [Jurassic]

CLYPEASTEROIDA
  Clypeaster rarispina de Meijere
  C. rosaceus (Linnaeus)
  Dendraster excentricus (Eschscholtz)
  Echinarachnius parma (Lamarck)
  Echinocyamus pusillus (Müller)
  Echinodiscus bisperforatus (Leske)
  Encope michelini Agassiz
  Fellaster zelandiae (Gray)
  Jacksonaster sp.
  Leodia sexiesperforatus (Leske)
  Mellita quinquiesperforata (Leske)

HOLASTEROIDA
  Infulaster excentricus (Woodward)[Cretaceous]
  Pourtalesia miranda Agassiz

SPATANGOIDA
  Brissopsis atlantica Mortensen
  B. lyrifera (Forbes)
  Brissus latecarinatus (Leske)
  B. unicolor (Leske)
  Echinocardium cordatum (Pennant)
  E. pennatifidum Norman
  Maretia planulata (Lamarck)
  Metalia spatangus (Linnaeus)
  M. sternalis (Lamarck)
  Micraster coranguinum (Leske) [Cretaceous]
  M. cortestudinarium (Goldfuss) [Cretaceous]
  Moira atropos (Lamarck)
  Paramaretia peloria (Clark)
  Paraster doederleini Chesher
  Spatangus purpureus Müller
  S. raschi Lovén

II. TUBERCLE MICROARCHITECTURE AND ITS INTERPRETATION

1. *Tubercle structure*

Much of the morphology of tubercles has been summarized by Melville & Durham (1966) and is illustrated in figure 1. There is a central mamelon which may have a large central perforation or may be imperforate. The mamelon surmounts the boss, which in most species is composed of galleried stereom. At the summit of the boss and surrounding the mamelon there may be a platform. The platform can be smooth (figure 2), crenulate (figure 4), or may have a parapet (figure 3). A rim around only part of the platform is termed a ridge (figure 5). Platforms may have only one of these features or may have any combination (figure 6). The areole, which is composed of a fine labyrinthic stereom, surrounds the boss, from which it is often separated by a ring of coarser stereom.

The spine attaches to its tubercle by an inner ring of collagenous catch apparatus fibres and an outer ring of smooth muscle fibres. Spine attachment has been described by Kawaguti & Kamishima (1965) and Takahashi (1967). The muscle fibre layer is overlain by a thin layer of nerve fibres, which swell to form a nerve ring near the plate surface (figure 1). A thin, ciliated epithelial layer forms the outer surface. Catch apparatus fibres insert into the boss and are 'sewn' around the trabeculae. Muscle fibres attach onto the stereom of the areole via a connective tissue ligament. A fluid-filled space separates the muscle fibres from the catch apparatus. Perforated tubercles bear spines with a corresponding perforation in their base (figure 10). The perforation houses connective tissue fibres, histologically indistinguishable from catch apparatus fibres.

2. *Functional interpretation of tubercle microarchitecture*

Much of the variation in tubercle morphology can be explained in mechanical terms by considering the spine–muscle system as a simple lever system. The mechanical advantage of the spine–muscle system, which is the ratio of the resultant force to the applied force, approximates to the moment arm of the muscle (M) divided by the length of the spine (L) (figure 7). Where the mechanical advantage of the system is small, as, for instance, when the spine is long and slender, movement at the spine tip will be rapid but will have little force behind it. Increasing the mechanical advantage, either by reducing the length of the spine or by increasing the moment arm of the muscle, results in a slower but stronger pull from the same applied force.

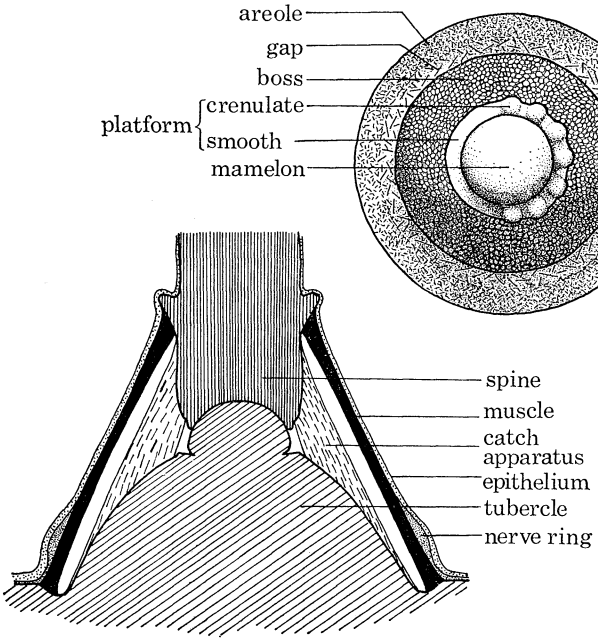

Figure 1. Tubercle structure and associated soft tissue. The lower diagram shows a longitudinal section through a tubercle and the base of its spine.

(*a*) *The areole*

A spine with no preferred directional pull is associated with a radially symmetrical areole. Where the spine has to work against the substratum in a preferred direction, the power of the stroke is enhanced in that direction. This is achieved in two ways. Firstly, there is an increase in the number of muscle fibres in the direction in which the spine works, and, secondly, the muscle fibres are moved further from the mamelon, thus increasing the moment arm (figure 8). Muscle displacement is achieved by enlarging the gap separating the areole and boss and by extending the milled ring on the spine, making it noticeably oblique. These changes increase the power of the spine stroke in the direction in which areole enlargement and displacement has occurred.

In regular echinoids, the areole is least well developed in certain rock-dwelling echinoids, such as *Colobocentrotus atratus* (Linnaeus) or *Stomopneustes variolaris* (Lamarck), in which the tube feet are the main organs of locomotion. Sediment-dwelling echinoids that move primarily by means of their spines, notably cidaroids, echinothurioids, diadematoids and salenioids, typically have well developed areoles.

(*b*) *The boss*

In some tubercles the boss is slightly enlarged to one side of the mamelon (figure 84). This occurs where the associated spine is strongly curved or is held oblique to the test and, as would be expected, catch apparatus fibres are increased on the side opposite to the direction in which the spine lies.

Oral tubercles of the lateral interambulacra of *Maretia planulata* (Lamarck) are unusual in

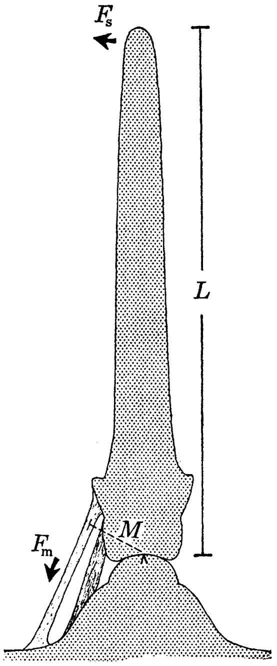

FIGURE 7. Mechanical advantage of the spine muscle system. F_m = applied force, F_s = resultant force, L = length of spine, M = moment arm. $F_s/F_m = L/M$. Seen in longitudinal section.

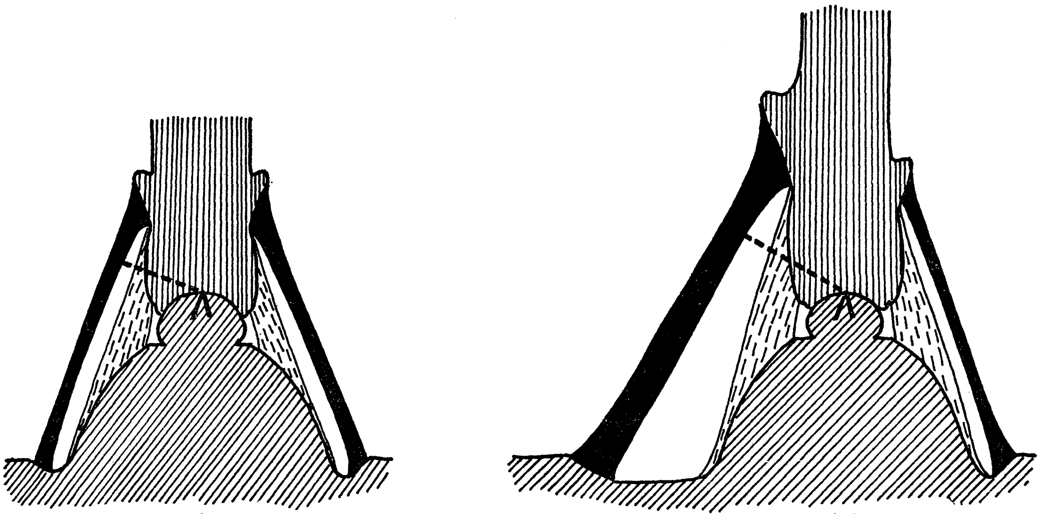

FIGURE 8. Displacement and enlargement of the spine muscle in (*b*) strengthens the power stroke in that direction.

that the boss is incomplete and is interrupted by a depressed region of coarse labyrinthic stereom (figures 13 and 14). No catch apparatus fibres insert into the stereom of this depression. A corresponding break occurs in the platform. The functional significance of this feature is not clear. Possibly, catch fibres are redundant where the spine cannot be clamped down upon the platform.

(*c*) *The platform*

(i) *Parapet.* A parapet is found in oral tubercles of *Phormosoma placenta* (Thomson) and *Calveriosoma hystrix* (Thomson) and in the large, aboral interambulacral tubercles of *Paramaretia peloria* (Clark) (figure 3). The parapet is thought to strengthen the rim and to provide support for the relatively large and heavy spine. The fact that the parapet is composed of smooth, imperforate stereom, like the mamelon, suggests that the spine base has a sliding contact with the parapet. The parapet is radially symmetrical in all three species and the spines are presumably held more or less perpendicular to the test.

(ii) *Ridge.* Only spatangoid tubercles develop a ridge. A ridge is associated with strongly curved spines or spines held obliquely. The ridge is always developed on the side to which the spine is inclined, independent of the direction of areole enlargement. It is composed of smooth, imperforate stereom, and the spine base rests upon this ridge during its recovery stroke, when the spine lies furthest from the perpendicular. The ridge appears to strengthen the platform and to support the spine, acting either as a stop or as a fulcrum. Where the ridge is positioned opposite to the direction of areole enlargement (figure 5), spine movement is restricted mainly to a raising and lowering action. In other instances (figure 6), spines move with an oar-like rotary action.

(iii) *Crenulation.* Radially symmetrical development of crenulation is associated with relatively straight spines held more or less perpendicular to the test, as with anterior scraping spines of *Echinocardium cordatum* (figure 16). In contrast, the lateral sand-moving spines of *E. cordatum* are supported on tubercles where both crenulation and a ridge are developed (figure 6). These spines have a rotary action, being lowered into the sediment, pulled outwards, lifted and recovered. During the recovery stroke, when the spine is held furthest from the perpendicular in order to avoid contact with the sediment, the spine base lies against the ridge, but during the power stroke, when leverage against the substratum is required, indentations on the spine base (figure 10) interlock with the platform crenulation. The cog-like action of crenulation acts to prevent lateral slippage of the spine base, where purchase is required.

Crenulation is not always radially symmetrical. It may be enlarged and displaced to one side of the platform (figure 11), and, in more extreme examples, the enlarged crenulation may be semi-fused, verging towards the development of a ridge (figures 17 and 18). Where such crenulation is found, the accompanying spine is curved or is held oblique, in the direction of enlarged crenulation. In general, the further a spine lies from the perpendicular, the more crenulation is enlarged, displaced and fused in the direction of inclination. A ridge is an extreme case of this trend.

In regular echinoids there is no obvious functional explanation for the presence or absence of crenulation. Although smooth-platformed tubercles are generally found in short-spined species, there are numerous exceptions.

(iv) *Incomplete platform.* Ventro-lateral tubercles of *Maretia planulata* have a most unusual construction, previously noted by Mortensen (1951). In side view, the platform is clearly not horizontal but has a spiral structure, the lowest and broadest part lying posteriorly (figure 12).

The platform is incomplete and the break occurs on the same side of the mamelon as the direction of areole enlargement, separating the narrowest area from the broadest area (figure 14). The associated spines are long and weakly spatulate and are inclined posteriorly. They lie at a shallow angle to the test surface.

No accounts of the behaviour of this urchin have been published and any interpretation of this unusual structure can only be speculative. Presumably, the spines excavate sediment from beneath the animal, with an oar-like action, judging from the direction of areole enlargement. Interestingly, the ventro-lateral tubercles in most spatangoids show some degree of asymmetry, though never to the extent seen in *Maretia* (figure 15). The pronounced asymmetry in tubercles of *Maretia* may be due to the relatively large size of the associated spines combined with the very small angle at which the spine is held to the test. The tilted platform is almost certainly an adaptation for supporting an oblique spine. The purpose of the break in the platform is uncertain. As it corresponds with the direction of strongest muscle pull, the gap may allow the spine to be pulled flatter against the test than would normally be possible.

(*d*) *The mamelon*

The presence or absence of a central perforation housing a collagenous ligament is the most obvious variable in the construction of the mamelon. Perforated mamelons are best developed in long-spined regular echinoids, in which the spines act as the primary deterrent to predators. The presence of a central ligament presumably increases the rigidity of the spine and helps to prevent its dislocation from the mamelon. Takahashi (1967) has reported that *Anthocidaris* can dislocate its spines from their imperforate tubercles to flatten them close to the test. Similar flattening has been observed in *Psammechinus miliaris* (Gmelin). The ability to flatten their spines must be advantageous to coral- or rock-dwelling echinoids, which seek protection from predators and excessive turbulence beneath boulders or within nooks and crannies. Nearly all such echinoids possess imperforate tubercles. A number of short-spined echinoids, found largely on sedimentary substrata, also have imperforate tubercles and commonly show a covering reaction.

In most irregular echinoids, the mamelon is perforated. They have more active spines than do regulars, which continually have to work against the substratum. The central ligament must help to prevent dislocation of the spine, which often has to work in an oblique position. Of those examined, only *Echinoneus cyclostomus* has imperforate mamelons and also lacks crenulation. Although this urchin commonly lives buried within coarse sands, it has been reported in crevices (Clark 1950) and on hard substrates beneath loose coral blocks (Taylor 1968).

(*e*) *Tubercle shape*

The majority of tubercles project above the plate surface and are more or less horizontal (figure 4), though they may be distorted where the plate is strongly curved as at the ambitus (figure 20).

(i) *Tilted tubercles.* Tubercles of irregular echinoids are often tilted with respect to the plate surface. In some, only the boss and mamelon are tilted while the areole remains more or less horizontal (figure 19), whereas, in others, the whole tubercle may be tilted (figure 39). In *Moira atropos* (Lamarck) and *Fellaster zelandiae* (Gray) the plate surface is weakly ridged and tubercles are linearly aranged along one of the sloping sides. These are all adaptations for supporting an oblique spine. Rather than having the spine base affixed obliquely to the tubercle, the tubercle is tilted to allow the spine to attach squarely onto the mamelon. Platform crenulation is usually more or less radially symmetrical.

(ii) *Sunken tubercles.* Not all tubercles lie above the plate surface. Tubercles of many irregular echinoids, such as *Echinoneus* or *Cassidulus,* possess a raised rim for muscle attachment (figure 51). In more extreme examples, the tubercle may be so deeply sunken that only the mamelon protrudes above the plate surface (figures 21 and 22). Sunken tubercles are best developed aborally. The associated spines may be closely packed and protective, as in *Clypeaster rosaceus* (Linnaeus) or *Echinolampas crassa* (Bell), or large, aboral and defensive, as in *Paramaretia peloria* (Clark) or *Lovenia elongata* (Gray).

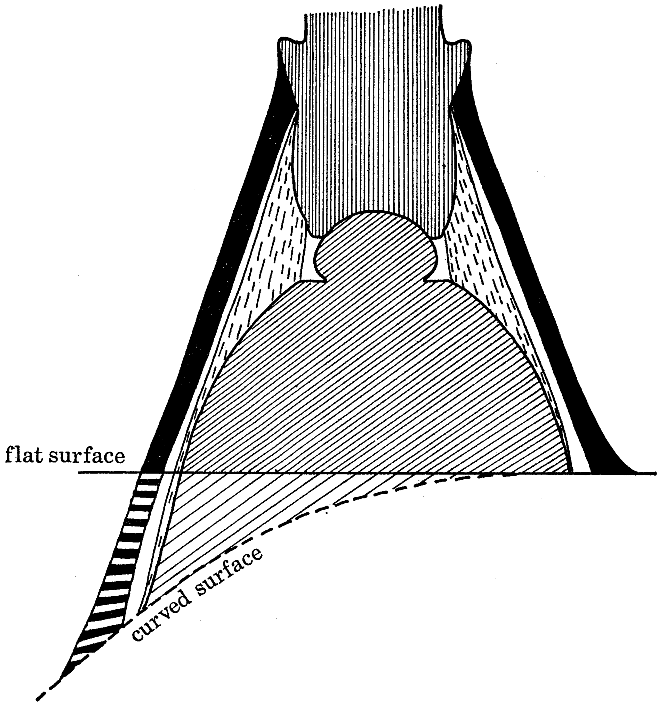

FIGURE 20. Distortion of a radially symmetrical tubercle on a curved surface, seen in longitudinal section.

In cross section (figure 24), the advantages of a sunken tubercle are obvious. Because muscle fibres attach just below the rim, the surface area of the tubercle is greatly reduced, while the mechanical advantage of the system is maintained. If the muscle were to maintain the same mechanical advantage, were the tubercle not sunken, the surface area of the tubercle would be markedly increased (dashed lines). By sinking tubercles, an increased tubercle and spine density can be achieved without loss of mechanical advantage and without the loss of interspersed miliary spines, pedicellariae and ciliated epithelium. Large aboral tubercles that bear stout defensive spines in the spatangoids, are sunken to reduce the surface area taken up by spine muscle. In *Clypeaster*, *Conolampas* and *Echinolampas*, the situation is somewhat different. Sunken tubercles are not produced by resorption, as they are in spatangoids (Smith, in preparation), but are the result of active outward growth of the outer plate layer. The marked height of the boss is not required to accommodate catch apparatus fibres, since these penetrate only a short distance into the stereom, but occurs to raise the mamelon above the plate surface, keeping pace with outward plate growth. The zone for muscle fibre attachment progressively shifts outwards to maintain optimum mechanical advantage.

3. *Tubercles, miliaries and granules*

The terminology adopted in this paper is modified from that of Melville & Durham (1966). Tubercles bear spines, miliaries bear either spines or pedicellariae, while granules have no appendages and are covered with integument. In regular echinoids, a primary tubercle is the large, first formed tubercle situated over the growth centre of each plate. Other large tubercles are termed secondary. The minute tubercles, which cover the plate surface and support small slender spines or pedicellariae, are termed miliaries. In irregular echinoids, it is impossible to differentiate between primary and secondary tubercles, and the use of these terms in spatangoids (Fischer 1966) is misleading. Miliaries of regular echinoids lack a distinct areole and have no real platform (figure 2). The miliaries of irregular echinoids are cap-like and may or may not have a distinct areole. Miliaries that bear spines can be distinguished from small tubercles by the absence of a platform and from those bearing pedicellariae by the presence of a mamelon (figure 25). Even the smallest miliaries of the fasciole have a distinct mamelon (figure 26). Miliaries that bear pedicellariae lack both a distinct areole and a differentiated mamelon (figure 27). They are simple cones of labyrinthic stereom, often possessing a denser apex, and range from low profile forms (figure 25) to large, conical forms (figure 42) that, in *Echinus acutus* Lamarck, bear globiferous pedicellariae.

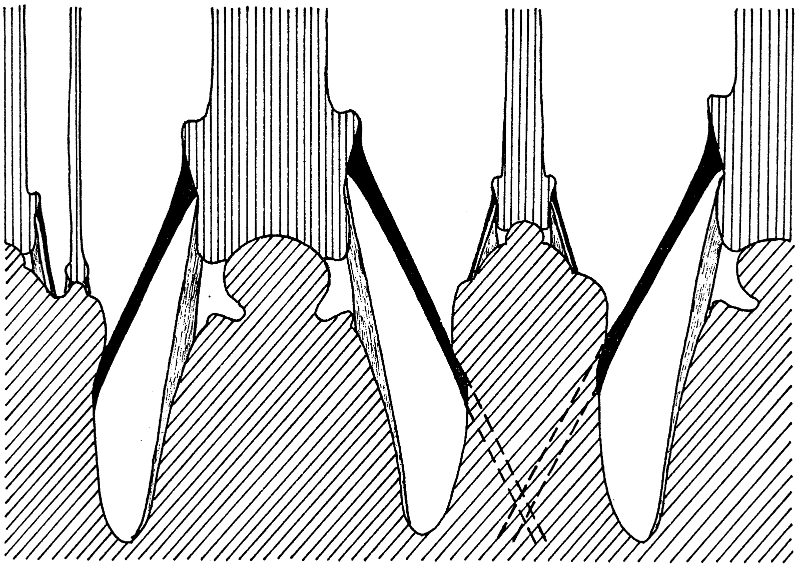

FIGURE 24. Schematic cross section of a plate of *Echinolampas*. Tubercles are deeply sunken and dashed lines show the area required for muscle attachment on a planar surface.

Tubercles and miliaries have to provide a suitable surface for the insertion of muscle and catch apparatus fibres, and are composed of moderately porous stereom. The stereom of granules, on the other hand, is much denser, with a surface pore space of less than 10%. Indeed, many have no surface pore space whatsoever. Granules may have a smooth surface (figure 31) or may have stereom thorns perpendicular to the surface (figure 28). Several types of granules can be identified. Simple, low-profile granules, oval or slightly irregular in outline, are present in the cassiduloids *Conolampas*, *Echinolampas* and *Apatopygus* (figure 29). The aboral surface of species of *Arbacia* is covered in large, warty granules of imperforate stereom covered in thorns (figure 28). In *Echinoneus*, there are very distinctive domed granules, previously described by Westergren (1911). Smooth imperforate stereom forms their domed surface, while the sides have vertical grooves and rows of thorns that become more pronounced towards the base (figure 30). Finally, there are large, thorn-shaped granules on clypeasteroid plates again composed of smooth imperforate stereom (figures 31 and 32). Because of their dense stereom, all granules have a glassy appearance under the light microscope.

Granules are covered with integument, which, in species examined, is not obviously differentiated histologically from integument over the rest of the plate. Nichols (1959) suggested that granulation acts to increase the surface area of ciliated epithelium. This agrees with the fact that granules are best developed on aboral surfaces and are restricted to areas adjacent to tube feet on oral surfaces. However, in *Echinoneus*, granules are covered by a single layer of sparsely-ciliated squamous epithelial cells and may serve a different function.

Structures bearing a close resemblance to the granules of *Echinoneus* have been reported, by Macurda (1977), in the Carboniferous blastoid *Astrocrinus*. Macurda postulated that these structures bore spines, but, from the evidence presented here, it is more probable that they were covered in integument.

On the aboral surface of the Cretaceous holectypoid *Conulus albogalerus* Leske, there are protuberances, previously described, by Forbes (1850) and Hawkins (1917), as spines. According to Hawkins, these 'spines' attach to 'encircled pits' and not to the more usual type of tubercle (although no such pits could be found on the specimen available for this study). These structures are barrel-shaped with smooth, rounded top and sides (figures 33–35). They show no tendency to flair outwards at their base, as illustrated by the two previous authors. Unfortunately, stereom has been completely obliterated in the specimen at hand, so that it is impossible to determine whether these are highly modified and sutured spines or, as is suspected, granules. Irrespective of their nature, they undoubtedly serve a similar function to granules and increase the surface area of ciliated epithelium.

III. TUBERCLES OF REGULAR ECHINOIDS

The tubercle structure in regular echinoids shows relatively little variation compared with that found in irregular echinoids. Tubercles are always radially symmetrical, unless the ambitus is strongly curved, and the circular areole surrounds the boss with little or no gap (figure 2). There appears to be an inverse relation between the number of muscle fibres and the number of catch apparatus fibres developed. Where the areole is well developed, as in *Centrostephanus* and in *Salenocidaris*, the boss is usually small, whereas, where the areole is small and indistinct, as in *Stomopneustes* and *Colobocentrotus*, the boss is extensive.

Spine articulation falls broadly into two categories, sliding-pivot systems and restricted-pivot systems (figure 38), though intermediates are not uncommon.

(i) *Sliding-pivot systems* (figure 40). In general, the tubercle has a low profile with a broad and gently curved imperforate mamelon. There is little platform and usually no well-defined neck. The base of the spine equals the mamelon in breadth (figure 38). Spines of *Psammechinus* can move up to 50° or so from the vertical while maintaining firm contact with the mamelon. Spines can be angled further, but only by disarticulation.

(ii) *Restricted-pivot systems* (figure 41). Typically, the mamelon has a well developed neck and a central perforation and is surrounded by a broad platform which may be smooth, crenulate or may possess a parapet. The base of the spine is larger than the mamelon and rests on the steep, outer sides of the mamelon (figure 38). Manual manipulation of the spines of *Centrostephanus* suggests that they have only to move through 25° to 30° from the perpendicular before the crenulation interlocks, restricting further movement. Tubercles may have a low profile or may be tall and conical (figure 43).

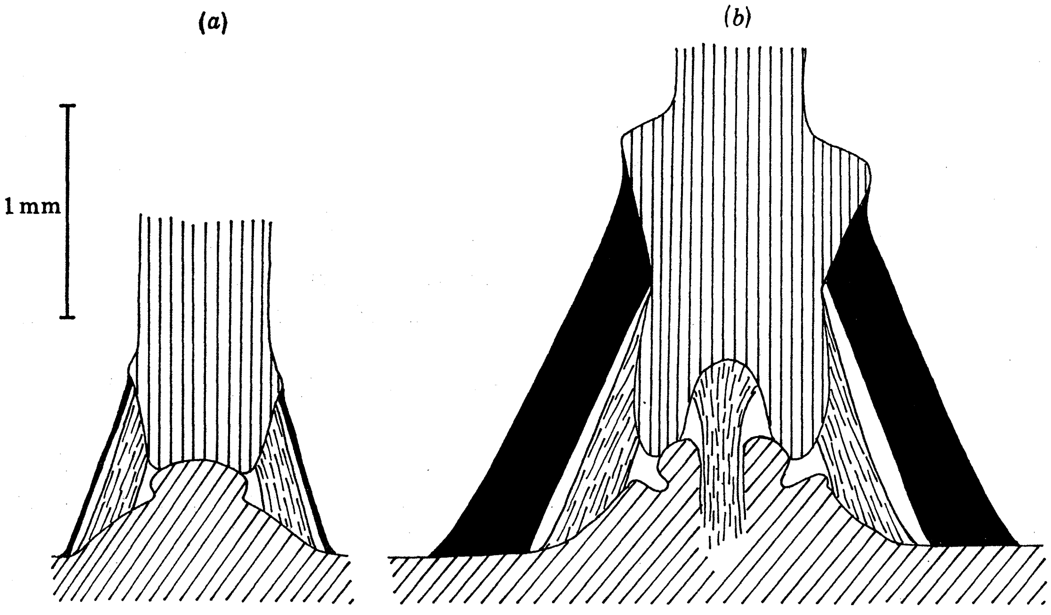

FIGURE 38. (*a*) Sliding-pivot system of *Psammechinus miliaris*; (*b*) restricted-pivot system of *Centrostephanus nitidus*. Drawn from scanning electron micrographs of longitudinal sections.

The restricted-pivot system provides a stronger and more firmly supported spine, but limits the movement of the spine. A sliding-pivot system gives the spine more mobility, but little support when the spine lies obliquely. Restricted-pivot systems are best developed in species that rely on their large spines for defence. Echinoids from shallow, rocky substrata, which seek protection under boulders or in crevices, typically have short spines and sliding-pivot systems. Sliding-pivot systems are also found in a number of echinoids known to cover themselves.

The primary tubercles of ambulacral plates of *Eucidaris metularia* (Lamarck) bear flattened spines which are held obliquely as a protective 'roofing' to the row of tube feet. The perradial side of these tubercles and adjacent miliaries is composed of coarse, granular stereom (figure 44). This produces a granular border to the naked, perradial channel. The functional significance of this is unknown.

IV. TUBERCLES OF NON-SPATANGOID IRREGULAR ECHINOIDS

1. *Pygasteroids*

The morphology and arrangement of tubercles in the Jurassic pygasteroid *Plesiechinus ornatus* (Buckman) has been described previously (Smith 1978*a*). Oral tubercles differ from aboral tubercles and, in oral tubercles, the areole is enlarged and displaced adambitally. Aboral tubercle density is low (*ca.* 0.4 mm^{-2}).

2. *Holectypoids*

Echinoneus cyclostomus Clark, the only extant species of holectypoid examined, has a uniform covering of perpendicular, straight spines. Oral spines are somewhat larger than aboral spines (figure 49 (3)). The tubercles are also fairly uniform in their construction. All have a large imperforate mamelon and lack a platform. Aboral tubercles are relatively dense and are more or less radially symmetrical (figure 46), whereas oral tubercles have areoles that are slightly enlarged and displaced on the adambital side of the boss (figure 45). This bilateral symmetry is least pronounced around the peristome and posterior to the periproct (figure 48).

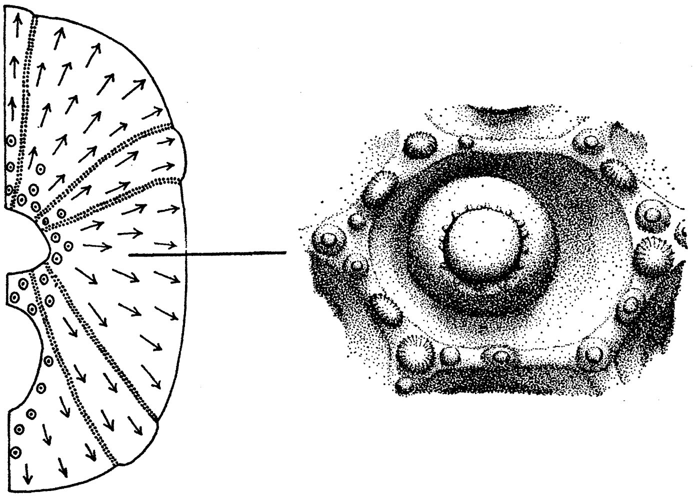

FIGURE 48. Tubercle arrangement on the oral surface of *Echinoneus cyclostomus*. Arrows show the direction of areole enlargement; circles indicate areas of radially symmetrical tubercles.

The morphology of oral tubercles indicates that oral spines are used largely for excavating sediment from beneath the animal and that, unlike Recent cassiduloids and clypeasteroids, *Echinoneus* does not plough continuously forward through the sediment in which it lives. Burial should, therefore, involve little forward motion, and this has recently been confirmed by Rose (1978). As individuals are almost never found within the sediment surrounding rock fragments, but always occur underneath rock fragments (Westergren 1911), it seems likely that adults are not particularly active, though Rose (1978) noted that, in an aquarium, some individuals emerge at night to move over the surface.

In the Jurassic echinoid *Holectypus depressus* Leske, tubercle arrangement is similar to that found in *Plesiechinus*. Tubercles on the concave oral surface have a displaced and enlarged areole on the marginal side of the boss, producing a radial arrangement of bilaterally symmetrical tubercles. Aboral tubercles are smaller and are radially symmetrical. The non-uniformity in aboral tubercle size and the rather sparse distribution of these tubercles suggest that, like *Plesiechinus*, *Holectypus* lived semi-infaunally.

Aboral tubercles of the Cretaceous holectypoid *Conulus albogalerus* Klein are radially symmetrical and have a low profile (figure 37). The mamelon is perforate and is surrounded by a weakly crenulate platform. Tubercles are small and well spaced, with many interspersed prominences (described previously, § II, 3). Oral tubercles are larger and more closely spaced. Crenulation is well developed and radially symmetrical (figure 36). Unlike in the previous two species, oral tubercles are also radially symmetrical.

3. *Cassiduloids*

In all species of cassiduloid examined, oral and aboral tubercles differ in structure and, in contrast to holectypoids, the areoles of oral tubercles are enlarged to the posterior of the boss.

The aboral surface of *Apatopygus recens* (Milne-Edwards) is covered in straight, stubby spines (figure 49 (4*a*)). Only the floor and lower portion of the walls of the posterior sulcus lack these spines. This area is covered in very small, straight miliary spines. *Apatopygus* is known to discharge an almost continuous stream of sediment from its anus (Higgins 1974) and the sulcus helps channel this material posteriorly. Miliary spines are generally covered in cilia-rich epithelium, and this is true in *Apatopygus*. The ciliary currents induced by cassiduloids have never been reported, but it seems likely that the tract of miliary spines in the sulcus may help in creating a backward-directed current for drawing the finer faecal discharge away from the respiratory surface.

Oral spines are longer and have obviously oblique, milled rings (figure 49 (4*b*)). Apart from those at the peristome, oral spines are uniform in structure, though they become smaller adambitally. All are held perpendicular to the test. Long, slender and slightly curved spines (figure 49(4*c*)) originate from the lip of the peristome and form a grill across the mouth.

The tubercle arrangement in *Apatopygus* is illustrated in figure 50. Oral tubercles are larger than aboral tubercles and most show a pronounced areole enlargement posterior to the boss (figure 57). Crenulation is radially symmetrical since spines are held vertically. Interambulacral tubercles around the peristome are much smaller and more densely packed. These differ from other oral tubercles in their low elevation, weakly developed areole and greater radial symmetry.

Aboral tubercles are also bilaterally symmetrical, though their areole enlargement is less pronounced than that of oral tubercles (figure 47). The areole is enlarged adapical to the boss, except posteriorly, where the situation is complicated by the posterior sulcus (figure 50). Tubercles on the lip of the sulcus commonly show no obvious areole enlargement. Miliaries, which are more common on the aboral surface than on the oral surface, cover the floor and walls of the sulcus.

The structure and arrangement of tubercles in the Jurassic species *Nucleolites scutatus* Lamarck closely match those described for *Apatopygus* and there is little doubt that both have a similar mode of life.

The tubercle arrangement in *Galeropygus agariciformis* (Forbes) has been described previously (Smith 1978*a*) and a similar arrangement is also present in *Clypeus ploti* Klein. Unlike *Apatopygus* and *Nucleolites*, their aboral tubercles are more or less radially symmetrical. Oral tubercles of the two anterior interambulacra are large, closely packed and approximately radially symmetrical, whereas lateral and posterior tubercles show some areole enlargement to the posterior of the boss. The arrangement and density of tubercles suggests that both species were infaunal.

Aboral spines of *Echinolampas crassa* (Bell) are relatively short and stout, whereas oral spines are much longer (figure 49 (2)). Both are straight and are held perpendicular to the test. Spines of the bourrelets are curved near their base and arch over the peristome to form a grill. Both oral and aboral tubercles are deeply sunken. On the flat oral surface the boss is situated closer

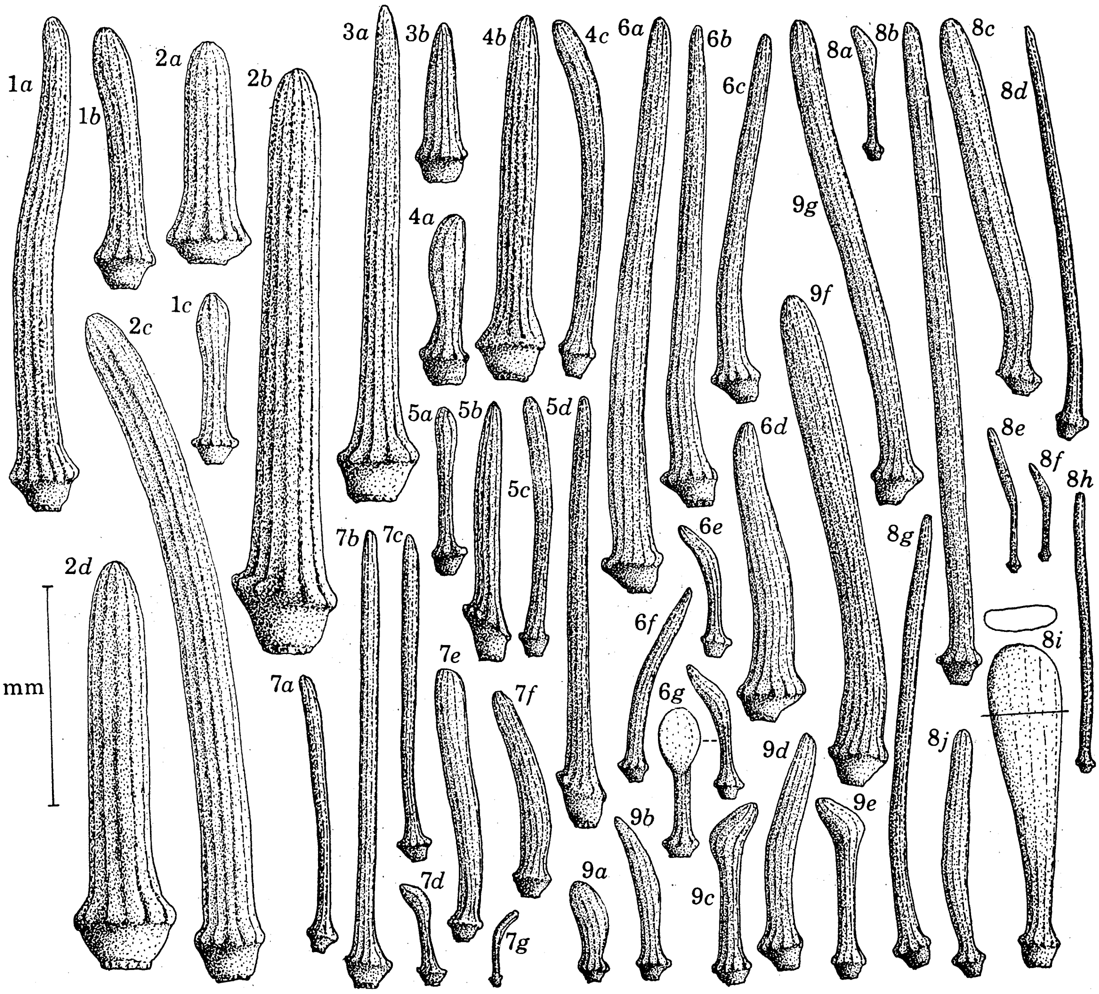

FIGURE 49. Spines of non-spatangoid irregular echinoids from camera lucida drawings. (1) *Echinarachnius parma*: *a*, peristomial lip; *b*, oral interambulacral; *c*, aboral. (2) *Echinolampas crassa*: *a*, aboral; *b*, oral; *c*, peristomial lip; *d*, oral margin. (3) *Echinoneus cyclostomus*: *a*, oral; *b*, aboral. (4) *Apatopygus recens*: *a*, aboral; *b*, oral; *c*, peristomial lip. (5) *Cassidulus cariboearum*: *a*, aboral: *b*, ambital; *c*, peristomial lip; *d*, oral interambulacral. (6) *Dendraster excentricus*: *a*, peristomial lip; *b*, oral interambulacral (central); *c*, oral interambulacral (anterior); *d*, ambital; *e*, aboral, marginal to food groove; *f*, oral, marginal to food groove; *g*, aboral. (7) *Echinodiscus bisperforatus*: *a*, oral interambulacral (marginal); *b*, oral ambulacral food tract; *c*, oral interambulacral (central); *d*, aboral; *e*, lunule lip, aboral; *f*, ambital; *g*, oral, marginal to food groove. (8) *Mellita quinquiesperforata*: *a*, aboral; *b*, oral interambulacral; *c*, ambital, towards the anterior; *d*, peristomial lip; *e*, oral ambulacral near interambulacrum; *f*, oral ambulacral, marginal to food groove; *g*, oral interambulacral, marginal; *h*, oral ambulacral, food tract; *i*, posterior lunule lip, aboral; *j*, ambulacral lunule lip, aboral. (9) *Fellaster zelandiae*: *a*, aboral marginal; *b*, oral ambulacral near interambulacrum; *c*, aboral interambulacral; *d*, oral ambulacral (perradial); *e*, aboral ambulacral; *f*, peristomial lip; *g*, oral interambulacral.

to the anterior wall, indicating that spines have a stronger pull in a posterior direction. Tubercle density increases adambitally. Small, densely packed interambulacral tubercles occur around the peristome. These are radially symmetrical and, unlike other tubercles, are not sunken. Aboral tubercles are large, closely packed and radially symmetrical. The tubercle arrangement in *Conolampas sigsbei* is similar to that in *Echinolampas*, except that oral tubercles as well as aboral tubercles are more or less radially symmetrical.

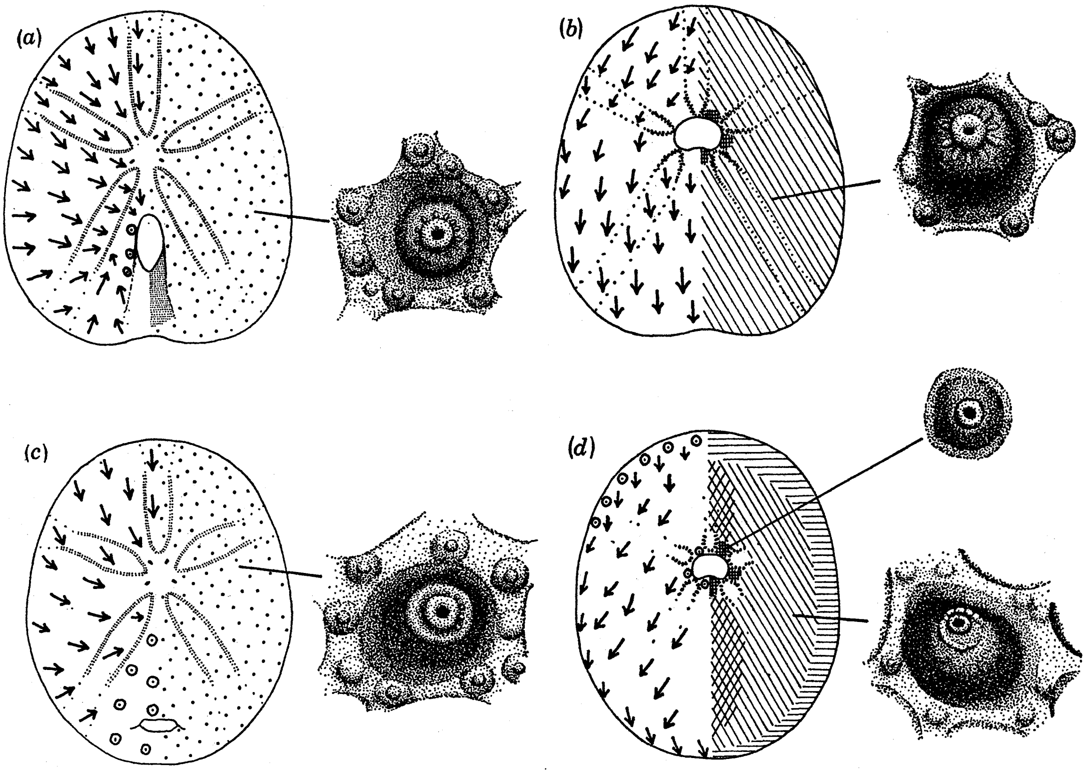

FIGURE 50. Tubercle arrangement in *Apatopygus recens* (*a, b*) and *Cassidulus cariboearum* (*c, d*): (*a*) and (*c*), aboral surface; (*b*) and (*d*), oral surface. Arrows indicate the direction of areole enlargement, circles denote regions of radially symmetrical tubercles. Hatching in the right hand side of each indicates differences in the spine coverage. Sparse stippling, aboral protective spines; dense aligned stippling, miliary spines alone; oblique lines, locomotory/excavatory spines; horizontal lines, sub-ambital spines; rectilinear hatching, peristomial lip spines; rhombic hatching, pitted area with sparse miliary spines.

Of the cassiduloids examined, *Cassidulus cariboearum* Lamarck has the most pronounced oral–aboral differentiation of tubercles and spines. Aboral spines are short and stubby with a slight distal swelling (figure 49 (5*a*)), and are held perpendicular to the test. Oral spines are long, gently curved and pointed (figure 49 (5*d*)), and lie in a meso-posterior direction at an angle of about 45° (in preserved specimens). They become progressively smaller towards the ambitus. Around the peristome, slender, weakly curved spines form a grill across the peristome.

The slightly sunken aboral tubercles of *Cassidulus* are small and densely packed, with only occasional miliaries interspersed (figure 53). The areole is often slightly enlarged to the posterior or adapical side of the boss, except in interambulacrum 5, where tubercles are radially symmetrical (figure 50). Two pitted areas, devoid of tubercles, are present on the oral surface, one lying anterior, the other posterior to the peristome. The pits, which appear to be formed by resorption, since they penetrate into the middle plate layer, are separated by thorned ridges of imperforate stereom (figures 55 and 56). This area is covered, in life, by apparently normal integument. Around the peristome, interambulacral tubercles are small and densely packed. They are more or less radially symmetrical, though distorted by packing, and are not sunken (figure 54). Large asymmetric tubercles cover the rest of the oral surface. These are roughly semicircular in outline and the boss lies in an anterior position (figures 51 and 52). The areole is broadest in a latero-posterior direction. Tubercles become smaller and less asymmetrical adambitally.

4. *Clypeasteroids*

(*a*) *Tubercle and spine arrangement*

Oral and aboral tubercles and spines are commonly differentiated in clypeasteroids, particularly in sand dollars, where there is often further differentiation of ambulacral and interambulacral tubercles and spines.

The simplest arrangement is found in species of *Clypeaster*. In both *C. rosaceus* (Linnaeus) and *C. rarispina* de Meijere, oral and aboral tubercles are sunken and are radially symmetrical. Apart from a slight variation in size, tubercles and spines are uniform in structure. In *C. rarispina*, the plates around the peristome curve inwards to form a lip. A single row of radially symmetrical tubercles lies on this lip and these tubercles bear slightly stouter and gently curved spines, which form a grill across the mouth. The spines of *C. rosaceus* are much larger and no specialized peristomial spines are developed. The oral surface is concave and a deep well is produced around the peristome, so that many of the oral spines pass across the mouth.

Echinocyamus pusillus (Müller) is covered in short, straight spines held perpendicular to the test. Oral and aboral tubercles are similar in size and are bilaterally symmetrical. Although crenulation is equally developed around the mamelon, the areole is displaced and enlarged to the posterior on both oral and aboral surfaces. Tubercles at the anterior ambitus and around the peristome are more radially symmetrical.

In *Fellaster zelandiae* (Gray), there is some ambulacral/interambulacral tubercle and spine differentiation. A smooth tubercle- and pore-free tract lies perradially. Aboral spines are short and straight and terminate in a swollen tip (figure 49 (9*c*)). Ambulacral and interambulacral tubercles are inclined in different directions, as are ambulacral spines on either side of the perradius. Adambitally, spines become shorter and stubbier. All aboral spines are similar in structure. Ambital spines are larger, curve gently towards the posterior and terminate in a point. On the oral surface, the interambulacral spines, which are also pointed, are long and slightly bent. Oral ambulacral spines are about half as long and have a prominent bend about halfway along the shaft (figure 49 (9*d*)). Slightly stouter, pointed spines, which are bent near their base, form a grill across the peristome.

Aboral tubercles of *Fellaster* are all bilaterally symmetrical with enlarged and displaced crenulation on the opposite side to the direction of areole enlargement. Whereas interambulacral tubercles are irregularly arranged, tubercles over much of each ambulacrum are organized into oblique rows, each row being separated from its neighbours by a row of miliaries and a row of unipores (figure 61). The more adradial tubercles are irregularly arranged. The areole in linearly-arranged tubercles is enlarged to the adambital side in a direction perpendicular to the lineation. In other aboral tubercles, the areole is enlarged to the posterior side. Crenulation is developed on the side towards which the spine leans, while the areole is enlarged in the opposite direction. Much the same arrangement is found on the oral surface. All ambulacral tubercles are arranged in oblique rows and the areole of each tubercle is enlarged adorally (figures 59, 60 and 64*b*). Larger and less densely packed tubercles cover interambulacral plates and, in these tubercles, the areole is enlarged in a posterior/adoral direction (figures 62 and 64*b*).

Spine and tubercle differentiation, which is pronounced on the oral surface of sand dollars, will be described for a number of species. However, the aboral arrangement of spines and tubercles follows a similar pattern in all species examined and can be dealt with collectively. Aboral spines are short with a swollen foot-shaped tip, except in *Echinarachnius parma* (Lamarck), where the tip is only slightly enlarged (figure 49 (1*c*)). Aboral tubercles are small, slightly sunken and densely packed. They are bilaterally symmetric, usually with a tilted boss and mamelon, with enlarged crenulation on the opposite side to areole enlargement. The areole is enlarged on the adapical side of anterior tubercles and on the meso-posterior side in lateral and posterior tubercles (figure 63*b*).

Ambital tubercles are larger and more radially symmetrical. They bear rather stout, pointed spines, held more or less perpendicular to the test. These are either straight or only slightly bent towards the posterior. All sand dollars examined also possess a grill of relatively long spines that cover the peristome. They attach to densely-packed tubercles, which form between two and five rows on the peristomial lip. These tubercles, which are never sunken, have poorly developed areoles and are more or less radially symmetrical (though packing may distort their shape).

The arrangement of oral spines is least specialized in *Echinarachnius parma* (Lamarck). Ambulacral and interambulacral spines are similar in shape though they differ in size. They are short, stout and gently curved, and end in a rounded tip (figure 49 (1*b*)). Interambulacral spines range in size from 1.2 mm near the peristome to 1.6 mm near the ambitus, whereas ambulacral spines are around 1–1.2 mm in length. All tubercles, except those of the peristomial lip, have enlarged areoles to the posterior side (figure 63*a*). The boss is tilted slightly towards the anterior, and crenulation is enlarged on this side. Tubercles decrease in size towards the food grooves.

Dendraster excentricus (Eschscholtz) has, on its oral surface, a complex system of branching food grooves, many of which extend aborally (figure 64*a*). As well as the peristomial spines, there are three other groups of oral spines (figure 49 (6*a–c*, *f*)). In central and posterior areas, the spines are long and slender and are bent near their base. Slightly shorter, but similarly shaped, spines are found towards the anterior and lateral margins, where they are extremely dense. Short, strongly curved spines on either side of each food groove form protective arches over them. Similar spines also form a roof to the aboral portions of food grooves. Spines of the anterior and lateral margins lean adambitally, whereas central and posterior spines lean in a meso-posterior direction.

Oral tubercles of *Dendraster* are bilaterally symmetrical and all are similarly structured. The areole is enlarged and displaced to one side, while crenulation is best developed on the opposite side, in the direction in which the boss is tilted. Anterior and lateral tubercles are densely packed, with few interspaced miliaries. Towards each food groove, tubercles become much smaller and there is usually a well defined row of very small tubercles immediately adjacent to the food groove (figure 68). The areole of central and posterior tubercles is enlarged to the posterior, whereas, in anterior and lateral tubercles, it is enlarged adorally (figure 64*a*).

Encope michelini Agassiz has a single lunule at the centre of interambulacrum 5 and a perradial notch in each ambulacrum (figure 63). On the aboral surface, around the lip of the lunule, there is a row of large tubercles, which bear stout spines with flattened tips. These spines bend towards the lunule before curving upwards to form a roof above it. There are five groups of spines on the

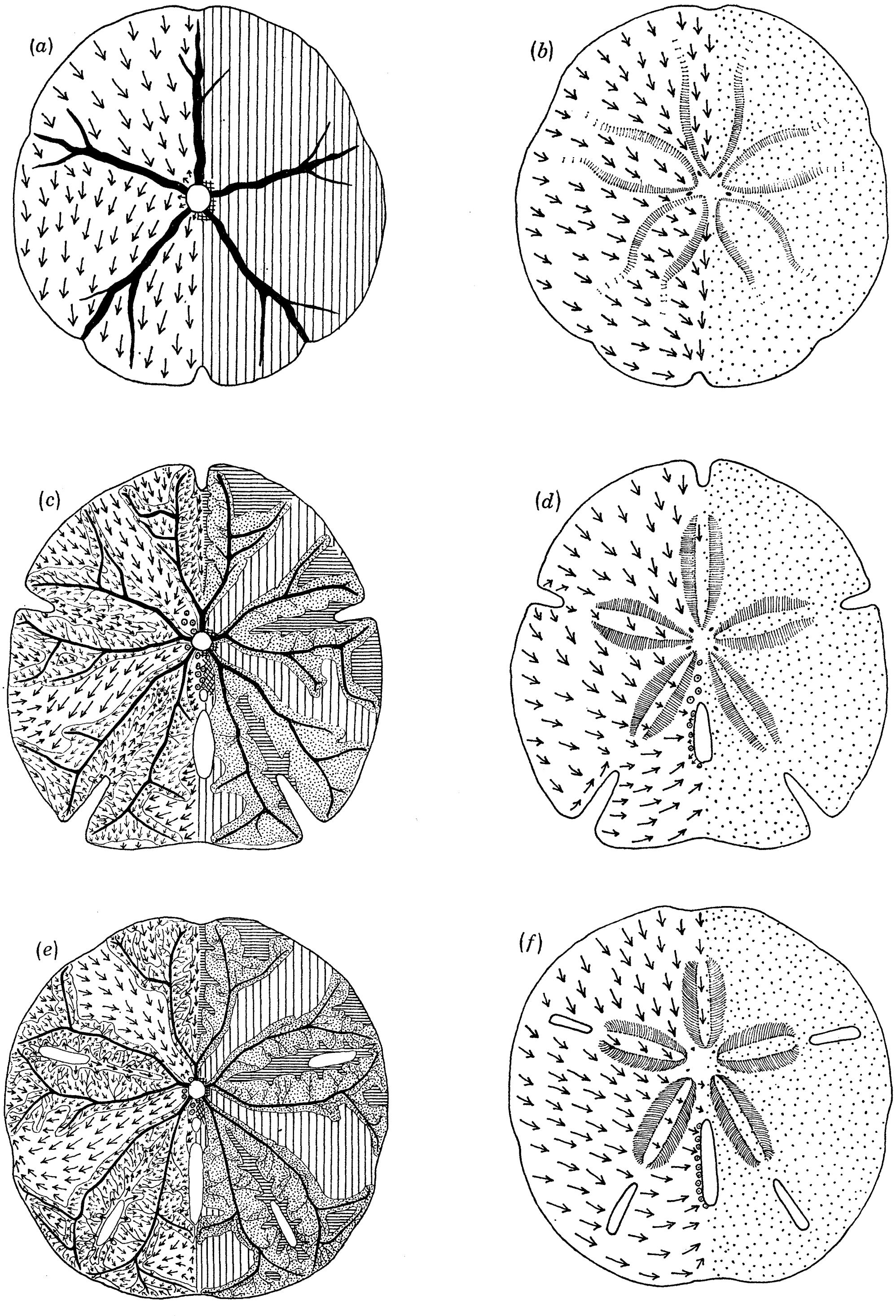

FIGURE 63. Tubercle arrangement in clypeasteroids: (*a*) and (*b*), *Echinarachnius parma*; (*c*) and (*d*), *Encope michelini*; (*e*) and (*f*), *Mellita quinquiesperforata*; (*a*), (*c*) and (*e*), oral; (*b*), (*d*) and (*f*), aboral. Heavy lines indicate food grooves. Arrows indicate direction of areole enlargement. Circles denote regions of radially symmetrical tubercles. Vertical lines, locomotory spines; horizontal lines, ambulacral food tract spines; fine stippling, area of accessory tube-foot pores and small ambulacral spines; rectilinear hatching, peristomial lip spines; rhombic hatching, large spines separating the peristome from the periproct; coarse stippling, aboral protective spines.

oral surface. Between the peristome and periproct, there are long, slender spines, which are held perpendicular to the test surface. The associated tubercles are large, closely packed, and more or less radially symmetrical (although marginally the areole may be enlarged towards the latero-posterior). Other interambulacral spines are long, spatulate and gently curved. There are two types of oral ambulacral spines. Short, gently curved spines with weakly spatulate tips are found perradially in each ambulacrum from the first bifurcation of the food groove to the marginal notch. They are also present marginally between the secondary branches of the food groove system. Their tubercles are small, weakly crenulate and relatively widely spaced. Areoles are enlarged adorally and slightly outwards towards the food grooves (figure 63*c*). Spines become smaller and strongly bent away from the direction of areole enlargement towards the food grooves. These have blunt, rounded tips. Associated tubercles are small and, in general, the direction of areole enlargement differs on either side of major food grooves (figure 63*c*). Small unipores are interspersed among these tubercles.

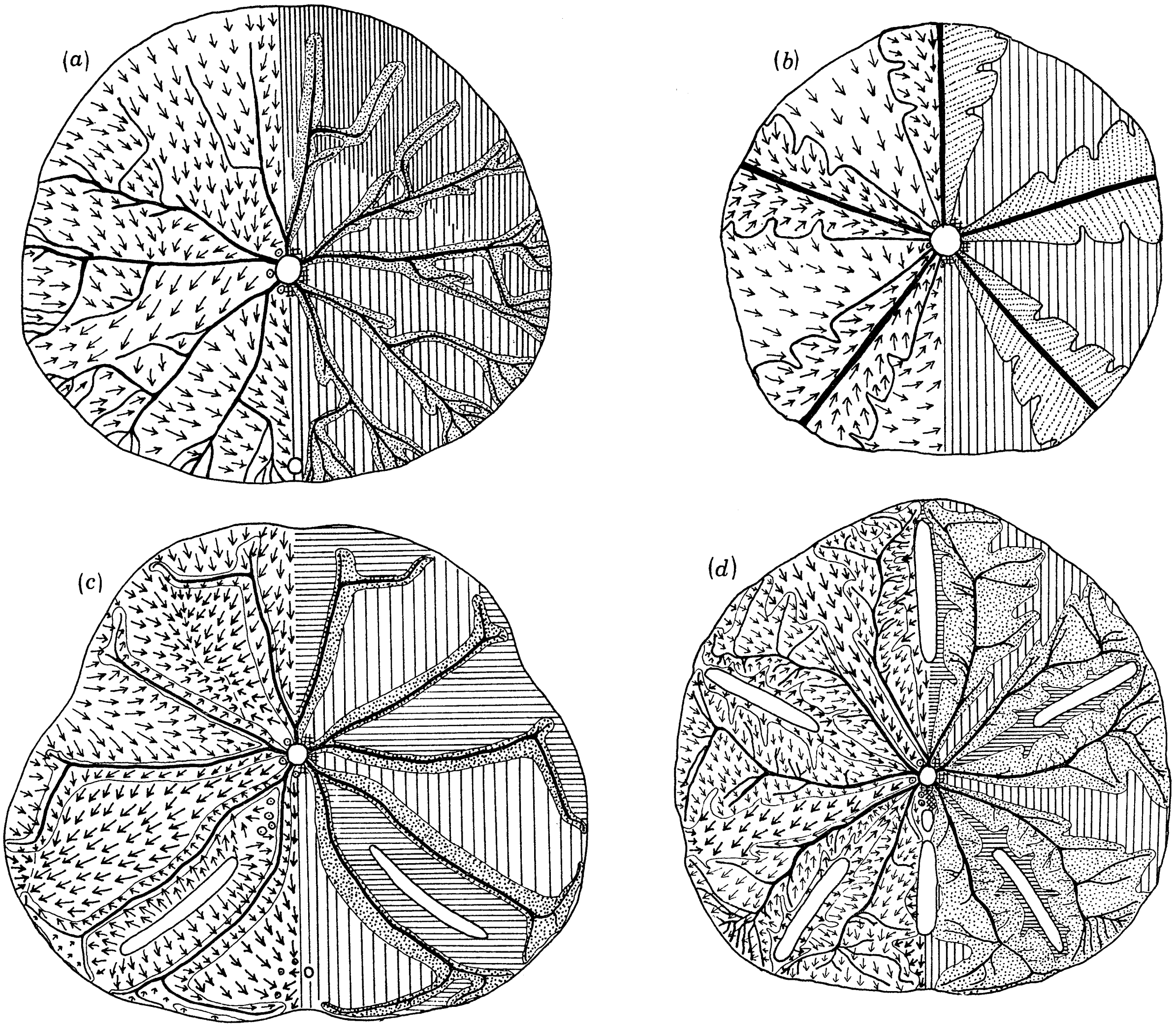

FIGURE 64. Oral tubercle arrangement in clypeasteroids. (*a*) *Dendraster excentricus*; (*b*) *Fellaster zelandiae*; (*c*) *Echinodiscus bisperforatus*; (*d*) *Leodia sexiesperforatus*. Hatching as in figure 63.

Mellita quinquiesperforata (Leske), *Leodia sexiesperforata* (Leske) and *Echinodiscus bisperforatus* Leske all possess lunules and, as the morphology and arrangement of spines and tubercles is similar in all three, only *Mellita* need be described in detail.

M. quinquiesperforata has five lunules: one in each of the lateral and posterior ambulacra and one interradially in interambulacrum 5. On the aboral surface, each lunule is roofed by an arch of relatively large spines. In ambulacral lunules, the spines are slightly flattened distally and bend near their base to curve across the lunule in an ambital direction (figure 49 (8*j*)). Spines of the posterior lunule are strongly flattened parallel to the major axis of the lunule and form a roof above the lunule (figure 49 (8*i*)). Tubercles at the lip of the lunule are obviously larger than other aboral tubercles. They are either radially symmetrical or have a slight areole enlargement away from the lunule.

Oral interambulacral spines of *Mellita* are long, pointed and gently curved (figure 49 (8*b*)). Spines are inclined towards the anterior margin in the anterior two interambulacra, but lie in a meso-posterior direction in the other interambulacra. Associated tubercles are relatively large and well spaced but become denser adambitally. The areole is enlarged and displaced on the side opposite to which the spine leans and in which crenulation is enlarged (figure 65). Large, densely packed and more or less radially symmetrical tubercles lie between the peristome and periproct. These bear long, relatively straight, pointed spines.

Ambulacral spines grade from slender, more or less straight spines, about 1.1–1.3 mm in length, which occur perradially, to small bent spines, 0.5 mm in length, found adjacent to food grooves (figure 49 (8*e*–*g*)). Apart from the loss of crenulation in smaller tubercles, all ambulacral tubercles are similar in structure, but they vary in size and density (figures 66 and 69). The smallest and most densely packed tubercles border the food grooves. The direction of areole enlargement is plotted in figure 63*e* and the detailed arrangement in ambulacrum II is given in figure 71. Tubercle arrangement is similar in the frontal ambulacrum, where there is no lunule. Here, perradial spines pull adorally. Within the lunules, slender, slightly bent spines, about 1 mm in length, extend into the cavity. Only miliary spines line the lunule walls of *Echinodiscus*.

Tubercle arrangement in *Leodia* is similar to that in *Mellita* (figure 64*d*). In *Echinodiscus* the interambulacral spines lean in different directions. Spines close to the margin are inclined adambitally, whereas, in the central and adoral regions, they are inclined towards the latero-posterior. There is a corresponding variation in the direction of areole enlargement in interambulacral tubercles (figure 64*c*). Tubercles become much smaller and more dense along the line separating areas of opposing spine inclination and this stands out clearly as a tract of finer tuberculation. Tubercle arrangement in the three anterior ambulacra follows a similar pattern, as is found in the ambulacra of *Encope* and in ambulacrum III of *Mellita* (figure 67).

(*b*) *Functional interpretation*

(i) *Aboral spines.* Aboral spines transport sand over the test during burial (Ikeda 1939; Goodbody 1960; Bell & Frey 1969). Sand is pulled up around the anterior margin and transported adapically and laterally. The last region of the test to be covered is the midline of the posterior interambulacrum (Ikeda 1939) and, in certain species, this ambulacrum may remain uncovered (Kenk 1944; Hyman 1958). The direction of areole enlargement indicates the direction of the spine power stroke and matches the direction in which sand grains are transported. These adambitally inclined spines are pulled erect, lifting sand grains adapically and posteriorly. A similar areole enlargement in the aboral tubercles of certain cassiduloids suggests that they, also, transport sediment aborally by means of their spines. The swollen tip of aboral spines can produce a mosaic pavement (Clark, in Melville & Durham (1966)). This not only increases their efficiency in moving sediment, but also provides better protection (from sediment abrasion) to the integument.

Miliary spines on the aboral surface are cilia-rich (Parker & van Alstyne 1932; Goodbody 1960; Chia 1969, personal observation) and may also produce mucus (Goodbody 1960). The cilia produce centrifugal currents in *Leodia* (Goodbody 1960) and *Echinocyamus* (Nichols 1959). These currents draw oxygenated water through sediment interstices and past respiratory tube feet, and also draw fine food particles adorally.

(ii) *Marginal spines*. Marginal spines are often denser around the anterior margin, and their stout design and vertical posture make them suitable for loosening and excavating sediment in front of the animal, as observed by Weihe & Gray (1968) and by Bell & Frey (1969). Kenk (1944) suggested that they also assist in locomotion, but this is largely effected by oral interambulacral spines.

(iii) *Oral interambulacral spines*. These are the main organs of locomotion in all sand dollars (Parker & van Alstyne 1932; Kenk 1944; Goodbody 1960; Salsman & Tolbert 1965; Weihe & Gray 1968; Bell & Frey 1969). Areole enlargement shows that the power stroke of the spines is developed to propel the animal forward. In the anterior interambulacra of *Echinodiscus*, only the marginal spines appear to be involved in locomotion, judging from the direction of areole enlargement. Where there is no pronounced differentiation of ambulacral and interambulacral spines, all oral spines are probably involved with locomotion.

(iv) *Periproct spines*. These spines are only developed in species in which the periproct lies in close proximity to the peristome. They act as a barrier preventing the reingestion of faeces (Goodbody 1960).

(v) *Spines of the peristomial lip*. A peristomial grill of spines is present in nearly all clypeasteroids and cassiduloids. (In *Echinocyamus pusillus* it consists of only ten spines.) It is not clear whether this is simply a protective grill or whether spines are used to push larger particles into the mouth. In *Dendraster*, food particles are pushed into the mouth by the tube feet and the spines are simply raised to allow admittance (Timko 1976). Similar behaviour was observed in *Mellita* by Bell & Frey (1969), though they also suggest that these spines may help to pass material into the peristome. In *Cassidulus cariboearum* and *Echinolampas crassa*, the peristomial grill of spines actively manoeuvres sediment into the peristome (Gladfelter 1978; Thum & Allen 1976).

(vi) *Lunules, notches and the ambulacral spine and tubercle arrangement*. Various functional interpretations of lunules have been advanced. Ikeda (1939, 1941) reported that, in *Astriclypeus manni* Verrill, sand could be passed through the lunules in either direction. Aboral transportation of sediment through the lunules was shown to increase the speed and efficiency of burial and righting. Although this may be the function of lunules in *Astriclypeus*, it is certainly not their primary function, as no other species has been observed to burrow in this way. In fact, in both *Mellita* and *Leodia*, sand actually passes adorally through the lunules during burial (Goodbody 1960; Weihe & Gray1968; Bell & Frey 1969). It has been suggested that lunules act to strengthen the test (Berrell & Berrell 1957, reported by Hyman 1958); the obvious problems with this theory have been pointed out by Hyman (1958). Lunules have also been implicated in maintaining communication with the surface (Bell & Frey 1969).

It will be argued below that the most plausible function of lunules is that they permit sand dollars to feed from the surface, organic-rich layer of sediment. The arrangement of spines and tubercles around the lunules, the close proximity of food grooves, which pass on either side of each lunule, and the development of food tracts leading from the lunule to the food grooves all lend strong support to the view that lunules are primarily involved in feeding activities. The very similar arrangement around notches indicates that notches and lunules serve the same function.

Goodbody (1960) demonstrated that smaller sediment particles pass adorally through the lunules, whereas larger particles pass over them. Ciliary currents transport the finer material directly to the food grooves (see Reese (1966), fig. 5 (8)), while slightly larger particles are probed by the tube feet and are deposited beneath the animal. The direction of areole enlargement indicates that the spines of the ambulacral food tract have their power stroke directed away from the lunule or notch and towards the food grooves, regardless of the direction of locomotion (figure 63*e*). Marginal spines, which lie within the catchment area of the food groove system, also have their strongest pull directed adorally towards the food grooves. It therefore seems reasonable to assume that particles, which fall down the lunules or around the margin and which are not transported by ciliary currents, are transported adorally and towards the food grooves by the action of the spines. Suckered tube feet are known to sample particles as they pass (Goodbody 1960) and are likely to select suitable particles, which they then transfer and incorporate into the mucous string (Bell & Frey 1969; Timko 1976). Particles not selected would continue to be moved by the spines and pushed across the food groove, where a protective arch of spines prevents non-selected particles from becoming incorporated into the mucous string. The direction of areole enlargement on the interambulacral side of the food grooves suggests that the power stroke of these spines moves particles either marginally or in a posterior direction, into the interambulacrum (figure 71).

Although *Leodia* incorporates into its mucous strings only small particles, which could have been transported by ciliary currents (Goodbody 1960), *Mellita* is known to be a sediment swallower (Bell & Frey 1969). The depressions in the sediment surface directly above each lunule, illustrated by Reinecke (1965) and by Bell & Frey (1969), show that surface sediment is passed adorally through the lunules. These depressions appear when the animal remains motionless for a short time. Dexter (1977) reports that *Encope stokesi* Agassiz rises to lie immediately beneath the surface of the sediment shortly before the time of low water, then, following the turn of the tide, quickly descends into the substratum. He correlates this with the tidal deposition of a film of diatoms and fine organic detritus over the surface, and suggests that this behaviour is an adaptation for feeding.

Notches and lunules greatly increase the length of the ambitus; extreme examples can be found in the family Rotulidae. This increase in length increases the area along which sediment can be transferred adorally to be incorporated into the mucous strings by tube feet or ciliary currents. In many instances, the food grooves branch towards the ambitus, so as to cover as much of the test circumference as possible (figure 64). This ensures that maximum usage is made of the peripheral area for collecting sediment. By this method of feeding, the richly organic surface layer of sediment can be selectively incorporated into the mucous string without the animal having to expose itself to the dangers of predation and desiccation.

Kier (1966) found a subtidal population of *Leodia* living deeply buried and making no trace on the rippled surface. *Mellita* is also known to burrow deeply during storms (Weihe & Gray 1968). Surface feeding does not, therefore, occur at all times and may only be adopted where a surface organic film is found and where the substrate has a low nutritional value.

The posterior interambulacral lunule apparently serves another function. When *Mellita* is stationary and, presumably, surface feeding, a surface depression forms above the posterior lunule as well as above the ambulacral lunules (Bell & Frey 1969), showing that sediment passes adorally through the former. However, the aboral protective spines of the posterior lunule are larger and much more flattened than similar spines of ambulacral lunules. These flattened spines beat up and down during defaecation, drawing faecal material aborally through the posterior lunule and dispersing this posteriorly (Bell & Frey 1969). The behaviour of certain populations that burrow leaving their posterior interambulacrum uncovered (Kenk 1944; Hyman 1958) may be an adaptation for more efficient waste disposal through the posterior lunule. However, similar activity was not observed, by Goodbody (1960), during defaecation in *Leodia*, and Hyman (1958) did not observe adapical sediment movement through the lunules of *Mellita*.

(vii) '*Pseudofascioles*'. The 'pseudofasciole' of the posterior interambulacrum, described at great length by Ikeda (1939), is a boundary marking a difference in the direction of aboral spine inclination accompanied by a corresponding difference in the direction of areole enlargement. The zigzag nature of this boundary, which bisects the interradial sutures, is simply a constructional feature produced by lateral plate growth. None of the postulated functions (strengthening of the posterior suture, acting as a rudder, inducing water currents, sweeping excreta away) are considered feasible. During burial, aboral spines pass sediment backwards on either side of the test, and the two fronts of sediment eventually meet along the posterior midline. The zigzag nature of the boundary separating spines with opposing pull most probably ensures that the covering of aboral sediment is complete, since a streamlining effect during progression would tend to leave the central posterior region uncovered in shallow burrowers. The term 'pseudofasciole' has, fortunately, never been adopted and there is no intention on the author's part to change this.

5. *Discussion*

Only holectypoids and pygasteroids show no development of a unidirectional spine pull on the oral surface. In these groups, the power stroke of the oral spines is radial and directed from the peristome. Burial is therefore likely to involve little forward locomotion and this has recently been confirmed by Rose (1978). Surface locomotion in *Echinoneus* is, unfortunately, unrecorded and it is not known whether it moves in one direction only, like clypeasteroids and cassiduloids. Both clypeasteroids and cassiduloids have oral locomotory spines whose power stroke is directed posteriorly. *Apatopygus* is known to move forwards within the sediment (Higgins 1974), and many clypeasteroids can move only forwards and must change direction by rotation (Parker & van Alstyne 1932; Kenk 1944; Hyman 1958; Salsman & Tolbert 1965).

Clypeasteroids appear to require forward movement to be able to bury themselves (Kenk 1944; Weihe & Gray 1968). They burrow by piling sediment anteriorly and 'bulldozing' into the substratum as they move forward (see review by Reese (1966)). Aboral spines help by pulling sediment aborally. Forward motion is also involved in the burial of *Apatopygus* (Higgins 1974, pl. II).

The oar-like oral spines of *Cassidulus cariboearum* have more in common with the latero-ventral spines of spatangoids than with oral spines of any other non-spatangoid echinoid. It is, therefore, not surprising to learn that *Cassidulus* excavates sediment from beneath itself and, with apparently little forward motion, 'sinks below the surface with a wobbling motion' (Gladfelter 1978), in a similar manner to spatangoids.

The arrangement of oral spines and tubercles in *Dendraster* is unlike that found in any other sand dollar. In moderate currents, *Dendraster* adopts an inclined posture with only the anterior third or so of the test inserted into the substratum (Merrill & Hobson 1970; Timko 1976). It is probably no coincidence that the arrangement of spines and tubercles is different around the anterior and lateral margins of the test (figure 64*a*). The anterior spines may be involved in raising the test into an oblique position and also in the lateral locomotion reported by Merrill & Hobson (1970).

The arrangement of oral tubercles (and spines) can be used to separate non-spatangoid echinoids into three behavioural groups:

(i) Unspecialized sediment swallowers with a uniform spine and tubercle arrangement on the oral surface, e.g. *Echinoneus*, *Apatopygus* and *Clypeaster*. *Echinarachnius* also falls into this group, although it may be a suspension feeder (Sokolova & Kuznetsov 1960).

(ii) Inclined suspension feeders with anterior/posterior differentiation of spines and tubercles and an unequal development of food grooves, e.g. *Dendraster*.

(iii) Infaunal surface sediment feeders with a complex food groove system, lunules or notches, and an obvious ambulacral/interambulacral differentiation of tubercles and spines, e.g. *Mellita*.

V. Tubercles of spatangoids

Tubercle and spine diversity reaches its most complex in the spatangoids. Twelve species were studied in detail (table 1). The arrangement of spines and tubercles in *Echinocardium cordatum* (Pennant), whose behaviour and ecology is well known, will be first described and then be contrasted with that in other species.

1. *Tubercles and spines of* Echinocardium cordatum

(*a*) *Plastron tubercles and spines*

Plastron spines are largest at the anterior and lateral margins of the pastron and decrease in size towards the posterior part of the interradial ridge. They are strongly spatulate (figure 76 (3*d*)) and are curved so that the spatulate face makes contact with the substratum. At rest, the spines lean slightly forward and outward away from the mid-posterior region of the plastron. They have a rotary motion. Each spine is pulled towards the mid-posterior region of the plastron, bringing the spatulate tip down into the substratum. The spine then moves laterally, towards the side of the plastron on which it is situated, in a semicircular sweep returning it to its original position. During this recovery stroke, the spine is held close to the test to avoid contact with the substratum. Spine movement is coordinated over the plastron.

Plastron tubercles are large and have a greatly enlarged areole directed towards the mid-posterior of the plastron (figures 72 and 73). This marks the direction in which spines are pulled into the substratum. The boss is tilted in the opposite direction, matching the direction of spine inclination at rest. There is a smooth ridge on the posterior and lateral sides of the platform. This direction corresponds with that part of the spine cycle where the spine is inclined closest to the test.

Plastron spines are locomotory in function (Nichols 1959) and propel the animal forward through the sediment at about 2 cm/h (Buchanan 1966).

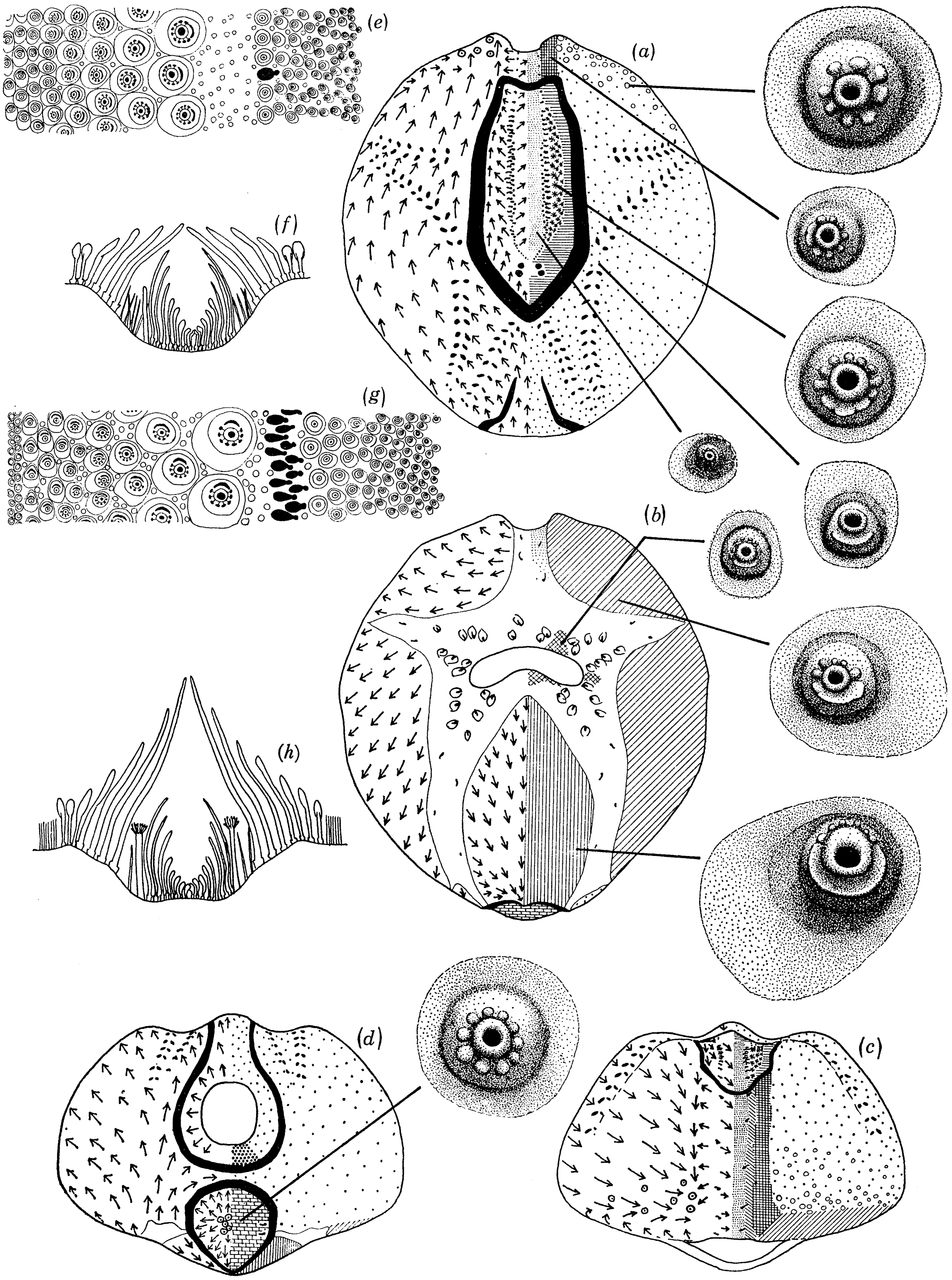

FIGURE 72. Tubercle arrangement in *Echinocardium cordatum*. (*a*) Aboral; (*b*) oral; (*c*) anterior; (*d*) posterior. Left hand sides of diagrams show direction of areole enlargement (arrows). Areas of radially symmetrical tubercles are indicated by circles. The right hand sides of diagrams indicate the distribution of different types of spines and their associated tubercles. Black bands, fascioles; vertical lines, locomotory spines; oblique lines, ventro-lateral spines; diamond hatching, spines marginal to the peristome; rectilinear hatching, protective spines forming an arch across ambulacrum III; circles, scraping spines; sparse stippling, dorso-lateral protective spines; asterisks, apical tuft spines; brickwork, sub-anal tuft spines; dense stippling, areas lacking large spines. (*e*) Tubercle arrangement in ambulacrum III below the fasciole, from the interambulacrum (left) to the midline of ambulacrum III (right). Apex to the top. (*f*) Spine arrangement in ambulacrum III below the fasciole. (*g*) Tubercle arrangement in ambulacrum III within the inner fasciole, from the fasciole (left) to the midline of the ambulacrum (right). Apex to the top. (*h*) Spine arrangement in ambulacrum III within the inner fasciole. Note radial arrangement of tubercles in lozenge-shaped sub-anal fasciole.

(*b*) *Latero-ventral tubercles and spines*

Oral spines of the lateral interambulacra are gently curved latero-posteriorly and have adambital-facing spatulate tips (figure 76 (3*c*)). They lie with pronounced obliquity in a meso-posterior direction. They move with an oar-like motion, being lowered into the sediment, pulled adambitally, raised and then recovered. Associated tubercles show marked areole enlargement in a postero-lateral direction in interambulacra 1 and 4 and in a lateral or sometimes antero-lateral direction in interambulacra 2 and 3 (figure 72). The power stroke of the spine is therefore directed marginally and upwards out of the sediment. There is a ridge to the posterior of the mamelon, and crenulation around the rest of the platform (figure 6). The spine base interlocks with the crenulate part of the platform, where purchase against the substratum is required, and, during the recovery stroke, slides across the ridge. These spines excavate sediment from beneath the animal and provide the sole means of burial (Nichols 1959).

(*c*) *Peristomial tubercles and spines*

Slender spines (figure 76 (3*k*)), which arise from interambulacral plates adjacent to the peristome, curve in towards the peristome to form an open grill across the mouth. The associated tubercles are small and cap-shaped. Those furtherst from the peristome are ovoid in outline, with a uniformly developed areole (figure 85). The platform, which is mostly crenulate, has an adorally situated ridge. Towards the peristome, tubercles become smaller and strongly tilted adorally, while the areole becomes enlarged adambitally.

(*d*) *Spines of the sub-anal tuft and their tubercles*

A posterior tuft of pointed spines is present within the sub-anal fasciole. The largest and straightest spines occur centrally and spines become progressively smaller and more inwardly curved towards the fasciole (figure 76 (3*e*)). This arrangement produces a cone of spines. Tubercle arrangement within the sub-anal fasciole matches the spine arrangement (figure 72). The largest tubercles are radially symmetrical and are found centrally. Towards the fasciole, tubercles become smaller and bilaterally symmetrical. The areole becomes progressively enlarged on the marginal side, while a ridge is developed on the side facing the centre.

During burial, the sub-anal tuft is splayed outwards to form a cylindrical sheath of spines. In this position, the spines rotate continually against the enveloping sediment. These spines help in the construction of a sanitary drain, which is used to remove excess water from the burrow (Chesher 1968). The outward splaying compacts sediment behind the animal to form a cylindrical tube. Mucus carried backwards from the sub-anal fasciole covers these spines and is pressed into the walls during compaction.

(*e*) *Anal spines and their tubercles*

Surrounding all but the adoral margin of the periproct there are slender, pointed spines (figure 76 (3*h*)), which curve gently towards the periproct. Anal spines shorten and rapidly grade into latero-dorsal spines away from the periproct. The associated tubercles have a slight bilateral symmetry that becomes more pronounced away from the periproct. The areole is enlarged on the side away from the periproct, while crenulation is better developed on the opposite side. These spines form a semicircular screen around the periproct, ensuring that faecal discharge drops behind the animal and does not foul the aboral respiratory surface.

(*f*) *Latero-dorsal tubercles and spines*

Small, strongly curved, spatulate spines are found on dorsal and lateral areas outside the inner fasciole (figure 76 (3*b*)). These spines are strongly inclined towards the posterior and, because of their high density, they overlap considerably. The flattened side of the spatulate tip faces the burrow wall. The associated tubercles are densely packed and highly distinctive (figure 5). The areole is greatly enlarged to the anterior or adapical side, while, on the opposite side, a ridge is developed (figure 75). The rest of the platform is smooth. The boss has a low profile and is gently tilted.

Latero-dorsal spines are raised and lowered with only slight rotation, and beat with a metachronal rhythm. They compact the walls of the burrow and pull mucus away from the inner fasciole. The whole aboral surface becomes cocooned in a mucous layer derived largely from the inner fasciole (Pequignat 1970). This layer is moved by the spines and helps to transport sediment posteriorly (Bromley & Asgaard 1975). Chesher (1968) found that much of the sediment excavated from the frontal wall by *Brissopsis alta* Mortensen is compressed into the lateral walls of the burrow by the action of the spines. The same is likely to be true in *Echinocardium*. The compaction and mucous plastering help to maintain the burrow walls. The curvature of the spines ensures that more of the spine tip can be used in burrow maintenance. It also produces a denser and more effective barrier, which prevents sediment from falling between spines and clogging the burrow.

(*g*) *Anterior scraping spines and their tubercles*

Robust, bluntly pointed spines, held more or less perpendicular to the test, occur on the anterior interambulacra above the ambitus. The shaft is bent slightly to point away from ambulacrum III (figure 76 (3*i*)). The associated tubercles are strikingly different from the surrounding tubercles of the latero-dorsal plastering spines (figure 16). They are larger (because of their stouter spines) and have crenulate platforms. Crenulation is usually radially symmetrical, though it may be slightly enlarged on the side furthest from ambulacrum III. The areole is moderately enlarged in a latero-dorsal direction.

During burial, these spines rotate through 25 to 30°, with a preferred oral and lateral movement. They loosen sediment of the front wall of the burrow, which can then be transported posteriorly, allowing the urchin to progress through the substratum.

(*h*) *Spines of the apical tuft and their tubercles*

Large, gently curved spines with pointed tips arise from the interambulacral plates marginal to ambulacrum III, within the inner fasciole. The largest spines are found adjacent to the anterior ambulacrum, and spines become progressively smaller towards the fasciole. Larger spines bend, near their base, towards ambulacrum III and then curve upwards (figures 72 and 76 (3*a*)). They are inclined meso-apically across the ambulacrum.

The associated tubercle arrangement is depicted in figure 72*g*. The largest tubercles are found centrally within the fasciole adjacent to the ambulacrum. Tubercles decrease in size, both adorally and adapically, as well as laterally towards the fasciole. The areole in the larger tubercles is moderately enlarged in an antero-lateral direction, but, towards the fasciole, areole enlargement changes to face laterally. The smallest tubercles, just within the fasciole, have an anterior areole enlargement. A ridge is present on the meso-posterior side of the platform of larger tubercles. The rest of the platform is crenulate. In smaller tubercles, the ridge is posterior and crenulation is feebly developed or absent.

When *Echinocardium* is at the surface, these spines lie flattened backwards and do not form a tuft. During burial, however, the spines are raised to form a tuft and, as sediment builds up aborally, they actively splay outwards and help in the construction of an apical funnel (Nichols 1959). The action of the apical tuft of spines has been described, by Chesher (1963), in *Moira atropos*. Mucus is transferred from the fasciole to the apical tuft by the jostling of the spines of graded size. The compacting and mucous-plastering activities of the apical tuft of spines can help to build a funnel during descent into the substratum, but new funnels must be constructed and maintained entirely by the tube feet (Nichols 1959; Chesher 1963). The apical tuft can only maintain the lower opening to the funnel and pass mucus to funnel-building tube feet (Chesher 1963).

(*i*) *Frontal arch of protective spines and their tubercles*

Below the inner fasciole, slender and curved spines arch over the anterior ambulacral groove, forming a grill (figure 76 (3*f*)). These pointed spines, which originate from interambulacral tubercles adjacent to ambulacrum III, curve towards the anterior groove. Tubercles in this zone are smaller than marginal tubercles inside the inner fasciole. Tubercles adjacent to the ambulacrum are larger than those more laterally situated. The areole is enlarged away from the ambulacrum, except in the larger tubercles, where the areole is enlarged in a more ventro-lateral position. Larger tubercles are crenulate and have a ridge on the ambulacral side (figure 72*e*). Smaller tubercles lose this crenulation and, away from ambulacrum III, the areole becomes enlarged in an adoral direction.

(*j*) *Spines of ambulacrum III and their tubercles*

(i) *Within the inner fasciole.* On the floor of the ambulacrum, between the two rows of tube feet, a dense and distinctive arrangement of spines is found. Long and slender spines, which curve perradially, occur by the tube feet. Spines become progressively shorter towards the midline and smaller spines become spatulate (figures 72*h* and 76 (3*j*)). Central spines are flattened distally in the vertical plane, and curve perradially. Tubercle arrangement is equally distinctive (figures 72*g* and 106). Tubercle size progressively decreases perradially. In all tubercles, the areole is enlarged on the meso-anterior side. This enlargement is more pronounced in smaller tubercles that are tilted in a latero-dorsal direction. In the larger tubercles, there is a platform that is broadest on the adapical side. Smaller tubercles lack any discernible platform.

The spatulate spines were observed to move sediment grains with an inward and adoral stroke followed by a semicircular recovery stroke. Their function has been described by Buchanan (1966). The larger, pointed spines, adjacent to the tube feet, are primarily protective. Smaller, spatulate spines push particles perradially, to concentrate them and enmesh them in a mucous string.

(ii) *Below the inner fasciole.* Between the adradial suture and the floor of the frontal groove there is a broad band of miliary spines (figure 72*f*). Large curved spines form a line by the tube feet. Spines rapidly decrease in size perradially and much of the central part has short spatulate spines. These are less densely packed than those within the inner fasciole. Even so, their arrangement matches that within the inner fasciole (figure 72*e*), except that the small, tilted tubercles of the central region occur over a much broader area.

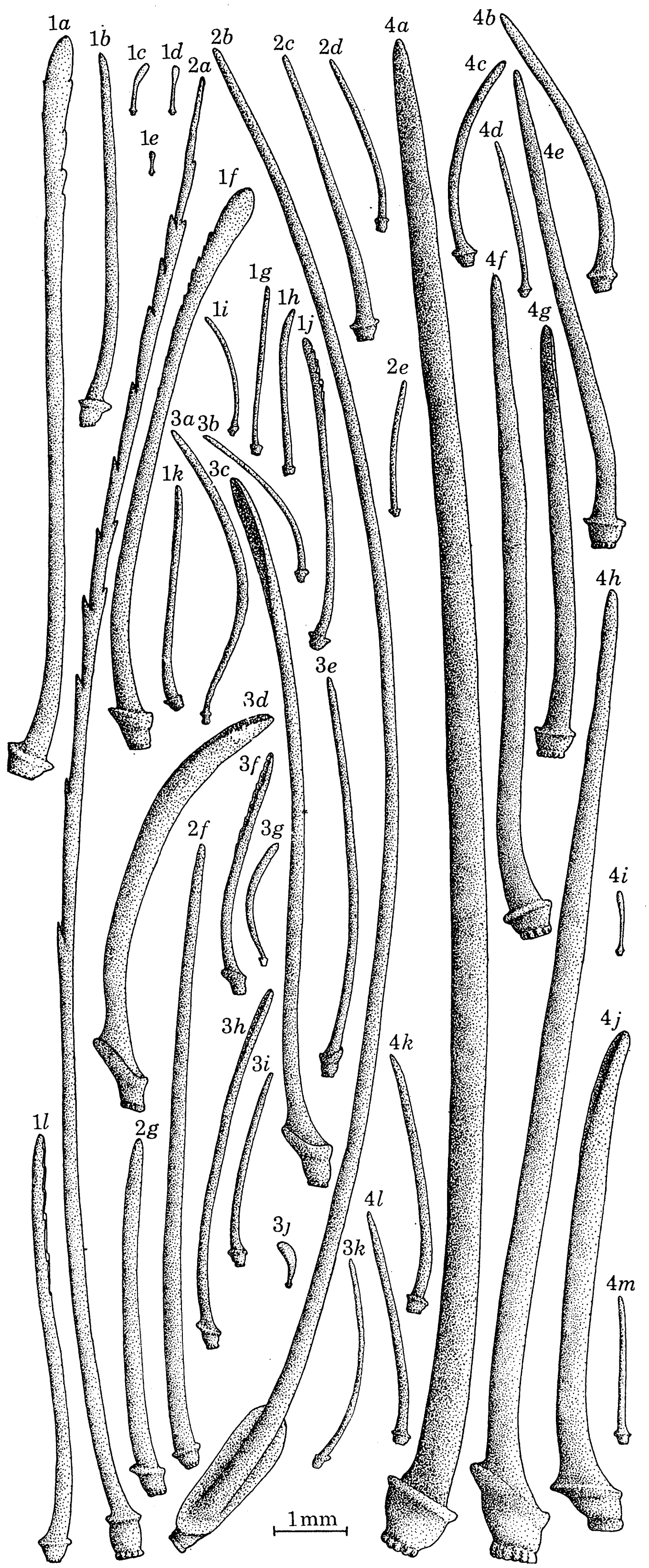

FIGURE 76. For description see facing page.

2. *Tubercles and spines in other spatangoids*

Tubercle arrangement is illustrated for *Spatangus purpureus* Müller (figure 77), *Brissopsis lyrifera* (Forbes) (figure 78), *Maretia planulata* (Lamarck) (figure 79) and *Metalia spatangus* (Linnaeus) (figure 80). These four species were selected from the eleven studied in detail to display the variation encountered.

(*a*) *Plastron tubercles and spines*

Plastron tubercles and spines are present in most spatangoids. However, in *Paramaretia peloria* (Clark), modified spines are absent and there is only a small posterior area where small undeveloped tubercles and spines are found. Similarly in *Maretia planulata*, plastron tubercles and spines are developed only in a small area immediately anterior to the sub-anal fasciole (figure 79). Despite their poor development of plastron spines, these species are not sluggish movers. *Lovenia elongata* (Gray), which also has few plastron spines, can move with great speed (Ferber & Lawrence 1976). In these species, latero-ventral spines must provide the propulsive force for locomotion as well as being used in burial.

In other spatangoids, plastron tubercles are similarly arranged (figures 77, 78 and 80). Most tubercles are crenulate. Crenulation is enlarged and semi-fused to one side of the platform in *Paraster doederleini* Chesher and *Spatangus purpureus* (figure 88), but, in other species, there is a clear ridge on the postero-lateral or antero-lateral side (figure 84).

Spatangoids from muddy substrates (e.g. *Moira atropos* (Lamarck), *Paraster doederleini* and *Brissopsis lyrifera*) have broad, spoon-shaped tips to their plastron spines. Those from coarser sands and gravels (e.g. *Spatangus purpureus*, *Echinocardium pennatifidum* Norman and *Maretia planulata*) have plastron spines that show little distal flattening. This confirms the observations of Nichols (1959).

(*b*) *Latero-ventral tubercles and spines*

Latero-ventral tubercles follow a similar pattern in all spatangoids examined (figures 77–80). The spines are spatulate to a greater or lesser extent. In species from muddy substrata (e.g. *Moira*, *Paraster* and *Brissopsis*), the boss is tilted and the platform crenulate. Crenulation is more marked on the side to which the spine leans (figures 19 and 74). Those from coarse sands or gravels (e.g. *Spatangus*, *Maretia*, *Paramaretia*, *Brissus unicolor*, *Metalia spatangus* and *Echinocardium pennatifidum*) have strongly asymmetrical platforms. There is a ridge or semi-fused crenulation to the posterior, while, around the admedial side to the anterior, crenulation becomes

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FIGURE 76. Camera lucida drawings of spines of spatangoids. (1) *Brissopsis lyrifera*: *a*, ventro-lateral interambulacral; *b*, sub-anal tuft; *c*, *d* and *e*, ambulacrum III within fasciole; *f*, plastron; *g*, marginal to peristome; *h*, ambulacrum III adjacent to tube feet; *i*, peristomial lip of the labrum; *j*, dorso-lateral protective; *k*, aboral protective inside the peripetalous fasciole; *l*, apical tuft. (2) *Maretia planulata*: *a*, aboral protective; *b*, ventro-lateral; *c*, aboral; *d*, marginal to peristome; *e*, aboral; *f*, sub-anal; *g*, plastron. (3) *Echinocardium cordatum*: *a*, ambulacrum III, within inner fasciole, adjacent to tube feet; *b*, aboral protective (spatulate); *c*, ventro-lateral; *d*, plastron; *e*, sub-anal; *f*, anterior interambulacral, forming arch across ambulacrum III; *g*, ambulacrum III, floor between midline and tube feet; *h*, marginal to the periproct; *i*, anterior scraping spine; *j*, ambulacrum III, inside the inner fasciole, at the midline; *k*, marginal to the peristome. (4) *Spatangus purpureus*: *a*, aboral defensive; *b*, marginal to the peristome; *c*, peristomial lip of the labrum; *d*, aboral; *e*, anterior interambulacrum, ambital; *f*, sub-anal; *g*, anterior interambulacrum forming protective arch across ambulacrum III; *h*, ventro-lateral; *i*, ambulacrum III, central; *j*, plastron; *k*, dorso-lateral protective; *l*, ambulacrum III, adjacent to tube feet; *m*, ambulacrum III, between tube feet and midline.

progressively smaller and closer to the mamelon. Crenulation is feeble or absent on the postero-lateral side (figure 89). The differences in tubercle structure appear to result from differences in spine size and posture. The spines of the three mud-dwelling urchins are relatively short and slender and are less strongly inclined than those of sand- and gravel-dwelling urchins. In sands and gravels, larger and more inclined spines, which excavate sediment with an oar-like action, are preferred, whereas, in muds, a more rotary action appears to be more efficient.

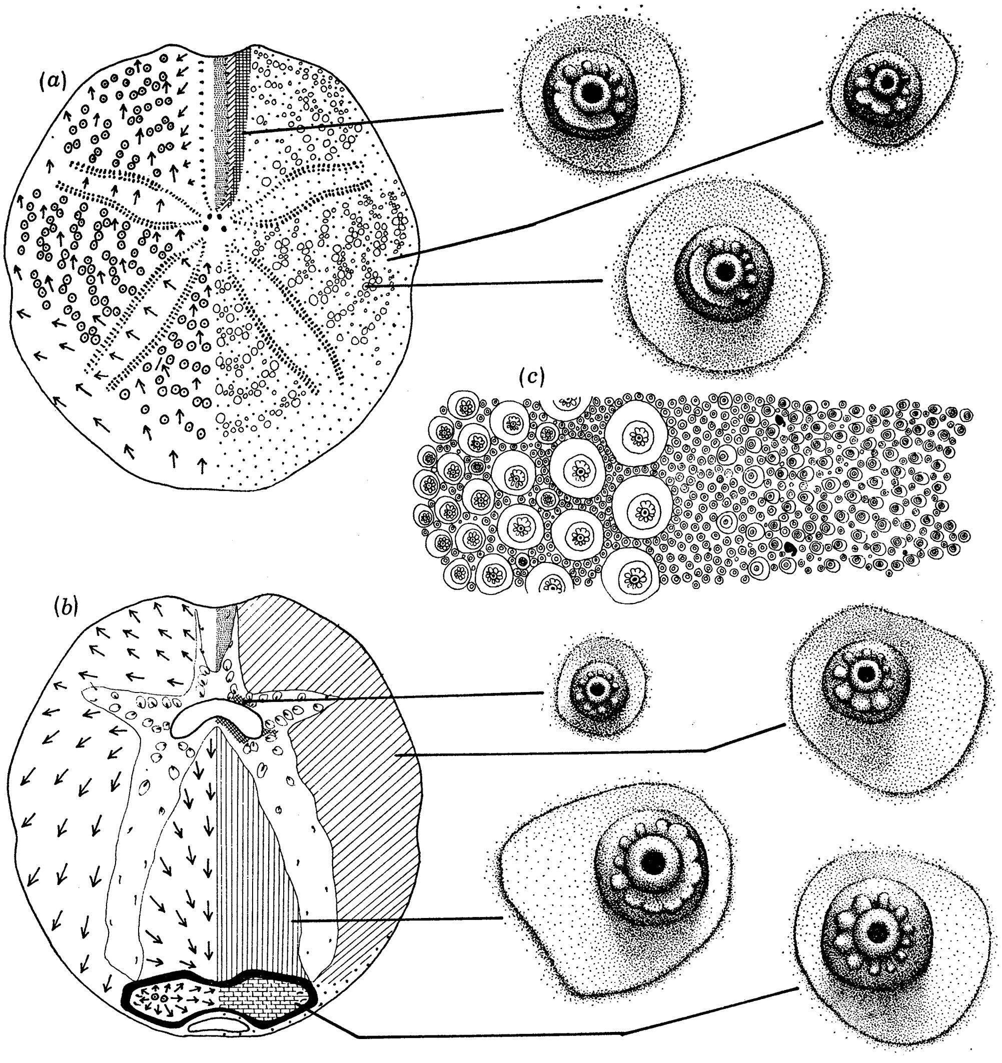

FIGURE 77. Tubercle arrangement in *Spatangus purpureus*. (*a*) Aboral; (*b*) oral; (*c*) tubercle arrangement in ambulacrum III from the interambulacrum (left) to the midline of the ambulacrum (right). Apex to the top. Symbols as in figure 72, but circles indicate large aboral spines.

(*c*) *Spines of the sub-anal tuft and their tubercles*

Nichols (1959) pointed out the correlation between the shape of the sub-anal fasciole and the number of sanitary funnels constructed. Tubercle arrangement also clearly reflects whether a single or double tuft of spines is present and hence whether one or two funnels are constructed (compare figures 72 and 78). Tubercles are radially arranged around either one or two centres within the sub-anal fasciole. Neither *Moira atropos* nor *Paraster doederleini* possess a sub-anal fasciole or tuft of spines, and *M. atropos* is known to burrow without constructing a sanitary funnel (Chesher 1963). However, spatangoids lacking a sub-anal fasciole are not always incapable of constructing a sanitary funnel. Specialized funnel-building tube feet are found in certain species lacking a sub-anal fasciole (Smith 1980), while, in the Cretaceous holasteroid *Infulaster*, sub-anal tubercle arrangement shows that there were two distinct tufts of spines. In *Maretia* and *Paramaretia*, sub-anal spines do not form such a distinct tuft and tubercles are not radially arranged (figure 79). It is not known whether these animals construct a sanitary funnel.

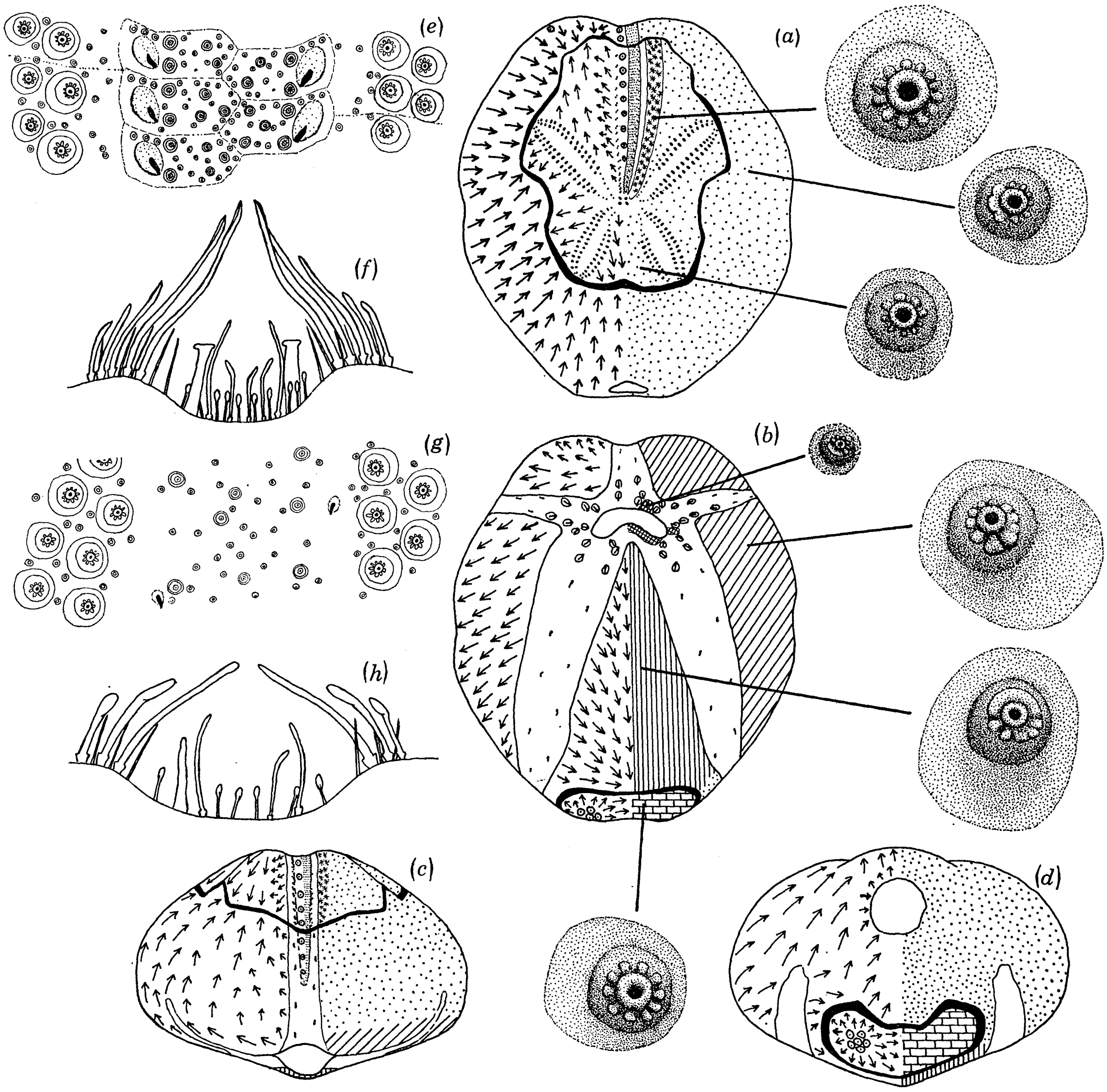

FIGURE 78. Tubercle arrangement in *Brissopsis lyrifera*. (*a*) Aboral; (*b*) oral; (*c*) anterior; (*d*) posterior. Symbols as in figure 72. (*e*) Tubercle arrangement in ambulacrum III within the fasciole, apex to the top. (*f*) Spine arrangement in ambulacrum III within the fasciole. (*g*) Tubercle arrangement in ambulacrum III below the fasciole, apex to the top. (*h*) Spine arrangement in ambulacrum III below the fasciole. Note the radial arrangement of tubercles around two loci in the bilobed sub-anal fasciole.

(*d*) *Latero-dorsal tubercles and spines*

A uniform protective covering of curved aboral spines is present in most spatangoids. Where there is a peripetalous fasciole, spine and tubercle arrangement differs on either side of the fasciole (figures 78 and 80). Within the fasciole, except by ambulacrum III, spines arch across the ambulacra, forming a protective arch to the respiratory tube feet. In *Echinocardium*, only spines immediately anterior to the ambulacra form the protective arch. Outside the peripetalous fasciole, spines are inclined away from the fasciole. Areole enlargement is developed in the opposite direction to the inclination of the spine, thus tubercle arrangement matches the arrangement of spines (figures 78 and 80). Latero-dorsal tubercles have a pronounced bilateral symmetry (figures 11, 75, 82 and 90). A ridge or large and often semi-fused crenulation is developed on the opposite side to areole enlargement. The latero-dorsal tubercles of *Moira atropos* have a unique structure. The platform has a horseshoe-shaped ridge open on the opposite side to the direction of areole enlargement (figure 87). The functional significance of this design is unknown.

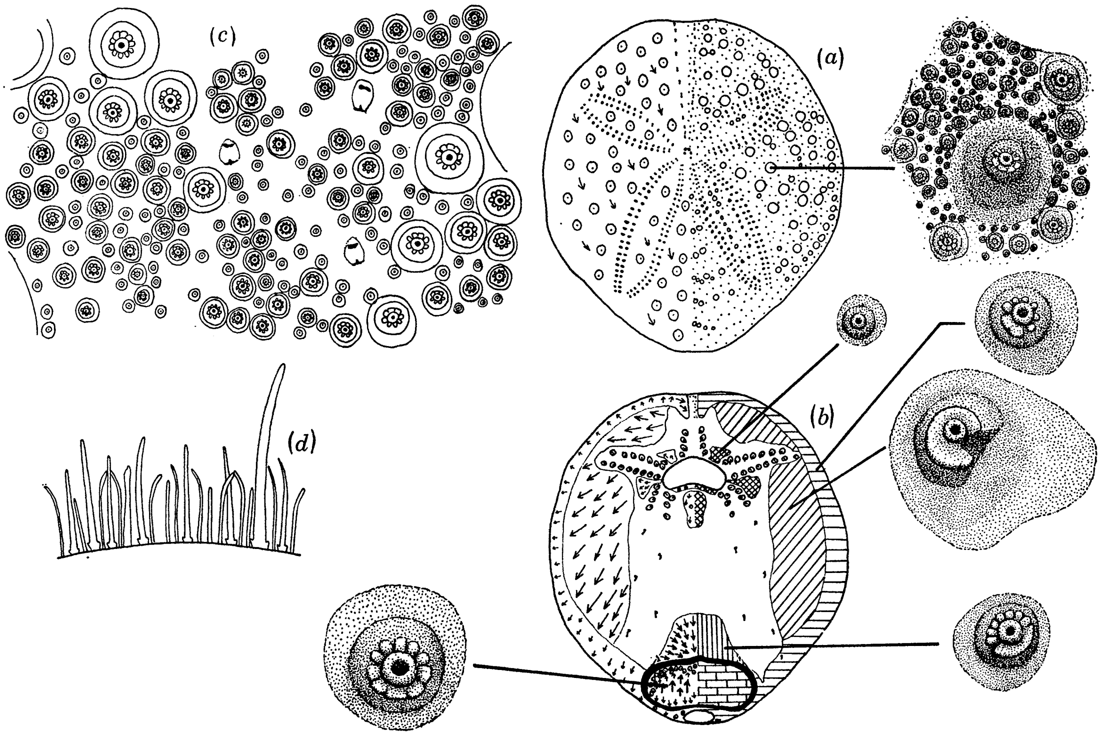

FIGURE 79. Tubercle arrangement in *Maretia planulata*. (*a*) Aboral; (*b*) oral. Symbols as in figure 72, but circles indicate large aboral spines. (*c*) Tubercle arrangement in ambulacrum III (aboral), apex to the top. (*d*) Spine arrangement in ambulacrum III.

Spatangus purpureus, *S. raschi*, *Maretia planulata* and *Paramaretia peloria* lack a uniform covering of spatulate aboral spines. They have numerous very large interambulacral tubercles (figure 86) which support long and stout spines with pointed tips (figure 76 (2*a*), (4*a*)). In *Spatangus*, there are areas with a uniform covering of weakly spatulate spines in more posterior and lateral parts, where large spines are rare (figure 77). Between the large tubercles there is a rather sparse arrangement of smaller tubercles and miliaries (figures 79 and 86). Large aboral spines in

Lovenia elongata can be brandished in defence and can also be used to right the creature if it becomes overturned (Ferber & Lawrence 1976). Aboral spines of *Spatangus purpureus* are also used in righting (Romanes & Ewart 1871, quoted by Reese (1966)). Undoubtedly, these spines provide a major deterrent to many predators. Neither *Lovenia* nor *Spatangus* burrow to great depth (i.e. 2–3 cm) (Nichols 1959; Gage 1966; Ferber & Lawrence 1976). *Paramaretia multituberculata* Mortensen, which also possesses numerous large aboral spines, is probably epifaunal, as it has been recognized in a sea bottom photograph (Fell 1960). In an aquarium tank, *Spatangus raschi* ploughed, half-buried (Nichols 1959). Finally, both *Breynia australasia* (Leach) and *Plagiobrissus grandis* (Gmelin) have moderately large aboral spines confined within the peripetalous fasciole and both are capable of living buried within sands and shell gravels (see appendix).

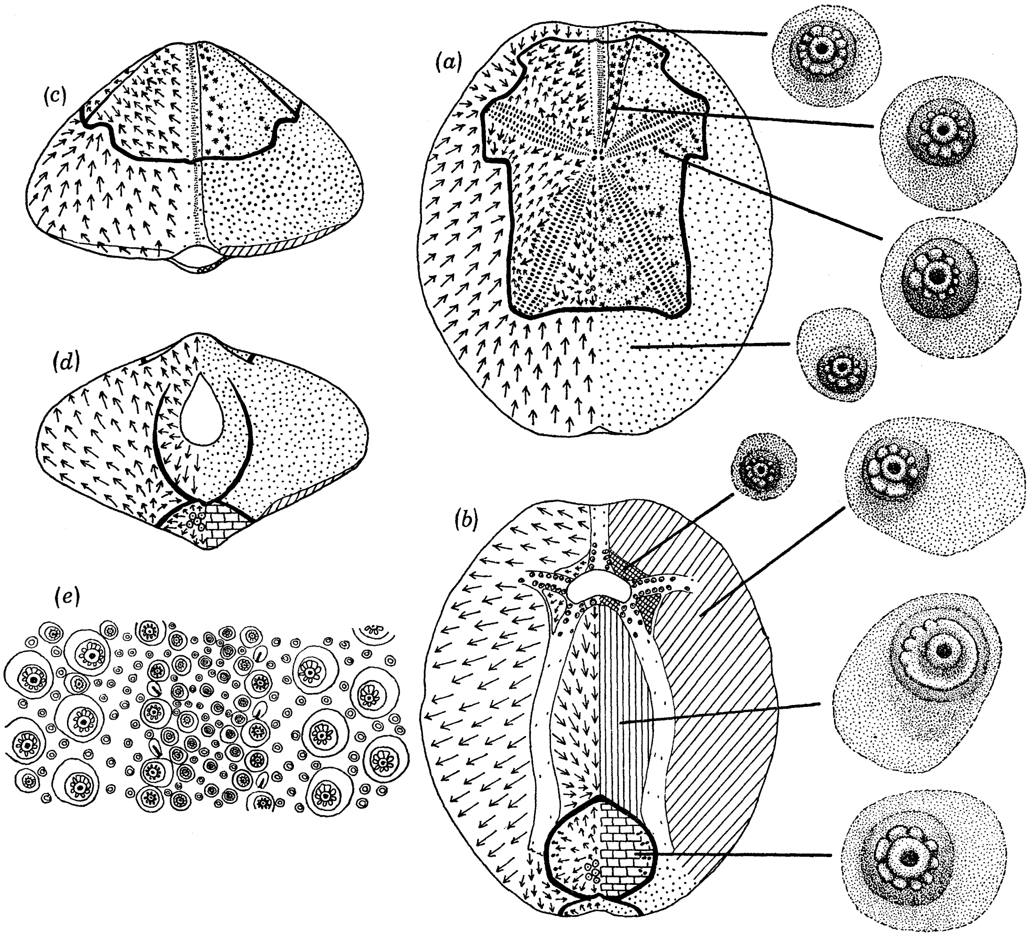

FIGURE 80. Tubercle arrangement in *Metalia spatangus*. (*a*) Aboral; (*b*) oral; (*c*) anterior; (*d*) posterior; (*e*) tubercle arrangement in ambulacrum III (aboral), apex to the top. Symbols as in figure 72; asterisks within the peripetalous fasciole indicate larger protective spines.

The lack of a uniform covering of spatulate spines and of an aboral fasciole suggests that *Maretia*, *Paramaretia* and *Spatangus* are less specialized for living infaunally than are other spatangoids. Most spatangoids can compact and maintain a burrow wall by the action of their laterodorsal spines and with the aid of a mucous coat derived principally from the dorsal fasciole.

The spines and mucous coat maintain a water space between the burrow wall and the surface of the test and also help to transport material posteriorly. Spatangoids without a dorsal fasciole and aboral compacting spines must rely on the interlocking properties of the sediment grains and can, therefore, burrow only in coarse sands or gravels.

(*e*) *Anterior scraping spines and their tubercles*

Only *Echinocardium cordatum* possesses specific excavatory spines. In other spatangoids, all spines at or immediately above the anterior ambitus are short and stout and are held approximately perpendicular. These spines are associated with more radially symmetrical tubercles than occur in other latero-dorsal areas. The anterior tubercles in *Brissus unicolor* are notably larger than other aboral tubercles outside the peripetalous fasciole.

(*f*) *Tubercle and spine arrangement in ambulacrum III*

(i) *Introduction.* The anterior ambulacrum plays a very important role in burial and feeding. Firstly, it often bears funnel-building tube feet and, secondly, it provides the major, if not sole, passageway for transporting sediment particles adorally. Echinoids that burrow in coarse, porous sediments do not need to build an apical shaft to the surface, since oxygenated waters can be drawn through interstitial spaces by cilia-induced currents. It has been suggested that water currents flowing through permeable substrata are of primary importance in irrigating the burrows of *Echinocardium cordatum* (Pequignat 1970). Pequignat proposed that currents approaching the anterior flow up the anterior ambulacra and then down the posterior ambulacra. The evidence put forward in support of this is rather insubstantial and the major channel linking the anterior and posterior ambulacra outside the fasciole, which he illustrated (Pequignat 1970, fig. 6), does not exist in British populations (compare with figure 72, this paper). Bromley & Asgaard (1975) adopt Pequignat's views and add the suggestion that water also flows from the anterior to the posterior ambulacra by twice crossing through the inner fasciole, which they assume would be inactive. However, unless the mucous coating is also to be lost, ciliary activity is unlikely to cease completely. Even if the fasciole were inactive, the thick band of very dense clavulae would have a pronounced dampening effect on the water flow. In addition, Pequignat (1970) confirmed earlier observations that the ciliature of aboral spines is centrifugal. It therefore appears that, although water currents through the sediment may be beneficial, centrifugal currents produced by the fasciole and drawn down on to the apex are probably of much greater importance.

Echinoids can burrow to considerable depths in coarse sands or gravels without an apical funnel. For example, *Meoma ventricosa* can live up to 10 cm below the surface (Chesher 1969), and *Brissus latecarinatus* commonly lives buried to 20 cm and has been found as deep as 50 cm (Takahashi 1938). Even in fine sands, some species, such as *Lovenia elongata* and *Brissus unicolor*, can burrow to around 2 cm depth without the need of an apical funnel (Ferber & Lawrence 1976; Tornquist 1911). However, nearly all urchins that burrow to any depth in fine or muddy sediments need to build an apical funnel to irrigate the burrow. Tubercle arrangement can help to identify those species that construct an apical funnel.

(ii) *The arrangement of spines and tubercles bordering ambulacrum III.* To be capable of constructing an apical funnel, Recent spatangoids must possess certain features, namely specialized funnel-building tube feet, an apical tuft of spines and a closely associated fasciole. The function of the apical tuft of spines has been described previously (§ V, 1 (*h*)). It plays an important role in maintaining a space in which funnel-building tube feet can manoeuvre. Where there is an apical tuft of spines, the tubercle arrangement on the adjacent interambulacra is fairly distinctive and has been described in detail for *Echinocardium* (§V, 1 (*h*)). The apical tuft of spines is always closely surrounded by a fasciole. This allows mucus to be readily transferred on to the tuft of spines.

Where no such apical tuft is developed, aboral spines are either uniformly arranged over the whole interambulacral area or form a protective arch across ambulacrum III. In the former, interambulacral tubercles continue, unmodified, right up to ambulacrum III (figures 79, 80, 92, 95 and 96). Interambulacral tubercles are somewhat larger and more closely packed at the margin of the ambulacrum, where spines arch over the frontal ambulacrum. The decrease in tubercle size away from the ambulacrum is much less pronounced than with tubercles of an apical tuft. Areole enlargement occurs on the side away from the ambulacrum, whereas a ridge, or, more usually, enlarged crenulation is developed facing the ambulacrum. Where an apical tuft of spines is present, adapical tubercles are obviously larger than those towards the ambitus. There is no such pronounced difference where the spines form a protective arch.

Although the anterior ambulacrum is commonly sunken, this is not thought to be related to the size of the funnel-building tube feet, as was suggested by Kier (1974). In many instances, the region with funnel-building tube feet may be less deeply sunken than the ambital region of the ambulacrum. *Echinocardium pennatifidum* has funnel-building tube feet yet has a planar frontal ambulacrum, whereas the holasteroid *Infulaster excentricus* (Forbes) has a deeply sunken frontal sulcus but pores suggesting that it possessed only sensory tube feet. The sunken ambulacrum is primarily concerned with the adoral transportation of particles, as proposed by Nichols (1959).

The presence of an appropriate fasciole and an apical tuft of spines does not always indicate that a particular species is capable of building an apical funnel. Judging from published photographs, *Lovenia elongata* appears to have a similar arrangement of tubercles adjacent to ambulacrum III, as *Echinocardium*, yet this species burrows without building an apical funnel (Ferber & Lawrence 1976). This is because *Lovenia* lacks funnel-building tube feet.

(iii) *The arrangement of spines and tubercles within ambulacrum III.* Tubercle arrangement within ambulacrum III is very variable and, so as to avoid wordy descriptions, stereo electron micrographs of the different arrangements are given (figures 91–107). The corresponding spine arrangement is illustrated, for a number of species, in figures 78, 79 and 99.

In those spantangoids that inhabit coarse sands and gravels (e.g. *Echinocardium pennatifidum*, *Metalia spatangus*, *Paramaretia peloria*, *Brissus unicolor* and *B. latecarinatus*), the frontal ambulacrum is usually flush with the rest of the aboral surface or may even be slightly raised. The ambulacrum is typically narrow with small, well spaced unipores bearing sensory tube feet. Ambulacral tuberculation differs from that of adjacent interambulacra only in the absence of larger tubercles (figures 91–94). It does not change adambitally. A row of larger tubercles occurs immediately perradial to ambulacral pores and these bear moderately long and often gently curved spines, which guard the tube feet. The narrow zone between these two rows has only sparse, scattered miliaries and small tubercles which bear small, more or less straight spines. Adjacent interambulacral spines do not curve over ambulacrum III to form a protective arch.

The coarseness of the substratum in which these species live precludes the use of ciliary currents for transporting particles adorally. Ambulacral spines are neither spatulate nor modified for mucus secretion and are thus not specialized for moving sediment. All available evidence suggests that sediment is not transported adorally in the frontal ambulacrum and that these species must feed entirely upon sub-surface particles collected by the phyllode tube feet when they are buried.

In *Brissopsis lyrifera*, *B. atlantica* and *Paraster doederleini*, the frontal ambulacrum is somewhat sunken and is much broader than those described above. Although only *B. atlantica* is known, for certain, to build an apical funnel (Chester 1968), all possess a small apical tuft of spines and funnel-building tube feet and are thus capable of constructing a funnel. Ambulacral pores are linearly arranged and closely spaced. Immediately perradial to the pores is a row of larger tubercles supporting moderately long and pointed spines which guard the tube feet. Marginal to the pores, there are only a few, sparsely distributed miliaries. The floor of the ambulacrum is covered with irregularly scattered miliaries and small tubercles (figures 100–103). The very small miliary spines are straight and terminate in a swollen, fleshy head with mucous glands and many cilia. The tubercles bear slightly larger and weakly spatulate spines, which curve adradially. In *Paraster*, these spines become progressively smaller perradially, while, immediately adapical to the fasciole, there are larger and stouter, spatulate spines, which curve perradially.

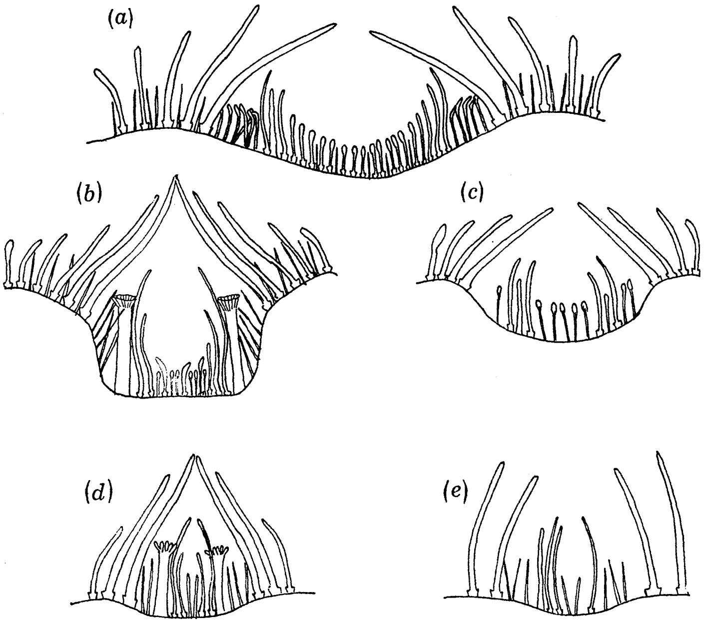

FIGURE 99. Spine arrangement in ambulacrum III: (*a*) *Spatangus purpureus*, aboral; (*b*) *Paraster doederleini*, aboral within the peripetalous fasciole; (*c*) *P. doederleini*, aboral, below the peripetalous fasciole; (*d*) *Echinocardium pennatifidum*, aboral within the inner fasciole; (*e*) *E. pennatifidum*, aboral below the inner fasciole. Tube feet appear in all parts of this figure.

Below the fasciole, the arrangement of tubercles and spines differs slightly (figure 78*g*, *h*). Spines of the adjacent interambulacra arch over the ambulacral groove. Each tube foot has its associated protective spine. On the floor of the ambulacrum, the tuberculation is sparser, with only the occasional tubercle amongst the miliaries. Miliary spines are noticeably longer than those within the peripetalous fasciole, but still end in a fleshy tip.

Brissopsis alta appears to have a similar tubercle arrangement (Chesher 1968, pl. 4, fig. *d*), and its mode of life has been studied in detail (Chesher 1968). *B. alta* does not apparently feed directly upon surface sediment, since it has no mucous string in the frontal groove and tube feet were never observed to extend from the funnel and rake material down into it. However, major cilia-induced water currents are drawn down the anterior ambulacrum, and particles introduced into the apical funnel were found on the floor of the burrow (Chesher 1968). The arrangement of tubercles and spines is clearly dissimilar to that found in species known to feed by means of a mucous string. However, the anterior ambulacrum is obviously modified for a particular function and it seems highly probable that finer particles can be transported adorally down the frontal groove by ciliary currents. Although the spines may also be involved in trapping and transporting sediment, this has not developed to the extent of producing a compact string of mucus-enmeshed particles.

Echinocardium cordatum and *Moira atropos* both feed by means of a mucous string (Buchanan 1966; Chesher 1963). The distinctive arrangement of spines and tubercles in *E. cordatum* has been described previously (§ V 1 (*j*)), and Chesher (1963) has fully described the spine arrangement in *M. atropos*. The spines on the floor of the ambulacrum have a U-shaped arrangement, and the associated tubercles progressively decrease in size perradially. In *Echinocardium*, the smaller spines are strongly spatulate, but, in *Moira*, the spines have a thick, fleshy covering. The U-shaped arrangement of spines presumably ensures that particles are moved to the midline, where the mucous string lies. Ambulacral tubercles are closely packed, with few interspersed miliaries. In *Moira*, alternating plates in each column have a neat row of tubercles which decrease in size perradially. Below the fasciole, tubercles and spines are rather less dense but have much the same arrangement. These spines are not linearly arranged and those near the perradius are bent meso-ventrally and have only slightly swollen tips.

A rather similar arrangement of tubercles and spines is found in the anterior ambulacrum of *Spatangus*. The ambulacrum is broad and only weakly sunken. Adjacent interambulacral spines arch over the ambulacrum. The largest ambulacral tubercles are found adradially, where they form a poorly defined row. They bear gently curved spines, which guard the tube feet (figure 76 (4*c*)). The size of tubercles decreases perradially, though much of the central region has uniformly sized tuberculation (figures 105 and 107). Areole enlargement is developed towards the midline and slightly adorally. Crenulation is more pronounced on the opposite side (figure 17). Tubercles are not particularly dense and miliaries occur between them. Miliaries also form a tract along the adradial margins of the ambulacrum. Larger, pointed spines are gently curved perradially, whereas smaller, central spines are slender and straight and terminate in a somewhat swollen tip. Miliary spines are slender and, distally, the shaft is bent adradially (figure 76 (4*m*)). The spines of the anterior ambulacrum describe a broad, U-shaped curve.

Surprisingly, the spine and tubercle arrangement in the coarse-sand-dwelling species *Spatangus purpureus* is more or less identical to that in the sandy-mud-dwelling *S. raschi*. There is no change in tubercle arrangement adambitally. Because the tubercle and spine arrangement has many similarities with that in *Echinocardium cordatum*, it seems likely that *S. purpureus* can actively transport particles adorally down the frontal groove though possibly not in a consolidated mucous string. Nichols (1959) thought that particles pass down the frontal ambulacrum, though he was never able to confirm this. If *S. raschi* is only semi-infaunal, as is suggested from the work of Nichols (1959), then it would appear that the frontal ambulacrum is non-functional.

Although *Pourtalesia miranda* Agassiz is a holasteroid, the arrangement of tubercles and spines in the anterior ambulacrum is worth recording here as it differs markedly from that observed in any other Recent echinoid. Above the ambitus, the anterior ambulacrum is more or less vertical and is flush with adjacent interambulacra. It is narrow, with a tubercle and spine arrangement much like that of adjacent interambulacra except that the larger spines and tubercles are absent. Spines are held perpendicular and do not arch over the ambulacrum.

Below the ambitus, the anterior ambulacrum turns inwards and becomes deeply sunken to form a funnelled opening to the peristome. Interambulacral spines around the lip of this recess curve in towards the midline but do not form a protective arch. The roof and walls of the recess are covered with curved and strongly spatulate spines borne on densely packed tubercles with marked areole enlargement. This arrangement was described by Lovén (1883).

Pourtalesia is epifaunal or, possibly, semi-infaunal, as it appears very clearly in photographs of the deep-sea floor (Southward *et al.* 1976; Billett, personal communication). It is obvious from the long, spindly spines, which form a rather sparse and non-uniform covering aborally, that *Pourtalesia* is not adapted for burial within the fine substrata on which it occurs. Without an aboral fasciole and a uniform covering of spatulate spines, *Pourtalesia* does not have the protection of a mucous coat and cannot maintain a water space between the spines and the test surface within the sediment. The mode of life postulated by Mirnov (1975) is, therefore, most unlikely.

The gut contents were found to consist of rather silty mud in the two species examined and, from this, it appears that *Pourtalesia* is a sediment swallower. *Pourtalesia* lacks phyllode tube feet for collecting sediment (Smith 1980). The recessed ambulacrum with its spatulate spines is ideally suited for shovelling sediment into the peristome. *Pourtalesia* probably feeds by ploughing forward through the sediment and, in this way, funnels the surface layer of sediment into the frontal recess, where the spatulate spines can be used to push material into the peristome. This explains why, in sea bottom photographs, a shallow furrow is left behind *Pourtalesia* as it moves forward.

Yet another tubercle arrangement is found in the frontal ambulacrum of a number of Cretaceous spatangoids and holasteroids, such as *Micraster* and *Infulaster*. In these, the whole of the frontal ambulacrum is covered in closely packed and uniformly sized miliaries, with only the occasional larger tubercle adjacent to ambulacral pores (figure 97). The associated miliary spines are likely to have been ciliated and mucus-secretory, like those of Recent spatangoids. The frontal groove was possibly used to transport sediment adorally.

3. *Fascioles and their palaeontological significance*

Fascioles are bands of very small and closely packed miliary tubercles (figure 26) bearing densely ciliated spines termed clavulae. The tubercles reach densities of well over 100 mm^{-2} and can be greater than 150 mm^{-2}. Fascioles act as ciliary pumps, enhancing water circulation within the burrow by drawing water, in one direction only, past the clavulae. The clavulae also produce copious amounts of mucus. Tornquist (1911) and Gislen (1924) observed that sediment tends to adhere to the fascioles and Chesher (1968, 1969) showed that this wall of mucous-bound sediment effectively compartmentalizes the burrow. The fascioles therefore act also as one-way valves. Mucus from fascioles is moved by the action of the spines to cover the whole aboral surface (Pequignat 1970). This mucous coat helps to transport sediment posteriorly (Bromley & Asgaard 1975), but, more importantly, it forms an effective barrier to prevent sediment particles from falling between the spines and clogging the burrow. Fascioles also supply mucus to funnel-building tube feet (Chesher 1963, 1968).

Records of the depth of burial and nature of the substratum, concerning 27 species of spatangoid, were found in the literature (see appendix). For each species, the arrangement of fascioles is indicated, together with the depth of burial and substratum (figure 108). This shows that there is little correlation between the type of fascioles and the depth of burial or substratum. For example, although most infaunal spatangoids possess either a sub-anal or a latero-anal fasciole, there is one (*Meoma ventricosa*) that possesses neither as an adult, yet lives at considerable depth within the substratum. Similarly, the suggestion by Nichols (1959) that the presence of a single or double sub-anal tuft of spines is correlated with the nature of the substratum does not appear to hold true. Species with an inner fasciole appear to be incapable of living in muddy substrata, whereas species with a peripetalous fasciole are found in all types of substrata. Buchanan (1966) suggested that *Echinocardium cordatum* does not live in mud because its method of mucous string feeding would not work in fine substrata, but this cannot be the prime reason, since *Moira atropos* feeds in this way in muds. Bromley & Asgaard (1975) suggest that *E. cordatum* may be excluded from muddy substrata because its respiratory tube feet lie outside the aboral fasciole.

For palaeontological purposes, the fasciole arrangement cannot be used to identify the depth of burial or preferred substratum of fossil spatangoids.

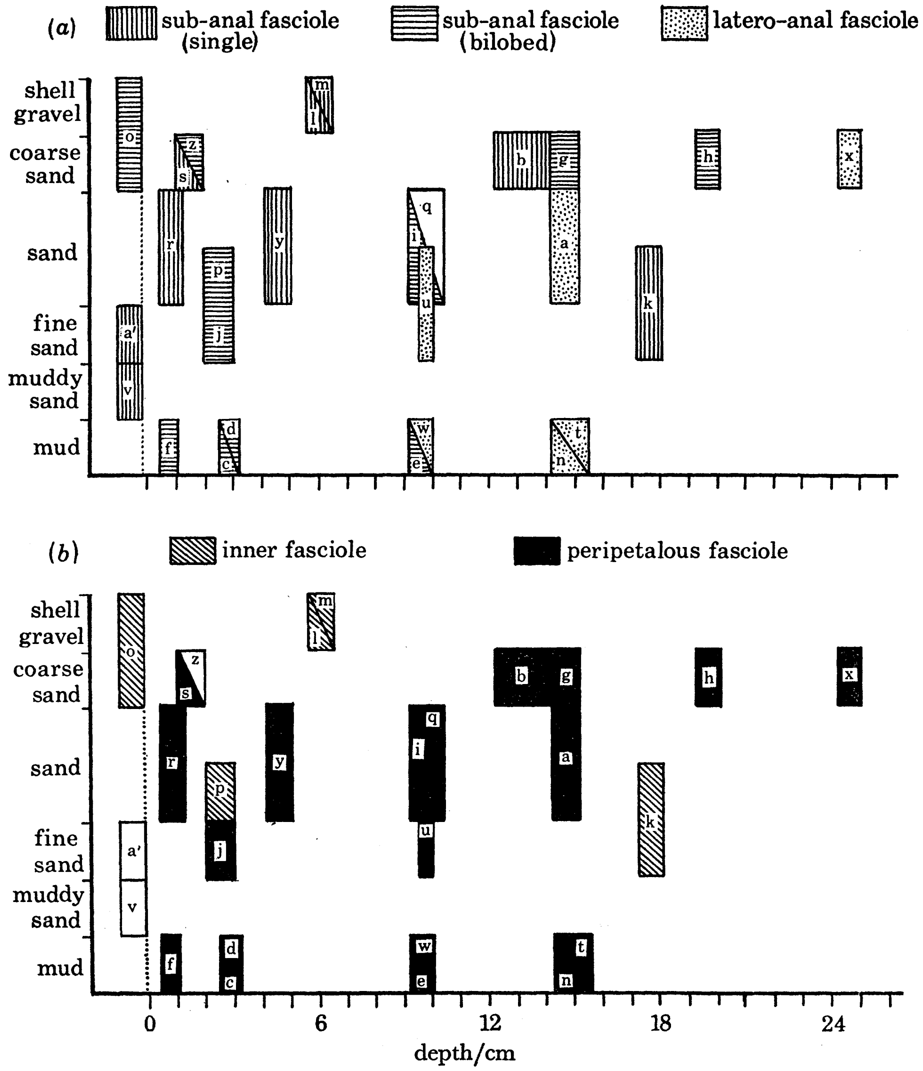

FIGURE 108. Preferred substratum and maximum depth of burial in 27 species of spatangoid, correlated with the type of fascioles in each. a, *Agassizia scrobiculata*; b, *Breynia australasia*; c, *Brissopsis alta*; d, *B. atlantica*; e, *B. elongata*; f, *B. lyrifera*; g, *Brissus brissus*; h, *B. latecarinatus*; i, *B. obesus*; j, *B. unicolor*; k, *Echinocardium cordatum*; l, *E. flavescens*; m, *E. pennatifidum*; n, *Hypselaster dolosus*; o, *Lovenia cordiformis*; p, *L. elongata*; q, *Meoma ventricosa*; r, *Metalia sternalis*; s, *M. townsendi*; t, *Moira atropos*; u, *M. stygia*; v, *Paramaretia multituberculata*; w, *Paraster doederleini*; x, *P. floridiensis*; y, *Plagiobrissus grandis*; z, *Spatangus purpureus*; a′, *S. raschi*.

VI. THE SIGNIFICANCE OF ABORAL TUBERCLE DENSITY

Infaunal echinoids need to protect their epidermis from abrasion by sediment particles and need to maintain a space for water circulation between the test and sediment of the burrow wall. They achieve this by means of their spines. A better protective coverage is obtained by having uniformly sized dorso-lateral spines and by increasing their packing density. This is brought about by reducing the size of spines and tubercles. A more effective coverage is also

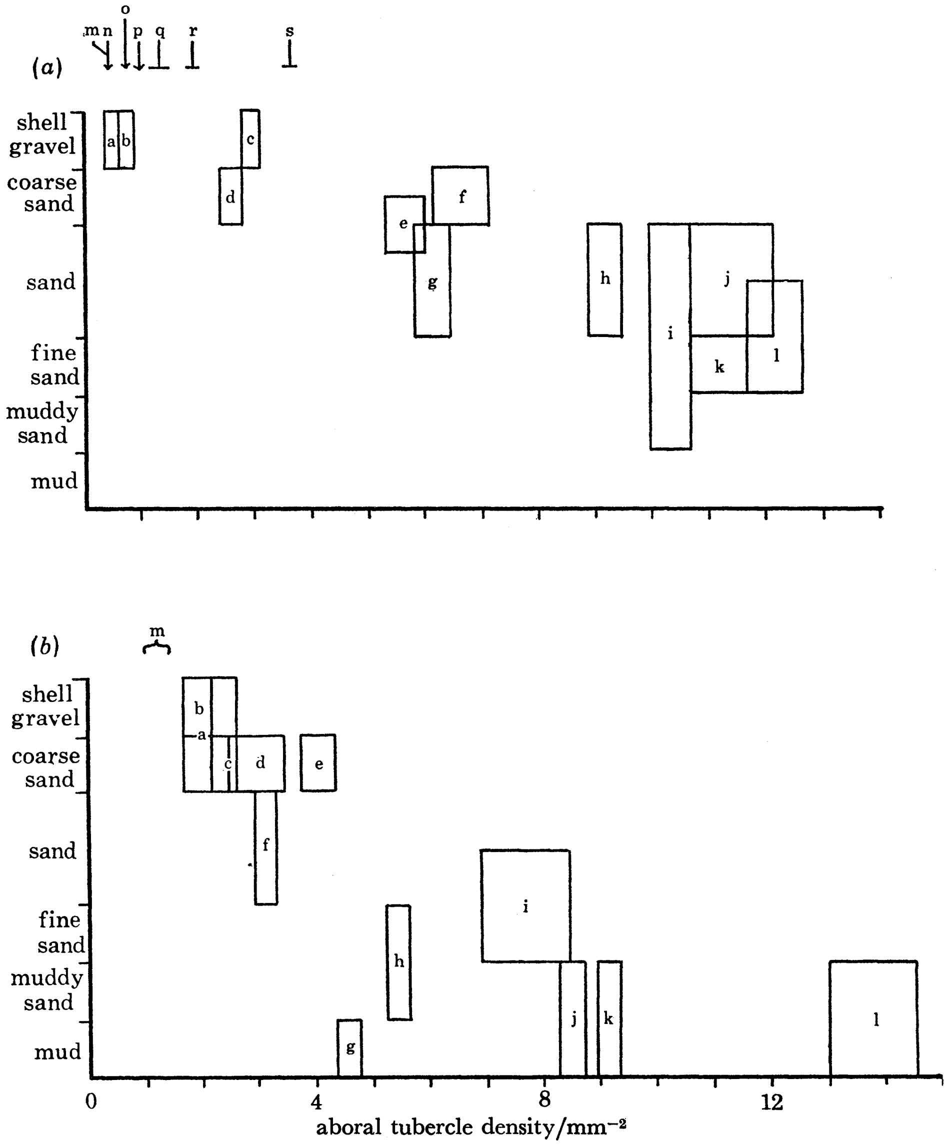

FIGURE 109. Aboral tubercle density in irregular echinoids correlated with the substratum in which they burrow. (*a*) Non-spatangoid irregulars: a, *Conolampas sigsbei*; b, *Echinolampas crassa*; c, *Apatopygus recens*; d, *Echinoneus cyclostomus*; e, *Encope michelini*; f, *Cassidulus cariboearum*; g, *Echinarachnius parma*; h, *Fellaster zelandiae*; i, *Echinodiscus bisperforata*; j, *Dendraster excentricus*; k, *Leodia sexiesperforatus*; l, *Mellita quinquiesperforata*; m, *Clypeaster rarispina*; n, *Plesiechinus ornatus*; o, *Holectypus depressus*; p, *Clypeaster rosaceus*; q, *Clypeus ploti*; r, *Galeropygus agariciformis*; s, *Nucleolites scutatus*. (*b*) Spatangoids: a, *Spatangus purpureus*; b, *Echinocardium pennatifidum*; c, *Metalia spatangus*; d, *Brissus unicolor*; e, *B. latecarinatus*; f, *Eupatagus valenciennesi*; g, *Paraster doederleini*; h, *Metalia sternalis*; i, *Echinocardium cordatum*; j, *Moira atropos*; k, *Brissopsis atlantica*; l, *B. lyrifera*; m, *Micraster cortestudinarium* and *M. coranguinum*.

achieved by increasing the surface area covered by each spine. In clypeasteroids, this is achieved by the development of a swollen tip to each spine (figure 49 (6*g*)). Spatangoids have adopted a different approach and aboral protective spines are strongly curved and held at an angle to the test, thus greatly increasing the surface area that each covers. This is further enhanced by the development of spatulate tips. Such an effective spine coverage has permitted spatangoids to live within muddy substrata.

It is therefore to be expected that a correlation between aboral tubercle density and the nature of the substratum in which a species lives should exist. Unfortunately, accurate quantitative data on the grain size and degree of sorting of the sediments in which echinoids live are sadly lacking. Much of the available data has been summarized by Lawrence & Ferber (1971) and little has appeared since. For present purposes, substrata have been classified qualitatively, taking the most accurate data available (see appendix). Some species are recorded from a variety of different sediments, and examples are known of species that will burrow to lesser depths in apparently less suitable substrata (Nichols 1975; Gage 1966; Chesher 1969). Ferber & Lawrence (1976) report that the speed of burial in *Lovenia* varies with the nature of the substratum. Tubercle density has therefore been correlated with the substratum in which each species is most commonly found.

A plot of aboral tubercle density against substratum is given for non-spatangoid irregulars (figure 109*a*) and for spatangoids (figure 109*b*). Although the number of species that have been examined is limited and the sediment data often imprecise, there does seem to be a general trend towards increasing tubercle (and spine) density with decreasing sediment grain size in both graphs. In the non-spatangoid irregulars, most infaunal species have a tubercle density of approximately 1 mm^{-2} or greater. *Clypeaster rosaceus*, which has an aboral tubercle density of approximately 1 mm^{-2}, is usually found living on, or partially buried within, the sediment (Kier & Grant 1965), though it is known to live buried in 'sand' (Chesher 1969). In contrast, the sparser-tuberculated *C. rarispina* appears to be epifaunal, as it is recorded from all types of substrata. *Echinolampas* lives infaunally (Thum & Allen 1976), as probably does *Conolampas*, and the low tubercle density achieved in these species reflects the large tubercle size and not a low packing density. Aboral tubercle densities in five species of Jurassic echinoids are also indicated in figure 109*a*. The least packed arrangement and the lowest tubercle density is found in *Plesiechinus ornatus*, which is considered to have been semi-infaunal (Smith 1978*a*). *Nucleolites scutatus* has a greater tubercle density than *Apatopygus recens*, a species inhabiting shell gravel. *Nucleolites* may, therefore, have been capable of exploiting slightly finer sediments, like the Recent *Cassidulus cariboearum*.

In spatangoids, low aboral tubercle densities are found in those species inhabiting coarser substrata. Differences in the size, curvature and development of the spatulate tip of latero-dorsal spines may be of more importance than actual tubercle density in determining the grade of substratum that can be inhabited. Spatangoids living in finer sands and muds have an aboral tubercle density of at least 4 mm^{-2}. Surprisingly, the two species of *Micraster* examined have extremely low aboral tubercle densities. The arrangement of latero-dorsal tubercles in *Micraster* is unlike that found in any Recent spatangoid. Latero-dorsal tubercles are almost radially symmetrical and miliaries are extremely dense and numerous. Whether *Micraster* was never truly infaunal or whether it tackled life in the fine sediments of the chalk sea in a different manner to Recent spatangoids is not clear.

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APPENDIX

Depth of burial and substratum preference of irregular echinoids

Only those species in which both the approximate depth of burial and the nature of the substratum have been recorded are included in the following list.

M, grain size in millimetres. *S*, coefficient of sorting.

species	sediment	depth of burial	references
Agassizia scrobiculata Valenciennes	Sandy shore.	Buried at spade depth.	Mortensen (1951)
Apatopygus recens (Milne-Edwards)	Coarse substrates of sand and shell with little or no mud; coarse shell sand or gravel calcarenite.	Buried to a depth of about 3 cm. No respiratory funnel.	Fell (1960), Pawson (1968), Higgins (1974)
Arachnoides placenta (Linnaeus)	Muddy sand; fine somewhat sandy mud; fine iron sand with practically no silt and just a trace of comminuted shell debris.	Never buried more than a few millimetres below the surface; covered by a thin film of sediment; outline readily recognizable; deeply buried, no surface elevation above specimens.	Tenison-Woods (1878), Mortensen (1921), Powell (1937), Clark (1938), Hayasaka (1948)
Astriclypeus manni (Verrill)	Sand.	Less than 5 mm of sediment covering; sometimes half buried.	Ikeda (1939)
Breynia australasia (Leach)	Sand and shells; sandy or more coarse bottoms; also from mud and from sand and mud.	At 5–6 in (12.7–15.2 cm) depth; completely buried but with slight convexity above each.	Bell (1884), Ramsay (1885), Clark (1925), Mortensen (1951)
Brissopsis alta Mortensen	Loosely packed, slimey mud; $\bar{M} = 0.054, S_0 = 1.96$; $\bar{M} = 0.19, S_0 = 6.7$; porosity = 58.1 %; permeability = 0.019.	Up to 28 mm sediment covering above apex; probably buries deeper in nature. Maintains a respiratory funnel.	Chesher (1968)
B. atlantica Mortensen	In the same sediments as *Brissopsis alta.*	Similar to *Brissopsis alta.*	Chesher (1968)
B. elongata Mortensen	Mud.	At depths of 40–100 mm.	Kier (1975)
B. lyrifera (Forbes)	Muddy bottoms; mud or sandy mud; silty substrates.	Aboral surface no more than 1 cm below the sediment surface.	Mortensen (1927), Nichols (1959), Buchanan (1967), Goldring & Stephenson (1970)
Brissus brissus (Leske)	Coarse sand.	Buried up to 15 cm depth but usually just below the surface.	Clark (1921), Chesher (1968)
B. latecarinatus (Leske)	Coarse sand or gravel; coarse coral sand; also from muddy shell sand.	7.5–10 cm below the surface: mostly buried to 20 cm but some to 50 cm. Mound of sand at surface with plug 7 cm in diameter of coarse coral sand.	Takahashi (1938), Mortensen (1951), Gibbs *et al.* (1976)
B. obesus Verrill	Sand.	About 10 cm below the surface.	Mortensen (1921)
B. unicolor (Leske)	Coarse sand.	Buried beneath or beside large coral slabs. Buries with apex 2–3 cm below surface in tank of fine sand.	Tornquist (1911), Westergren (1911), Mortensen (1951), Kier & Grant (1965), Chesher (1969).
Cassidulus cariboearum Lamarck	Coarse sand; coarse, fairly well sorted carbonate sand. Modal size class = 0.7–1.0 mm.	Buried with no respiratory funnel to 3.4 cm depth; buried 3–20 cm depth.	Kier (1975), Gladfelter (1978)

species	sediment	depth of burial	references
Clypeaster humilis (Leske)	Coarse shelly sand; sand; shell gravel.	Shallowly buried.	Clark (1923), Mortensen (1940), Clark & Bowen (1949)
C. rosaceus (Linnaeus)	Sandy substrates.	Mostly on the surface or partially buried; some buried.	Fontaine (1953), Chesher (1969), Kier (1975)
C. subdepressus (Gray)	Sandy areas with little or no grass. $\bar{M} = 0.82$; $S_0 = 1.9$.	Up to 8–10 cm below the surface; up to 2.5 cm below the surface or on the surface if the substrate is not suitable.	Kier & Grant (1965), Kier (1975), Lawrence & Ferber (1971)
Dendraster excentricus (Eschscholtz)	Fine, poorly sorted sand; clean, well sorted sand.	On or just below the surface; in inclined posture; buried to 10 cm depth maximum; completely buried at low tide, half buried at high tide; buried several inches deep.	Mortensen (1921), Ricketts & Calvin (1962), Chia (1969), Merrill & Hobson (1970)
Echinarachnius mirabilis Agassiz	Sand.	Buried at less than 5 mm depth.	Ikeda (1939)
E. parma (Lamarck)	Fairly pure sand.	On the surface, partially buried, or just covered.	Boone (1938), Ikeda (1939), Ricketts & Calvin (1962), Sokolova & Kuznetsov (1960)
Echinocardium cordatum (Pennant)	Largely found in sands or muddy sands. $\bar{M} = 0.1–0.45$; $\bar{M} = 0.135$, $S_0 = 1.62$; $\bar{M} = 0.149$, $S_0 = 1.16$; $\bar{M} = 0.125–0.177$.	To 18 cm in clean sand; to 13 cm in sand plus clay; 2 cm in fine sand plus clay. Builds a respiratory funnel.	Nichols (1959), Buchanan (1966), Lawrence & Ferber (1971), Higgins (1974)
E. flavescens (Müller)	Clean to muddy shell gravel; coarse to medium sand.	To 6 cm in shell gravel with no funnel; less deeply buried in coarse sand with respiratory funnel.	Koehler (1927), Gage (1966), Rowe (1971)
E. pennatifidum Norman	As *E. flavescens*.	As *E. flavescens*.	Koehler (1927), Gage (1966), Rowe (1971)
Echinocyamus pusillus (Müller)	Most common in coarse sands and shell gravels. $\bar{M} = 0.27–0.46$.	Nestles in interstices of shell gravel just below the surface.	Koehler (1927), Nichols (1959), Lawrence & Ferber (1971), Rowe (1971)
Echinodiscus auritus (Leske)	Sand or sandy mud.	Just buried forming an obvious mound; just below the surface or half buried.	Roxas (1928), Clark (1946, 1949), Balinsky (1958)
E. bisperforatus (Leske)	Sand or muddy sand.	Just buried forming a mound.	Bedford (1900), Balinsky (1958), Clark & Stock (1976)
Echinolampas crassa (Bell)	Coarse shelly sediment composed almost entirely of broken shell; slope zone of macro-ripples; $\bar{M} = 0.73–1.1$, $S_0 = 0.9–1.5$.	Sediment covering 3–5 cm deep.	Thum & Allen (1976)
Echinoneus cyclostomus Clark	Coarse sand; coarse, bioclastic, well sorted, grain-supported sand or shell gravel.	Completely buried in sand beneath coral blocks to 2 or 3 cm depth; also recorded in cavity in coral rock and adhering to hard substrates beneath loose coral blocks.	Westergren (1911), Clark (1921), Clark (1950), Taylor (1968), Rose (1978)
Encope grandis Agassiz	Sand; $\bar{M} = 0.24–0.36$.	Just buried, dimples visible on the surface.	Ebert & Dexter (1975)

species	sediment	depth of burial	references
E. michelini Agassiz	Sand; $\bar{M} = 0.5$.	Slightly buried, less than 2.5 cm below the surface; outline visible on the surface.	Kier & Grant (1965), Lawrence & Ferber (1971)
E. stokesi Agassiz	Fine sand ($\bar{M} = 0.17$–0.20) and in medium sand ($\bar{M} = 0.5$); not present where there is a high percentage of silt and clay.	Buried; ascends to just below the surface at low tide when its outline becomes visible.	Dexter (1977)
Hypselaster dolosus Clark	Mud.	To a depth of 10–15 cm.	Clark (1938)
Laganum laganum (Leske)	Fine, muddy, calcareous sand.	Not deep, but wholely covered.	Mortensen (1948)
Leodia sexiesperforatus (Leske)	Sand; silty sand.	Below the surface by 2.5 cm; 5–10 cm below the surface.	Kier & Grant (1965), Kier (1966)
Lovenia cordiformis Agassiz	Shell sand and sandy gravel; fairly pure sand.	Half buried (intertidal).	Clark (1917), Ricketts & Calvin (1962)
L. elongata (Gray)	Largely found in fine to medium sand; $\bar{M} = 0.15$–0.30 ($\bar{\bar{M}} = 0.25$), $S_0 = 1.3$.	Buried slightly more than its own body height (2–3 cm). Aboral spines may form a short groove at the surface. No respiratory funnel.	Lawrence & Ferber (1971), Ferber & Lawrence (1976)
L. subcarinatus (Gray)	Sand; mud.	Buries completely within mud.	Brown (1910). Mortensen (1951)
Maretia planulata (Lamarck)	Fine to coarse sandy bottoms; muddy sand.	Buried in sand.	Brown (1910), Mortensen (1951), Taylor (1968), Gibbs *et al.* (1976)
Mellita grantii Mortensen	Sand; $\bar{M} = 0.24$–0.36.	Buried with dimples visible on the surface.	Ebert & Dexter (1975)
M. lata Clark	Sand.	Buried in uppermost layer of sand with only a small part of the posterior surface visible.	Kenk (1944)
M. quinquiesperforata (Leske)	Medium to fine sand, neither coarse nor silty, subangular quartz sand with small amounts of shell fragments: $\bar{M} = 0.20$–0.30, also 0.39; $S_0 = 2.23$.	Partially or lightly covered with a thin sand layer, also up to 3–5 cm below the surface. Buries to 20–25 cm during storms.	Salsman & Tolbert (1965), Weihe & Gray (1968), Bell & Frey (1969), Lawrence & Ferber (1971)
Meoma ventricosa (Lamarck)	Sand; clean sand; $\bar{M} = 0.45$, $S_0 = 1.54$.	Buries to 10 cm in clean unsilted sand, less deeply buried or only partially buried in other substrata; apex near the surface or up to 4 cm below the surface in clean sand; no respiratory funnel.	Kier & Grant (1965), Kier (1966), Chesher (1969)
Metalia nobilis Verrill	More or less coarse sand.	Buried.	Mortensen (1951)
M. spatangus (Linnaeus)	Coarse loose sand; muddy sand; shell gravel in gut.	Burrows with no respiratory funnel.	Clark (1950), Taylor (1968), Gibbs *et al.* (1976 and pers. observation)
M. sternalis (Lamarck)	Coarse sand; muddy sand; fine sand.	Buried with apex near the surface.	Bedford (1900), Ferber (1973), Gibbs *et al.* (1976)
M. townsendi (Bell)	Coarse gravel; coarse sand with or without mud.	Buried to a depth of 1–2 cm with visible mound on the surface; form cone-shaped hollows in the sand at the surface.	Mortensen (1940), Clark & Bowen (1949)

species	sediment	depth of burial	references
Moira atropos (Lamarck)	Sand or mud; commonest in soft muddy bottoms. $\bar{M} = 0.22, S_0 = 1.55$.	Between 4 and 10 cm below the surface; up to 15 cm.	Chesher (1963), Lawrence & Ferber (1971), Kier (1975)
M. stygia (Lutken)	? Medium to fine sand (found with *Lovenia elongata*).	At a depth of 5–10 cm.	Ferber & Lawrence (1976)
Paramaretia multituberculata Mortensen	Fine sand and fine sandy mud.	Appears in a photograph of the sea floor.	Fell (1960)
Paraster doederleini Chesher	Mud.	Buried 2–10 cm below the surface; no funnel or other sign at the surface.	Kier (1975)
P. floridiensis Kier & Grant	Mud; also from coarse pockets of sand.	Adults buried in sand beneath coral slabs to depths of 25 cm; juveniles in mud at depths of 1–1.5 cm.	Kier & Grant (1965), Chesher (1966), Kier (1975)
Peronella lesueri (Valenciennes)	Sand; silty sand; sand and mud.	Buried a few cm down with a small elevation on the surface.	Mortensen (1921), Chang (1932), Gibbs *et al.* (1976)
P. japonica Mortensen	Fine sand.	Thin sediment covering over the test surface.	Kawaguti & Yamasu (1957)
Plagiobrissus grandis (Gmelin)	Clean sand; $\bar{M} = 0.82$, $S_0 = 1.9$.	From just below the surface to 5 cm: juveniles live at depths of 5–10 cm.	Kier & Grant (1965), Kier (1966, 1975), Lawrence & Ferber (1971)
Pourtalesia miranda Agassiz	Silty mud in gut.	Appears on the surface in photographs of the sea floor.	Southward *et al.* (1976) and pers. observation)
Ryncholampas pacificus (Agassiz)	Sand; sand and broken coral.	Half buried, up to the extremities of the petals.	Clark (1917), Kier (1962)
Rhynobrissus pyramidalis Agassiz	Sand.	Buried.	Clark (1946), Mortensen (1951)
Spatangus purpureus Müller	Coarse sand or shell gravel: adults in coarse sand, juveniles in fine or muddy sand.	Above the apex, 2 cm of sediment; no connection with the surface; surface may be slightly raised.	Koehler (1927), Nichols (1959), Ursin (1960), Gage (1966)
S. raschi Lovén	Fine sand or sandy mud.	Ploughs, never completely buried.	Nichols (1959)

DESCRIPTION OF PLATE 1

Tubercle morphology

FIGURE 2. Stereoview of a primary interambulacral tubercle of *Echinostrephus molaris* (de Blainville). This tubercle has a smooth platform and is surrounded by secondary tubercles and miliaries.

FIGURE 3. Stereoview of a large aboral interambulacral tubercle of *Paramaretia peloria* (Clark). The tubercle is deeply sunken and the platform has a pronounced parapet.

FIGURE 4. Stereoview of an aboral tubercle adjacent to a tube foot in ambulacrum III of *Spatangus raschi* Lovén. The platform is strongly crenulate.

FIGURE 5. Dorso-lateral interambulacral tubercle of *Echinocardium cordatum* (Pennant) with a ridge.

FIGURE 6. Ventro-lateral interambulacral tubercle of *Echinocardium cordatum*, with a ridge and crenulation.

Scale bar in figures 2 and 3, 200 μm, in figures 4–6, 100 μm.

DESCRIPTION OF PLATE 2

Tubercle morphology

FIGURE 9. Stereoview of a large aboral interambulacral tubercle of *Spatangus purpureus* Müller. The platform has a ridge and crenulation. Miliary tubercles surround this tubercle.

FIGURE 10. Stereoview of the base of a primary interambulacral spine of *Centrostephanus nitidus* Koehler. Connective tissue fibres insert into the central perforation and the outer rim is crenulate.

FIGURE 11. Stereoview of a latero-dorsal interambulacral tubercle of *Eupatagus hastingiae* (Forbes) [Eocene].

FIGURE 12. Stereoview of a latero-ventral interambulacral tubercle of *Maretia planulata* (Lamarck). Side view of the platform and incomplete boss.

Scale bar in figures 9 and 12, 200 μm, in figure 10, 400 μm, in figure 11, 100 μm.

DESCRIPTION OF PLATE 3

Tubercle morphology

FIGURE 13. Stereoview of the boss and platform of a latero-ventral tubercle of *Maretia planulata* (Lamarck). Stereom for collagenous catch apparatus insertion is absent from the lower part of the boss.

FIGURE 14. Latero-ventral tubercle of *Maretia planulata*.

FIGURE 15. Latero-ventral tubercle of *Paramaretia peloria* (Clark).

FIGURE 16. Stereoview of an anterior interambulacral tubercle of *Echinocardium cordatum* (Pennant). The large central tubercle bears a scraping spine, the smaller tubercles bear curved protective spines.

Scale bar in figures 13 and 16, 200 μm in figures 14 and 15, 400 μm.

DESCRIPTION OF PLATE 4

Tubercle morphology

FIGURE 17. Stereoview of an aboral tubercle near the centre of ambulacrum III in *Spatangus raschi* Lovén. This tubercle is surrounded by miliaries that bear spines. A miliary that supports a pedicellaria can be seen at the centre bottom.

FIGURE 18. Stereoview of two interambulacral tubercles adjacent to the peristome in *Spatangus purpureus* Müller. The crenulation of the upper tubercle is partially fused to form a ridge.

FIGURE 19. Stereoview of a latero-ventral interambulacral tubercle of *Brissopsis lyrifera* (Forbes). The platform is noticeably tilted to the plate surface.

Scale bar in figures 17 and 19, 100 μm, in figure 18, 200 μm.

DESCRIPTION OF PLATE 5

Sunken tubercles

FIGURE 21. Stereoview of aboral interambulacral tubercles of *Echinolampas crassa* (Bell). Between large tubercles, miliaries and granules can be seen.

FIGURE 22. Stereoview of an aboral interambulacral plate section of *Clypeaster rosaceus* (Linnaeus).

FIGURE 23. Stereoview of an oral interambulacral tubercle of *Clypeaster rarispina* de Meijere.

Scale bar in figure 21, 400 μm, in figure 22, 200 μm, in figure 23, 100 μm.

DESCRIPTION OF PLATE 6

Miliaries

FIGURE 25. Stereoview of aboral tubercles in the centre of ambulacrum III of *Maretia planulata* (Lamarck). The central tubercle is surrounded by miliaries (lacking a platform) that bear spines. Immediately above the tubercle is a small miliary that bears a pedicellaria.

FIGURE 26. Stereoview of miliaries from the sub-anal fasciole of *Brissopsis lyrifera* (Forbes).

FIGURE 27. Stereoview of a miliary that bears a pedicellaria. Aboral interambulacral plate of *Sphaerechinus granularis* (Lamarck).

Scale bar in figure 25, 100 μm, in figures 26 and 27, 40 μm.

Description of plate 7

Granules

Figure 28. Stereoview of warty granules of an aboral interambulacral plate of *Arbacia lixula* (Linnaeus).

Figure 29. Stereoview of a granule on an aboral interambulacral plate of *Echinolampas crassa* (Bell).

Figure 30. Stereoview of domed granules of an aboral interambulacral plate of *Echinoneus cyclostomus* Clark.

Figure 31. Stereoview of granules on an aboral interambulacral plate of *Mellita quinquiesperforata* (Leske).

Figure 32. Stereoview of granules on an oral interambulacral plate of *Encope michelini* Agassiz.

Scale bar in figures 28–30, 100 μm, in figures 31, 32, 40 μm.

Description of plate 8

Conulus albogalerus Klein

Figure 33. Stereoview of aboral interambulacral tubercles and protruberances.

Figure 34. Stereoview of aboral interambulacral protruberances and miliary tubercles.

Figure 35. Stereoview of two aboral interambulacral protruberances.

Figure 36. Oral interambulacral tubercle.

Figure 37. Aboral interambulacral tubercle.

Scale bar in figure 33, 200 μm, in figures 34, 36 and 37, 100 μm, in figure 35, 40 μm.

Description of plate 9

Figure 39. Stereoview of an oral interambulacral tubercle of *Mellita quinquiesperforata* (Leske).

Figure 40. Side view of an ambital ambulacral tubercle of *Echinostrephus molaris* (de Blainville).

Figure 41. Side view of an ambital interambulacral tubercle of *Centrostephanus nitidus* Koehler.

Figure 42. Side view of a miliary tubercle on an aboral interambulacral plate of *Echinus acutus* Lamarck. This miliary bears a pedicellaria.

Figure 43. Side view of an ambital interambulacral tubercle of *Austrocidaris canaliculatus* (Agassiz).

Figure 44. Stereoview of an ambital ambulacral tubercle of *Eucidaris metularia* (Lamarck).

Scale bar in figures 39, 40, 42 and 44, 100 μm, in figures 41 and 43, 400 μm.

Description of plate 10

Figure 45. Stereoview of oral interambulacral tubercles of *Echinoneus cyclostomus* Clark. Ambitus to the left.

Figure 46. Stereoview of aboral interambulacral tubercles and granules of *Echinoneus cyclostomus*. Apex to the left.

Figure 47. Stereoview of an aboral interambulacral tubercle of *Apatopygus recens* (Milne-Edwards). Apex to the left.

Scale bar in figures 45 and 46, 200 μm, in figure 47, 100 μm.

Description of plate 11

Cassidulus cariboearum Lamarck

Figure 51. Stereoview of oral interambulacral tubercles.

Figure 52. Stereoview of an oral interambulacral tubercle.

Figure 53. Stereoview of an aboral interambulacral tubercle.

Figure 54. Stereoview of oral interambulacral tubercles from the peristomial lip.

Scale bar in figure 51, 200 μm, in figures 52–54, 100 μm.

Description of plate 12

Figure 55. Stereoview of the oral pitted region lying posterior to the peristome in *Cassidulus cariboearum* Lamarck.

Figure 56. Pitted region lying posterior to the peristome in *Cassidulus cariboearum*, viewed perpendicular to the surface.

Figure 57. Oral interambulacral tubercles of *Apatopygus recens* (Milne-Edwards). Posterior to the lower left.

Figure 58. Oral interambulacral tubercles of *Mellita quinquiesperforata* (Leske).

Figure 59. Stereoview of an oral ambulacral tubercle of *Fellaster zelandiae* (Gray).

Scale bar in figures 55, 56 and 58, 100 μm, in figure 57, 400 μm, in figure 59, 40 μm.

DESCRIPTION OF PLATE 13

Fellaster zelandiae (Gray)

FIGURE 60. Stereoview of oral ambulacral tubercles. The food groove lies to the left, and larger interambulacral tubercles are just visible in the lower right corner. The peristome lies to the bottom.

FIGURE 61. Stereoview of aboral ambulacral tubercles. Apex to the bottom.

FIGURE 62. Stereoview of oral interambulacral tubercles.

Scale bar in figure 60, 400 μm, in figures 61 and 62, 100 μm.

DESCRIPTION OF PLATE 14

Clypeasteroid tubercles

FIGURE 65. Oral interambulacral tubercles of *Mellita quinquiesperforata* (Leske).

FIGURE 66. Oral ambulacral tubercles of *Mellita quinquiesperforata*. Food groove and two branches can be seen on the left. The larger tubercles on the right hand side lie in the food tract. The top of the electron micrograph is towards the peristome.

FIGURE 67. Stereoview of an oral food groove in *Echinodiscus bisperforatus* (Leske). Large tubercles at the top are interambulacral. The food tract lies to the bottom, the peristome lies to the left.

FIGURE 68. Oral food groove of *Dendraster excentricus* (Eschscholtz).

FIGURE 69. Junction between ambulacral (left) and interambulacral (right) tubercles on the oral surface of *Mellita quinquiesperforata* (Leske).

FIGURE 70. Stereoview of an aboral interambulacral tubercle of *Encope michelini* Agassiz.

Scale bar in figures 65, 67 and 68, 400 μm, in figure 66, 1 mm, in figure 69, 200 μm, in figure 70, 100 μm.

DESCRIPTION OF PLATE 15

FIGURE 71. Tubercle arrangement on the oral surface of *Mellita quinquiesperforata* in ambulacrum II.

DESCRIPTION OF PLATE 16

Spatangoid tubercles

FIGURE 73. Stereoview of plastron tubercles of *Echinocardium cordatum* (Pennant).

FIGURE 74. Stereoview of latero-ventral tubercles of *Brissopsis lyrifera* (Forbes).

FIGURE 75. Stereoview of a latero-dorsal tubercle of *Echinocardium cordatum*.

Scale bar in figures 73–75, 200 μm.

DESCRIPTION OF PLATE 17

Spatangoid tubercles

FIGURE 81. Stereoview of a latero-dorsal tubercle of *Brissopsis lyrifera* (Forbes).

FIGURE 82. Stereoview of a latero-dorsal tubercle of *Brissopsis lyrifera*.

FIGURE 83. Stereoview of an aboral tubercle, adjacent to a tube foot in ambulacrum III, of *Paramaretia peloria* (Clark).

FIGURE 84. Plastron tubercle of *Brissopsis lyrifera*.

FIGURE 85. Interambulacral tubercles adjacent to the peristome in *Echinocardium cordatum* (Pennant). The peristome lies to the bottom.

Scale bar in figures 81–83 and 85, 100 μm, in figure 84, 200 μm.

DESCRIPTION OF PLATE 18

FIGURE 86. Aboral interambulacral tubercles of *Paramaretia peloria* (Clark).

FIGURE 87. Latero-dorsal interambulacral tubercles of *Moira atropos* (Lamarck).

FIGURE 88. Plastron tubercles of *Spatangus purpureus* Müller.

FIGURE 89. Latero-ventral tubercles of *Spatangus purpureus.*

FIGURE 90. Stereoview of a latero-dorsal tubercle of *Spatangus purpureus.*

Scale bar in figure 86, 1 mm, in figures 87 and 90, 100 μm, in figures 88 and 89, 400 μm.

DESCRIPTION OF PLATE 19

Tubercle arrangement in ambulacrum III

FIGURE 91. Aboral ambulacrum III of *Echinocardium pennatifidum* Norman; apex to the top.

FIGURE 92. Aboral ambulacrum III of *Maretia planulata* (Lamarck); apex to the top.

FIGURE 93. Stereoview of aboral ambulacrum III tubercles in *Echinocardium pennatifidum*; apex to the top.

FIGURE 94. Stereoview of aboral ambulacrum III tubercles in *Maretia planulata*; apex to the left.

Scale bar in figures 91 and 92, 1 mm, in figures 93 and 94, 400 μm.

DESCRIPTION OF PLATE 20

Tubercle arrangement in ambulacrum III

FIGURE 95. Light micrograph of tubercle arrangement in the aboral ambulacrum III of *Metalia spatangus* (Linnaeus). Magn. × 10.

FIGURE 96. Electron micrograph of tubercle arrangement in the aboral ambulacrum III of *Paramaretia peloria* (Clark).

FIGURE 97. Stereoview of aboral ambulacrum III tubercles in *Micraster cortestudinarium* (Goldfuss), apex to the top. Midline of the ambulacrum can be seen to the right.

FIGURE 98. Stereoview of aboral ambulacrum III plate in *Paramaretia peloria*; apex to the top.

Scale bar in figure 96, 1 mm, in figures 97 and 98, 400 μm.

DESCRIPTION OF PLATE 21

Tubercle arrangement in ambulacrum III

FIGURE 100. Aboral ambulacrum III of *Brissopsis lyrifera* (Leske); apex to the top.

FIGURE 101. Aboral ambulacrum III of *Brissus latecarinatus* (Forbes); apex to the top.

FIGURE 102. Stereoview of aboral ambulacrum III tubercles in *Brissopsis atlantica* Mortensen; apex to the left.

FIGURE 103. Stereoview of aboral ambulacrum III tubercles in *Brissopsis atlantica*; apex to the left.

Scale bar in figures 100–102, 400 μm, in figure 103, 200 μm.

DESCRIPTION OF PLATE 22

Tubercle arrangement in ambulacrum III

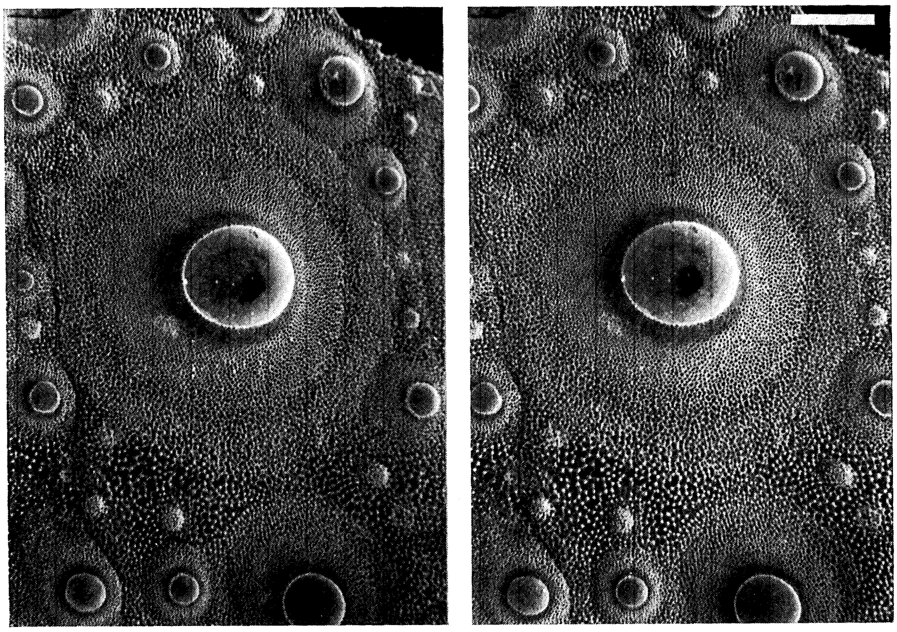
FIGURE 104. Aboral ambulacrum III of *Echinocardium cordatum,* apex to the bottom.

FIGURE 105. Aboral ambulacrum III of *Spatangus purpureus* Müller, apex to the bottom. The midline of the ambulacrum can be seen to the left.

FIGURE 106. Stereoview of aboral ambulacrum III tubercles of *Echinocardium cordatum;* apex to the left.

FIGURE 107. Stereoview of aboral ambulacrum III tubercles of *Spatangus purpureus*; apex to the right.

Scale bar in figures 104 and 105, 1 mm, in figures 106 and 107, 400 μm.



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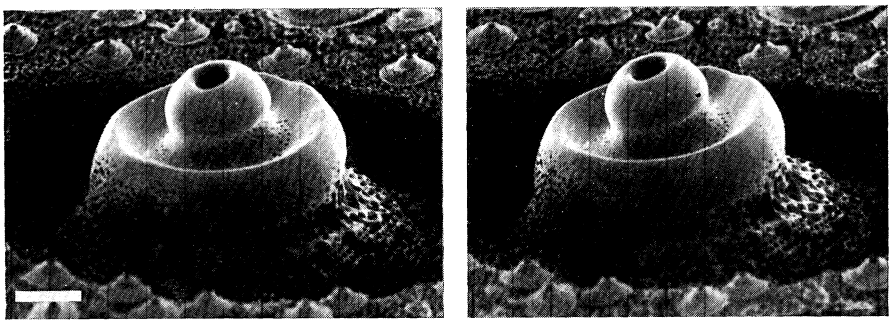

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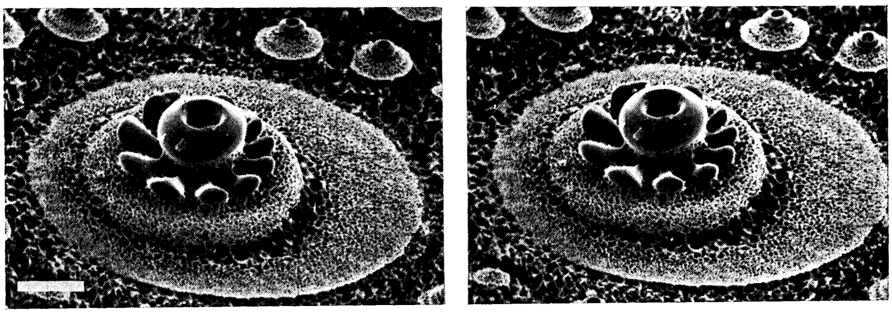

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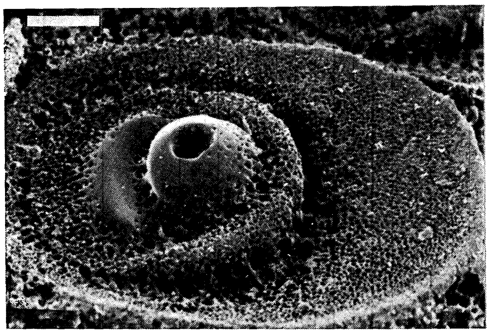

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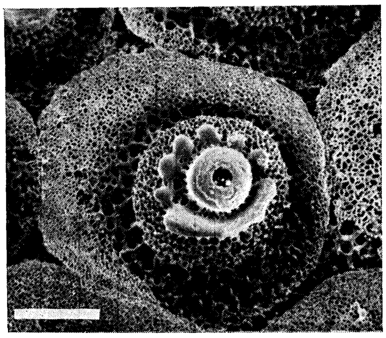

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PLATE 1. For description see page 51.

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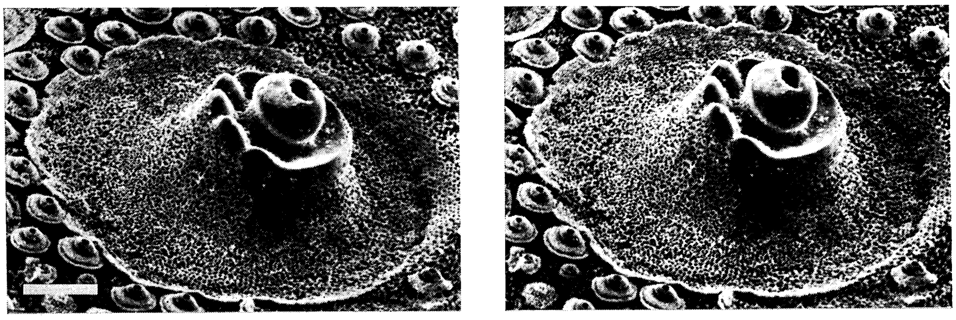

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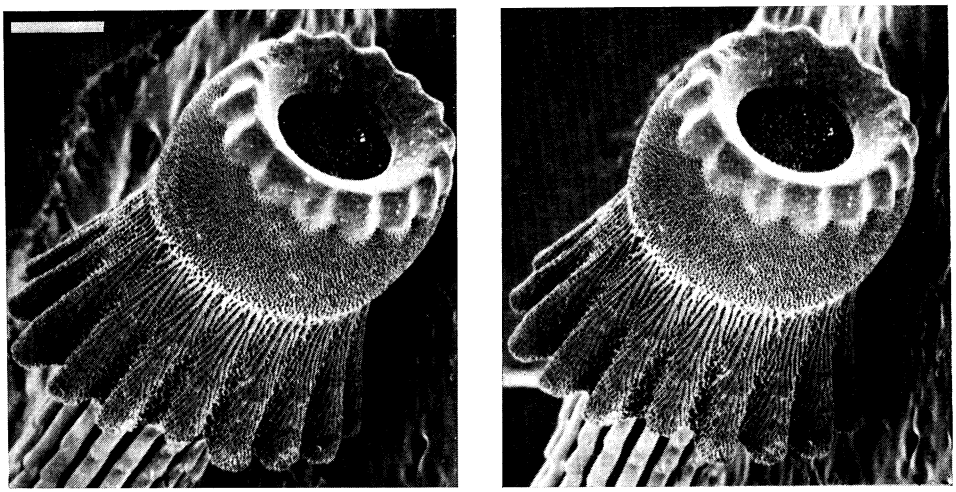

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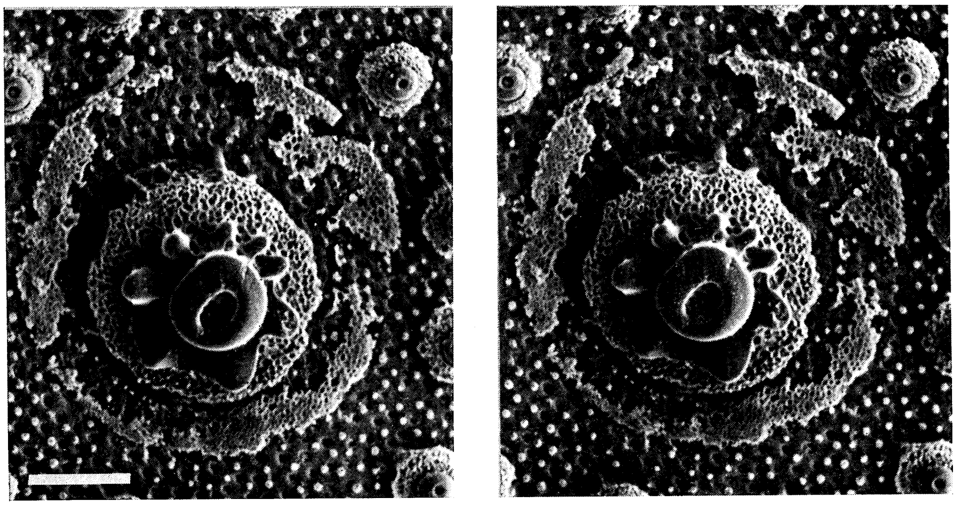

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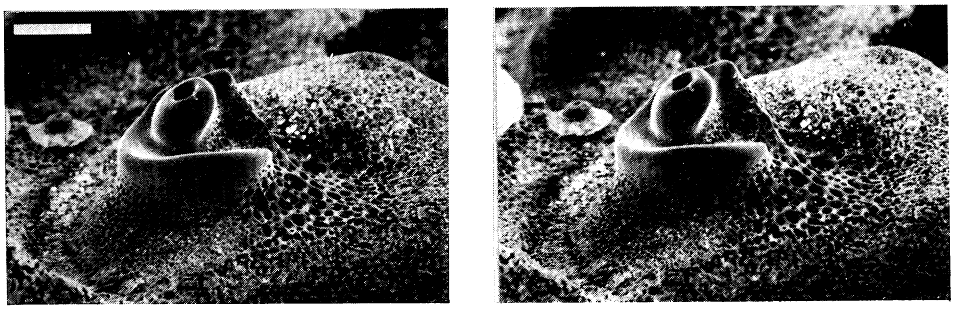

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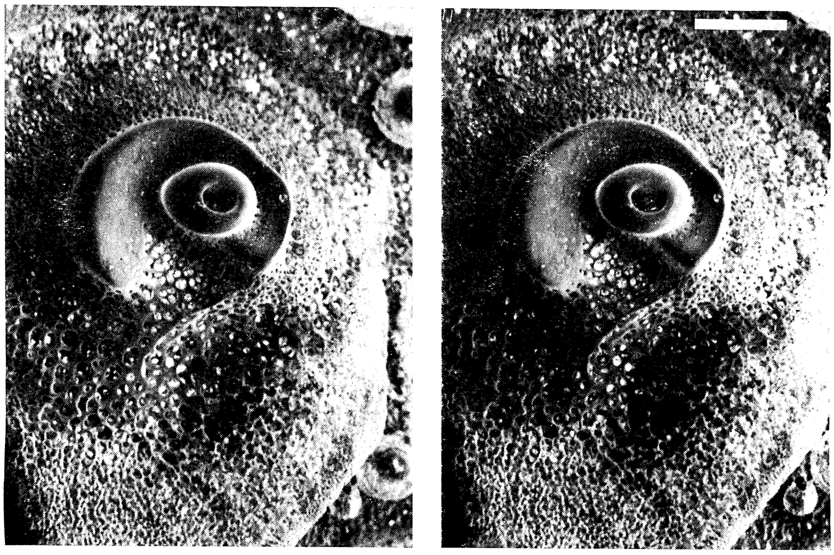
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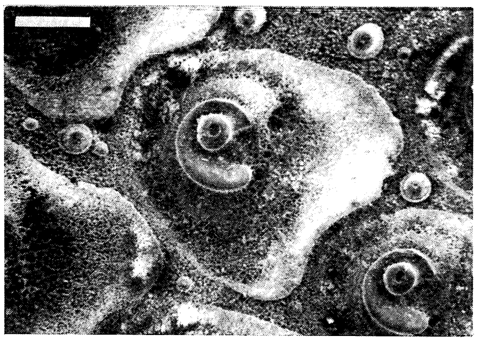
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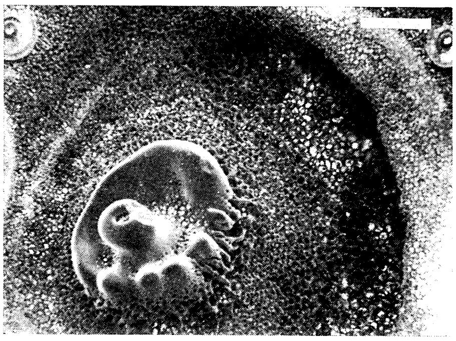
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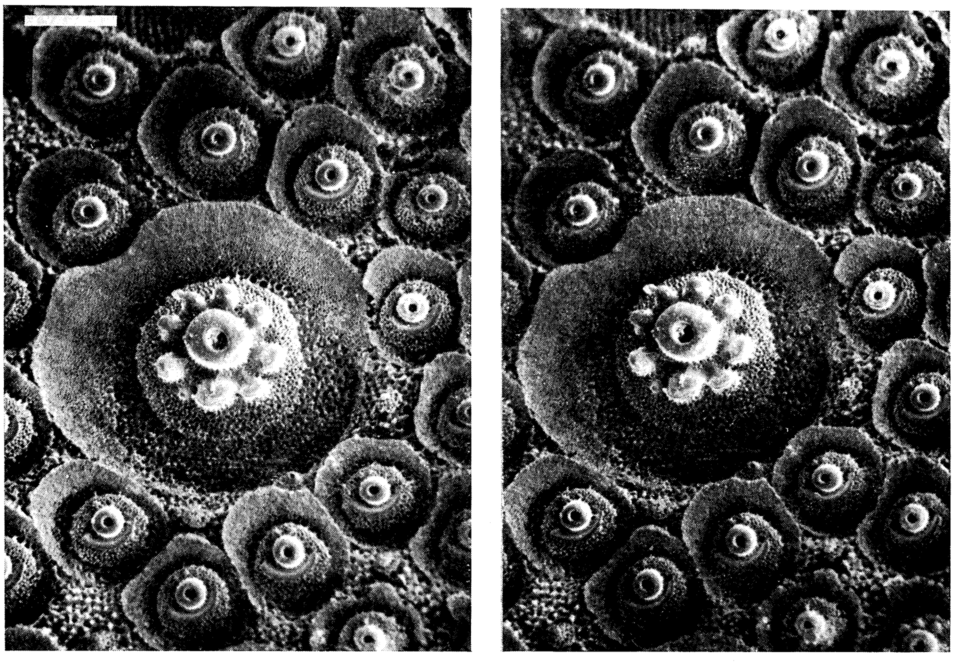
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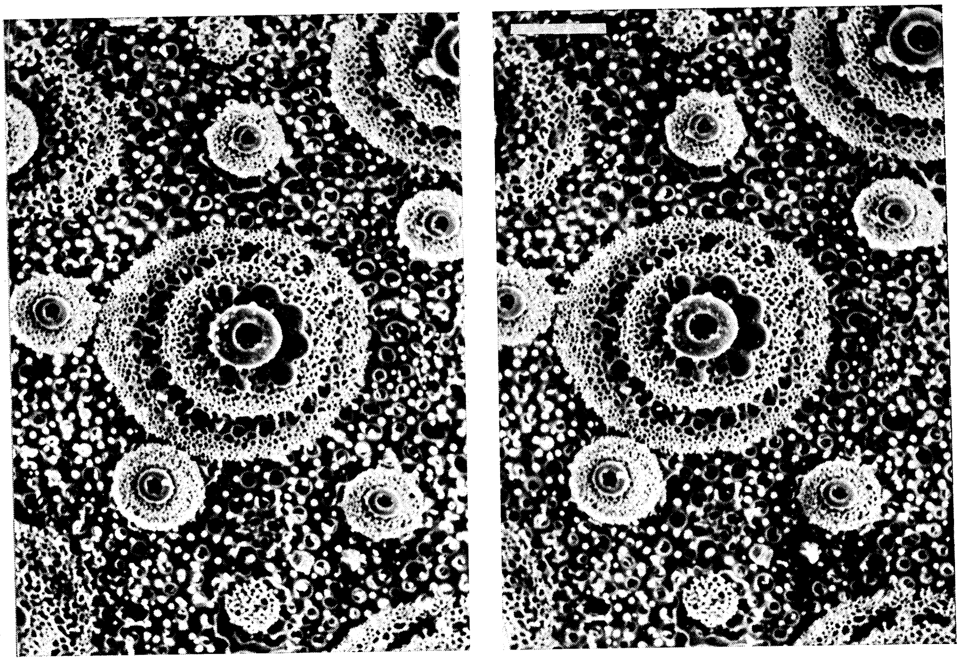

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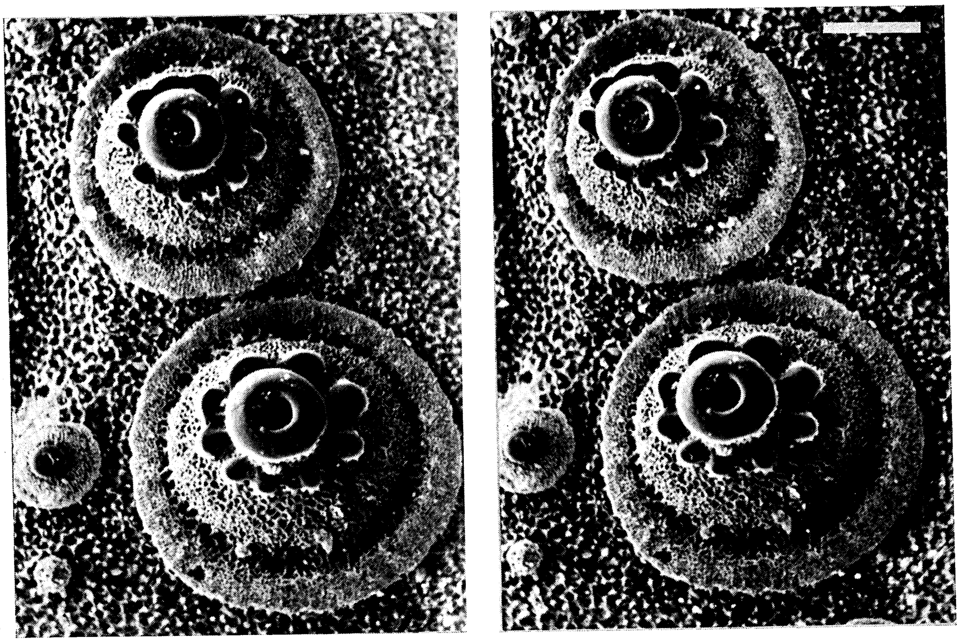

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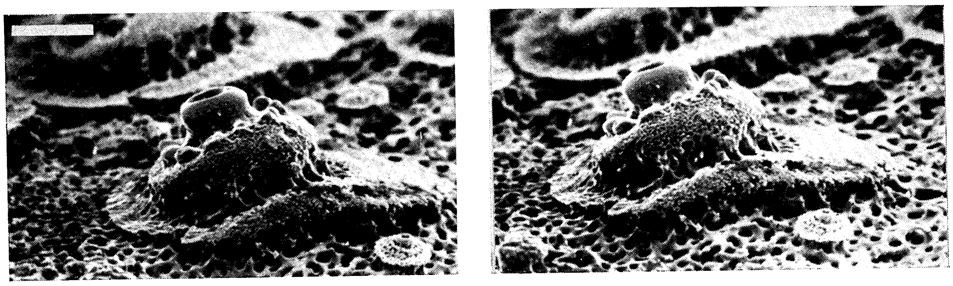

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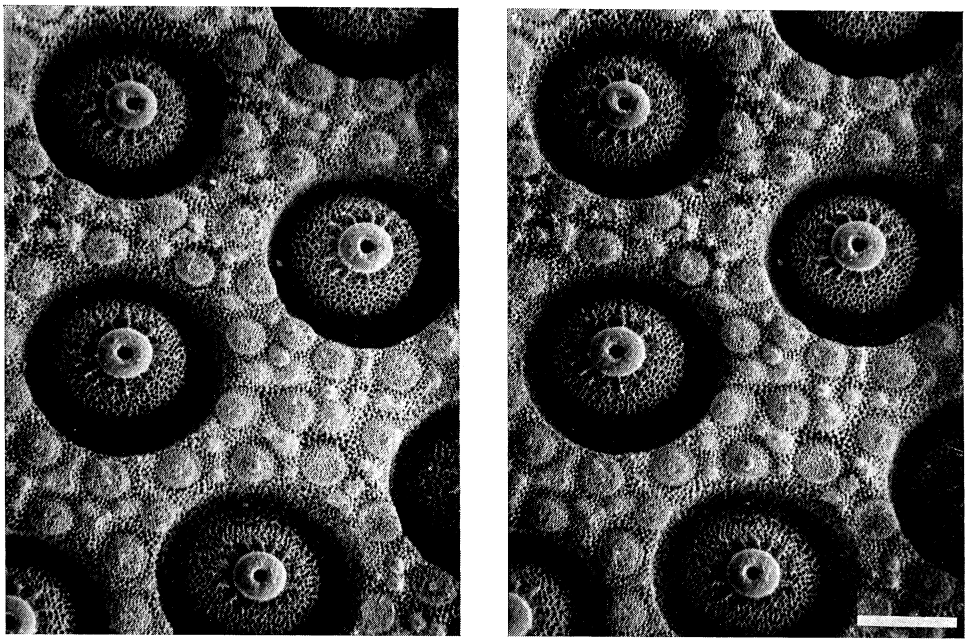

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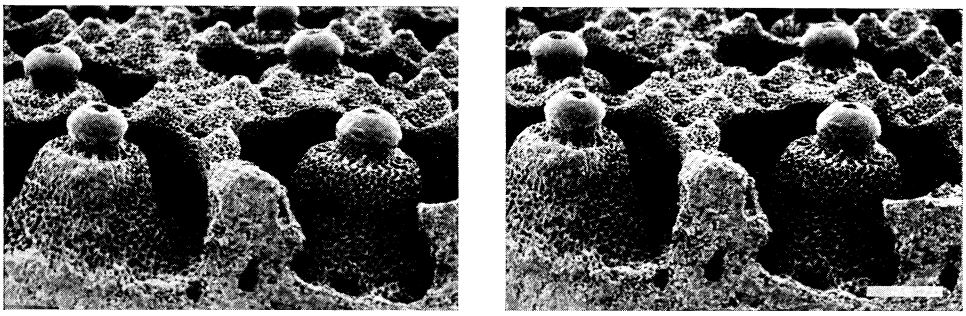

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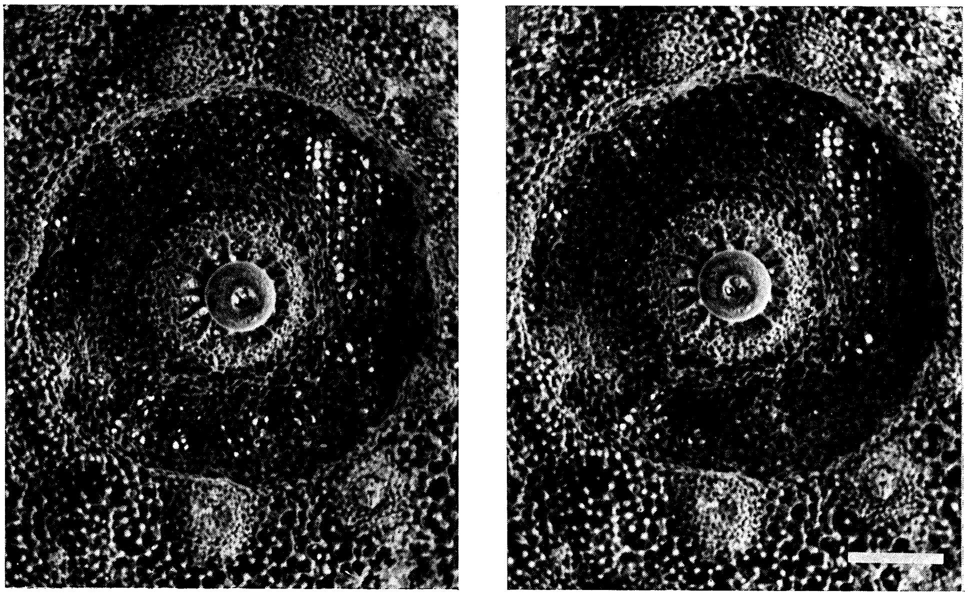

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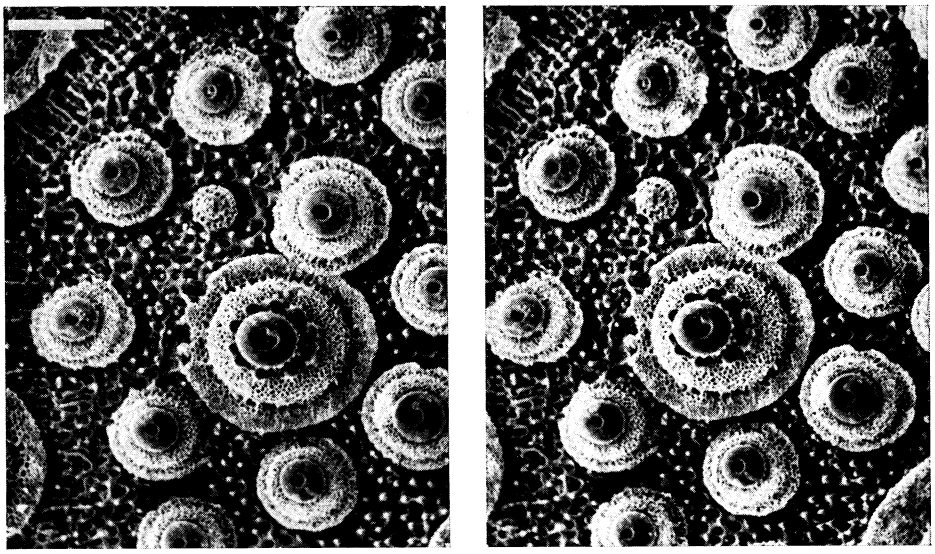

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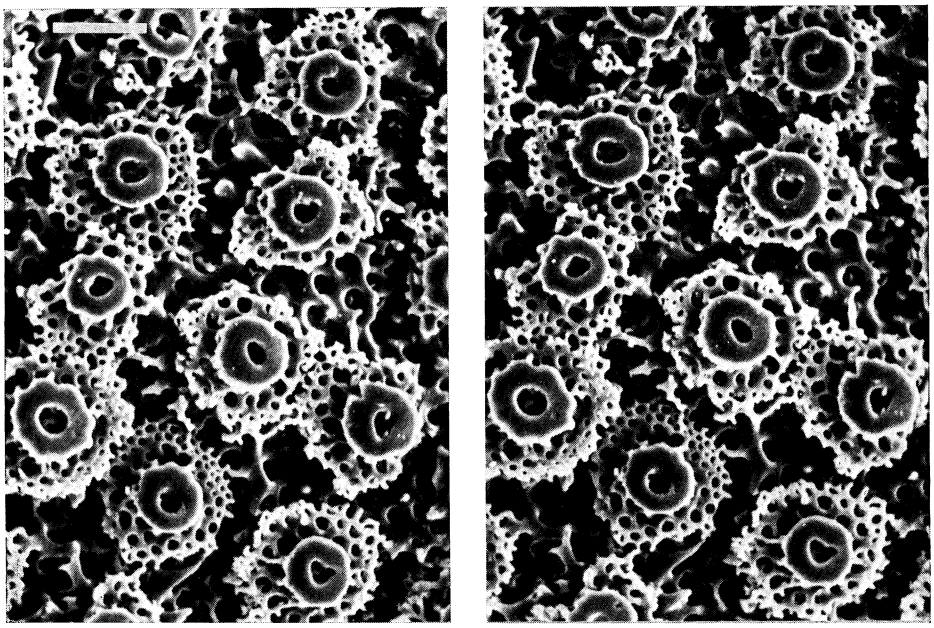

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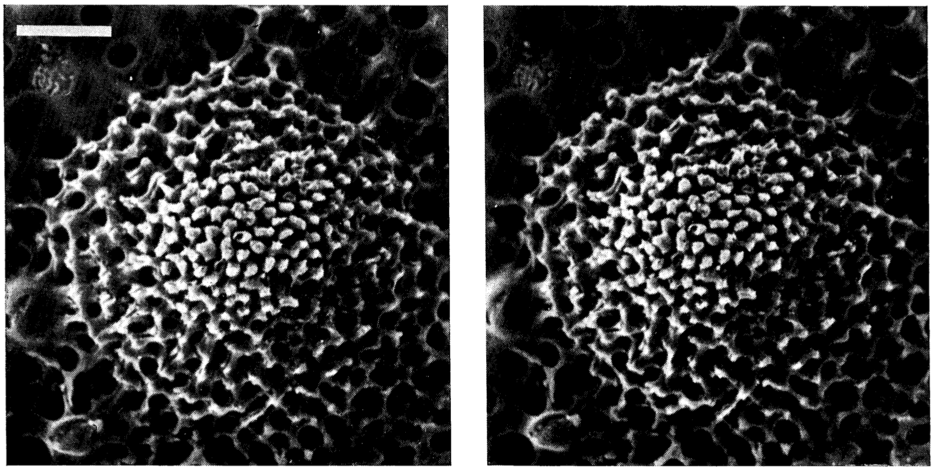

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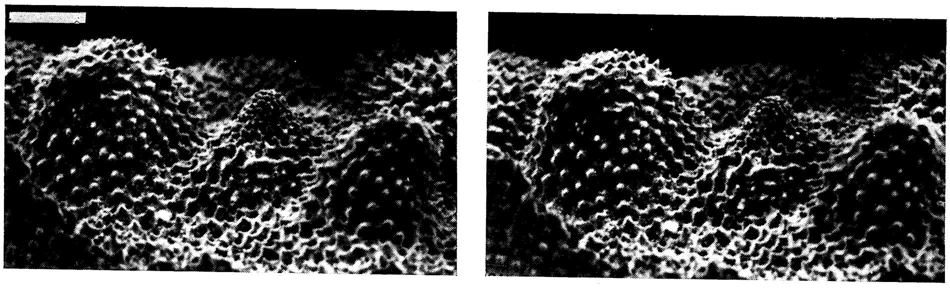

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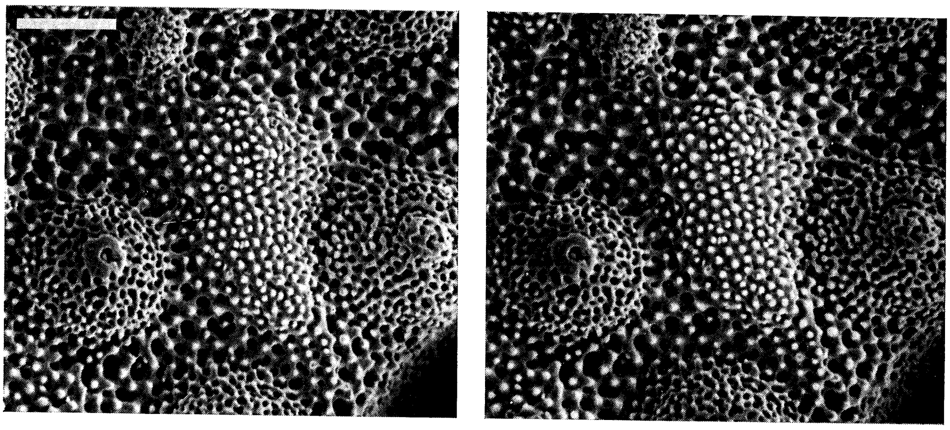

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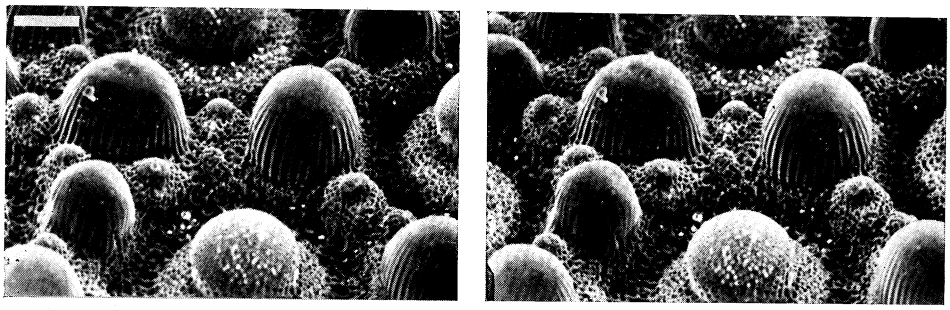

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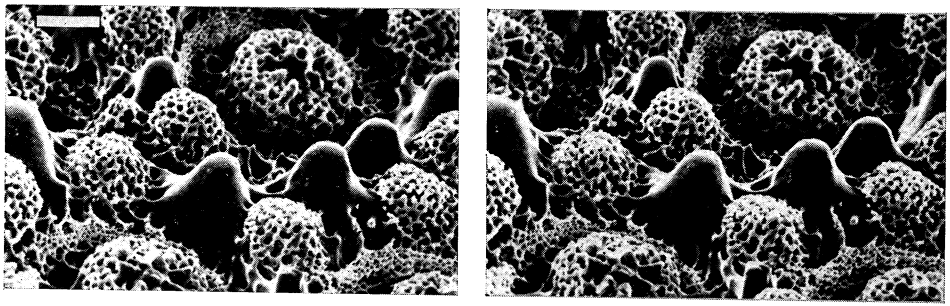

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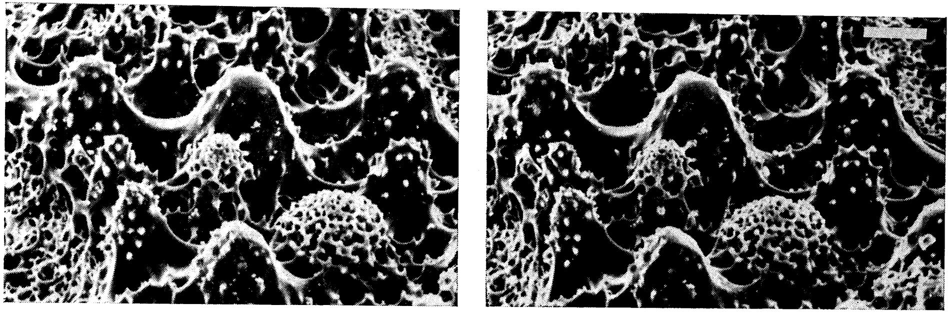

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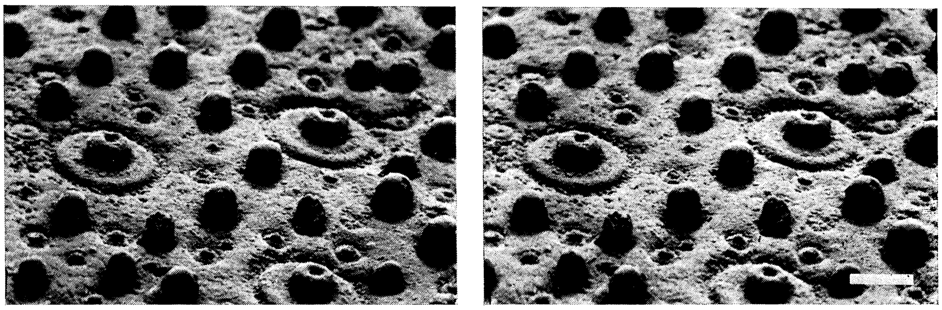
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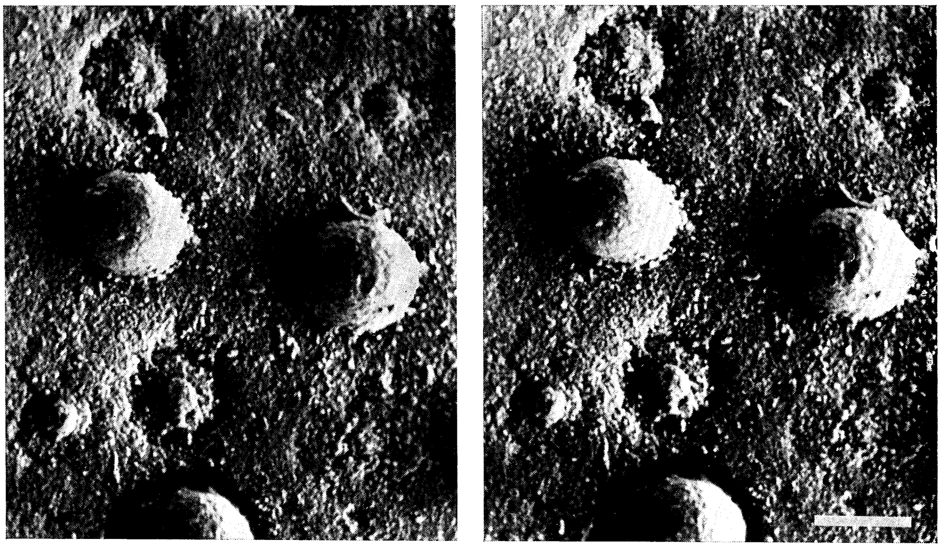
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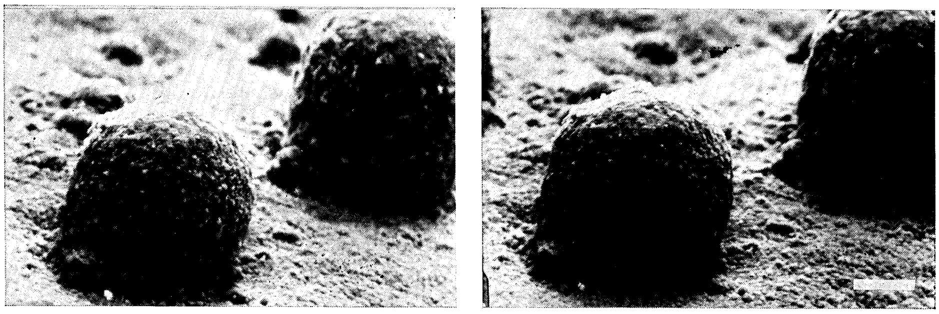
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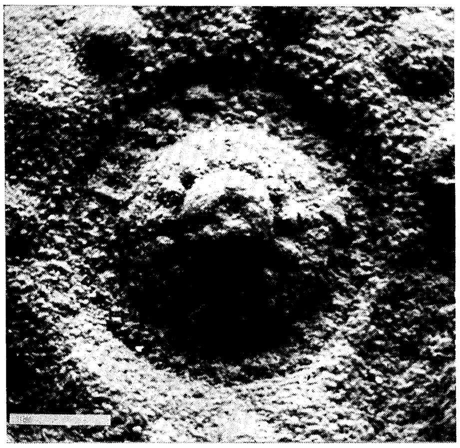
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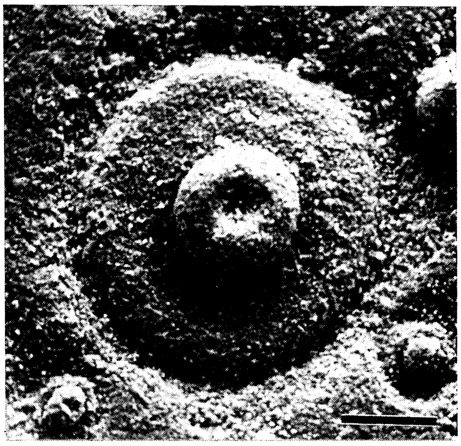
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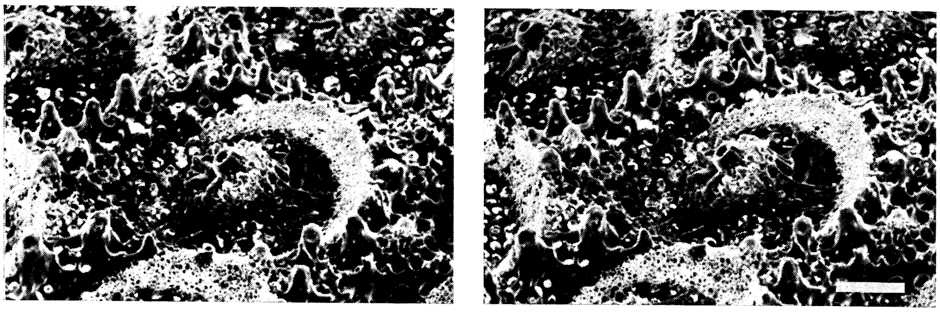
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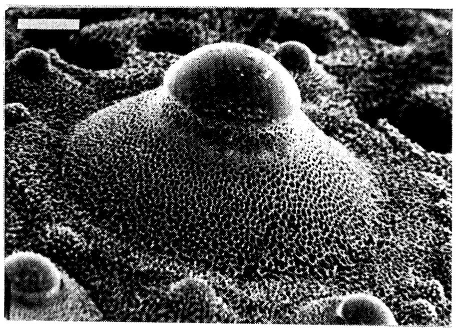
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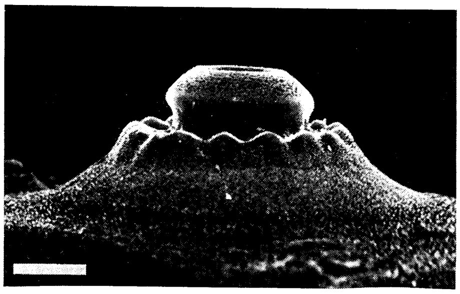
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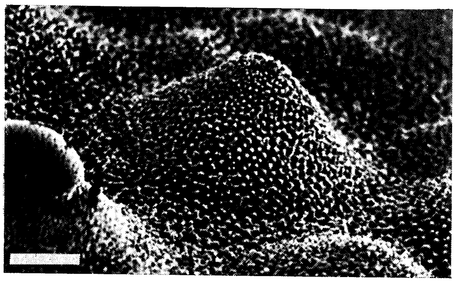
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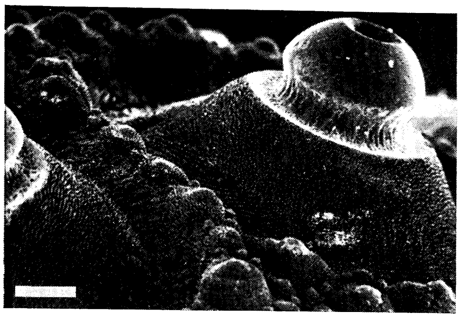
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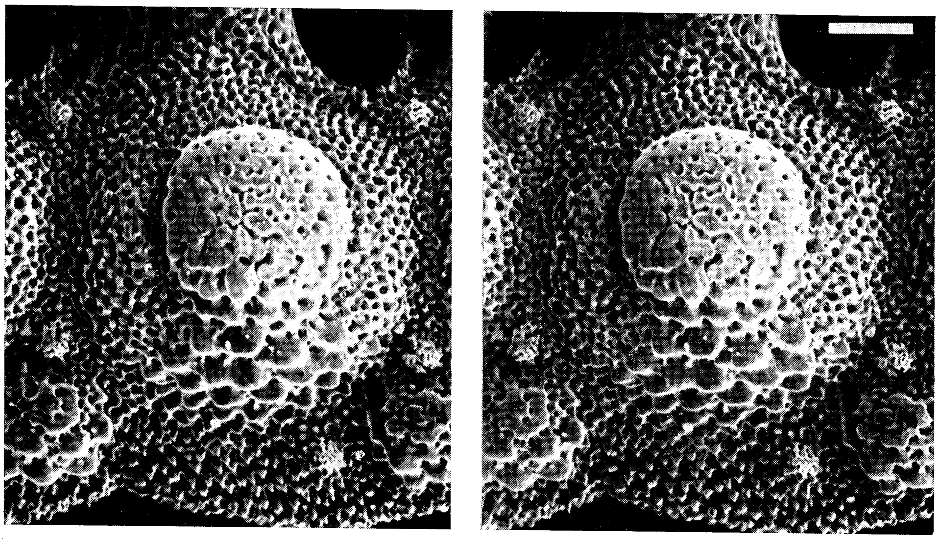
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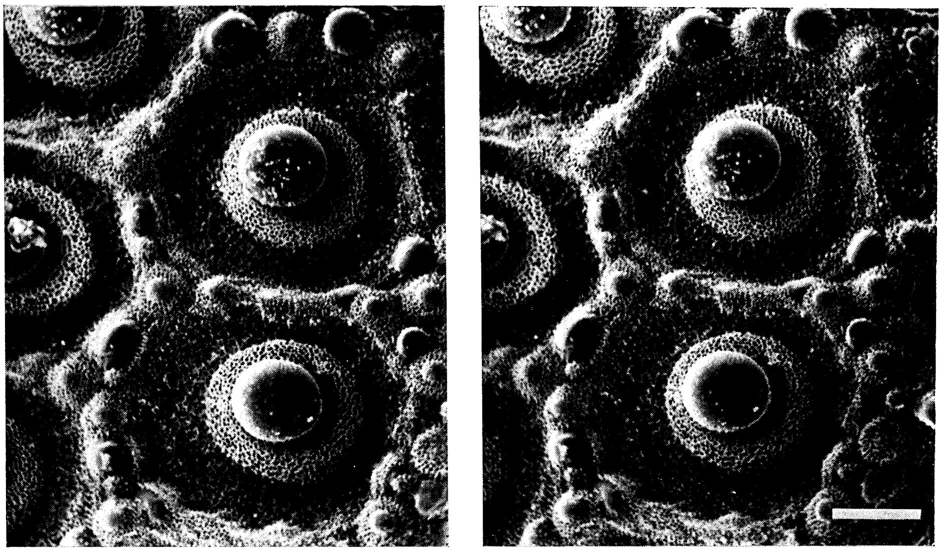

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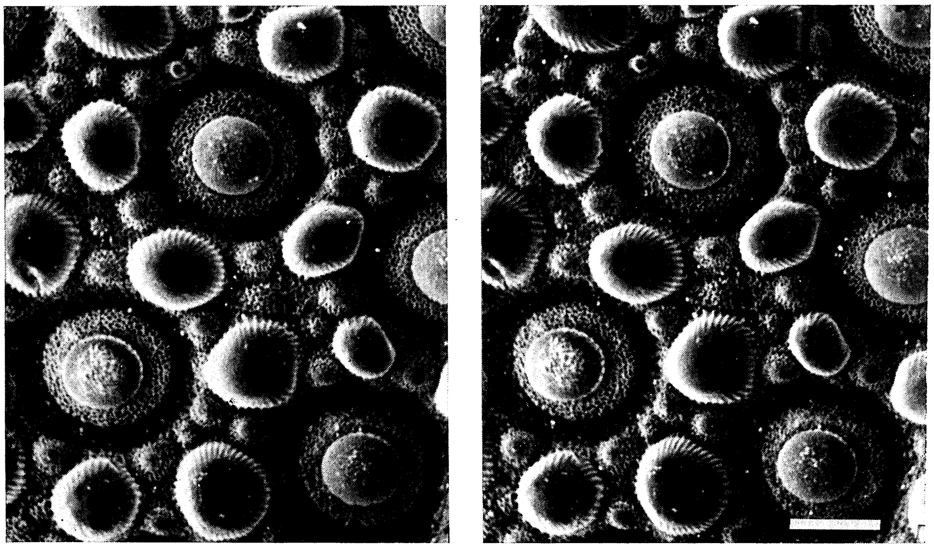

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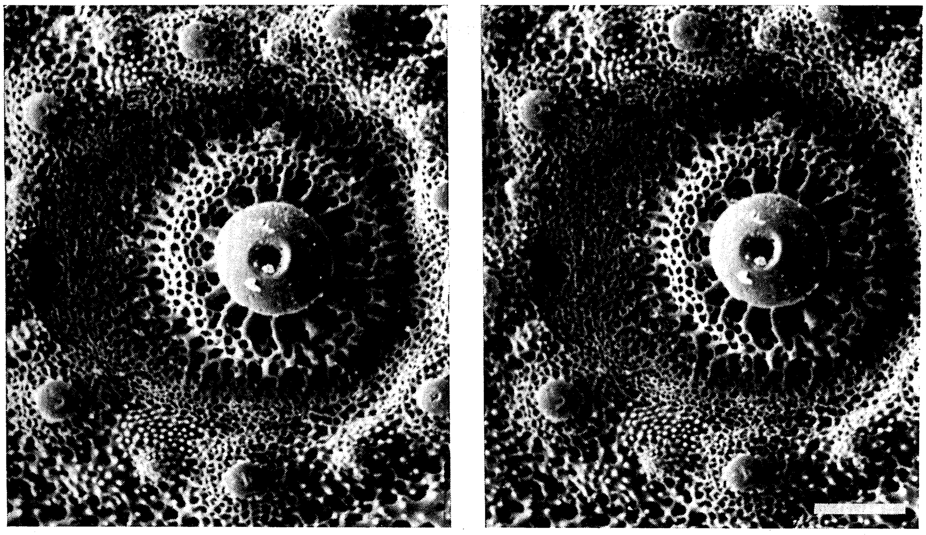

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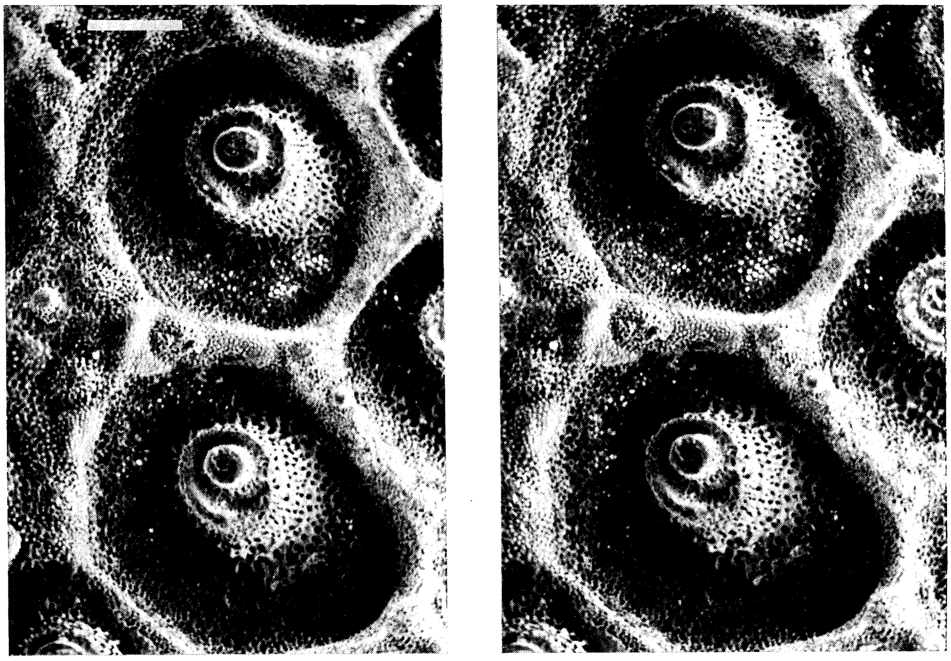
PLATE 10. For description see page 52.



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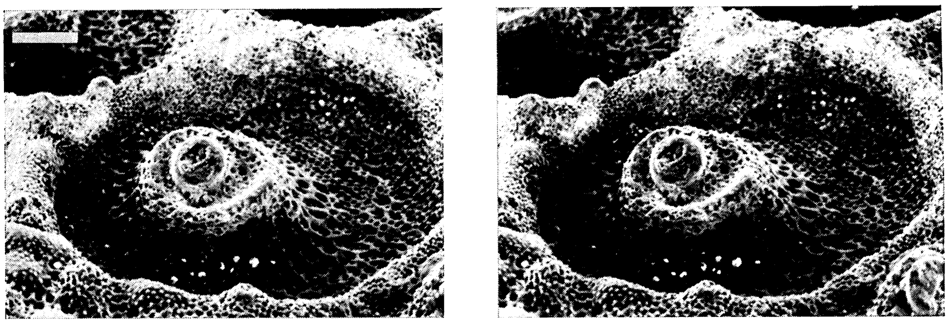

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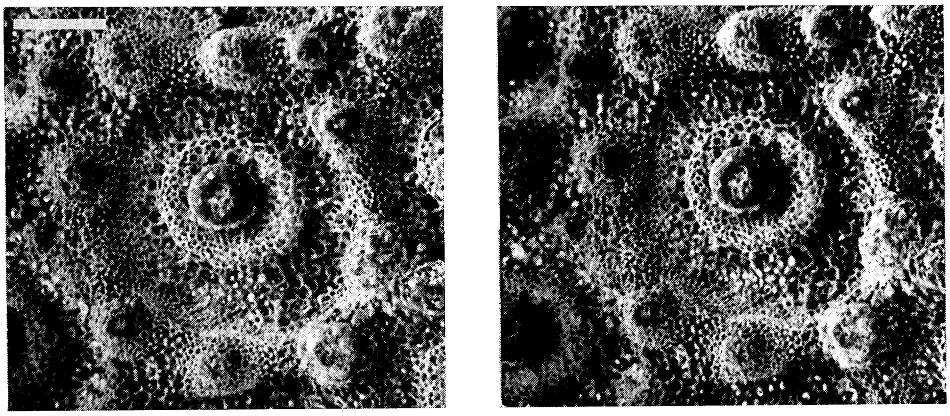

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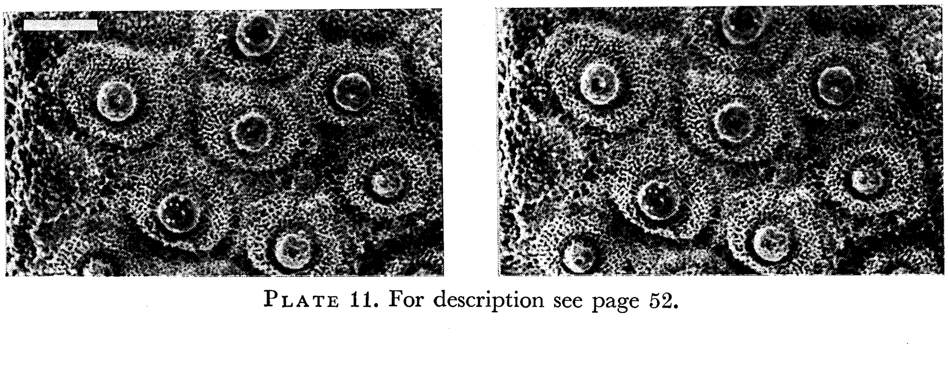

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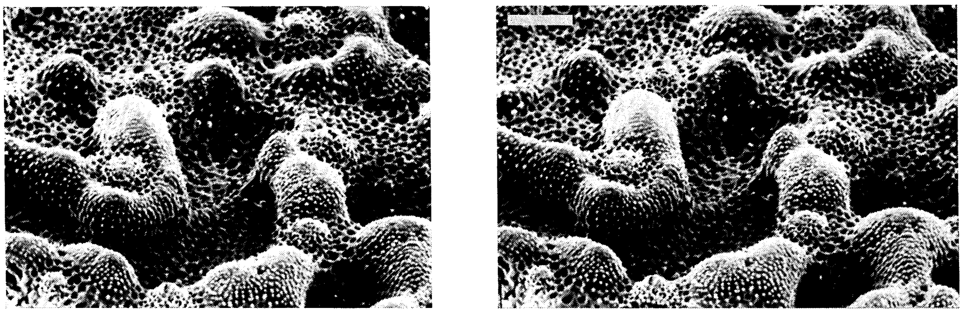
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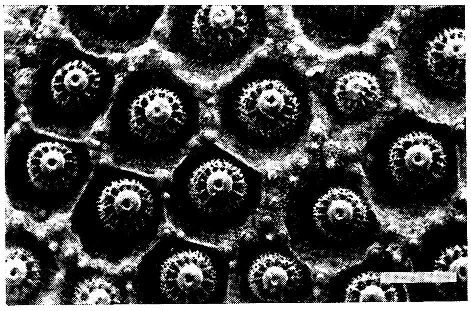
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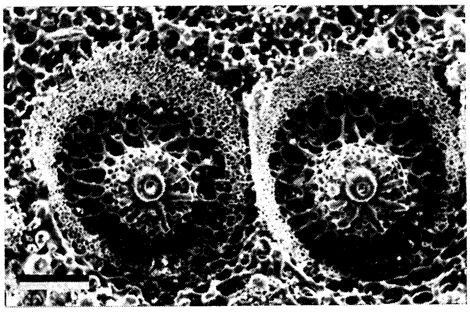
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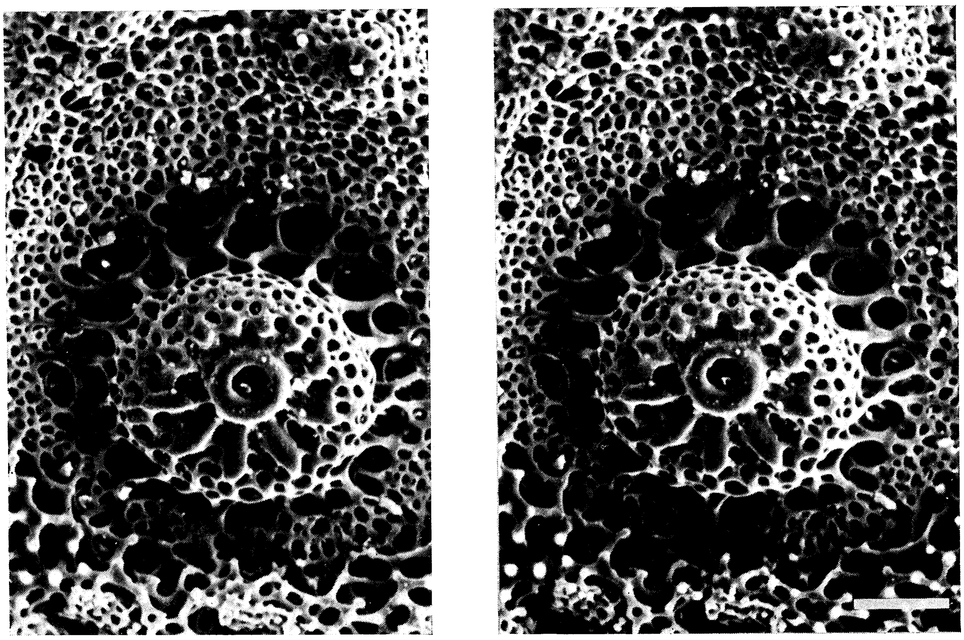
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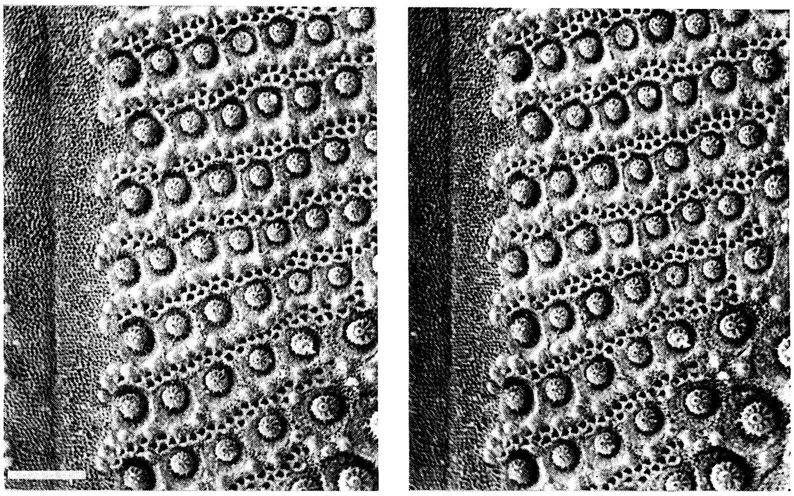

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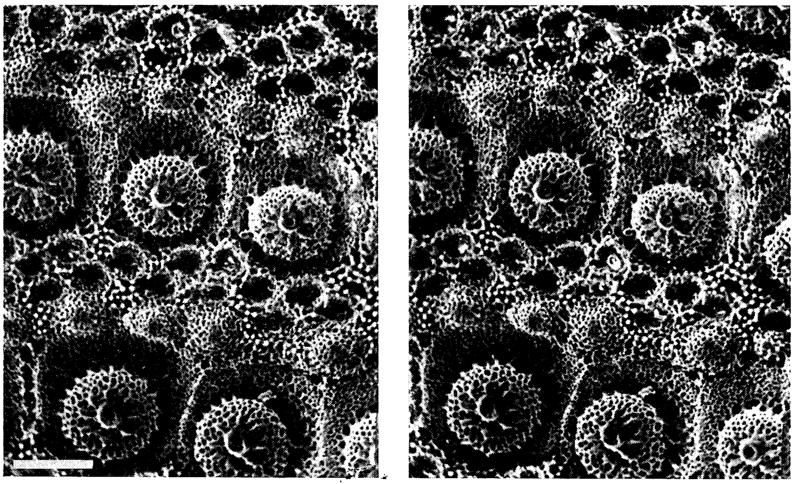

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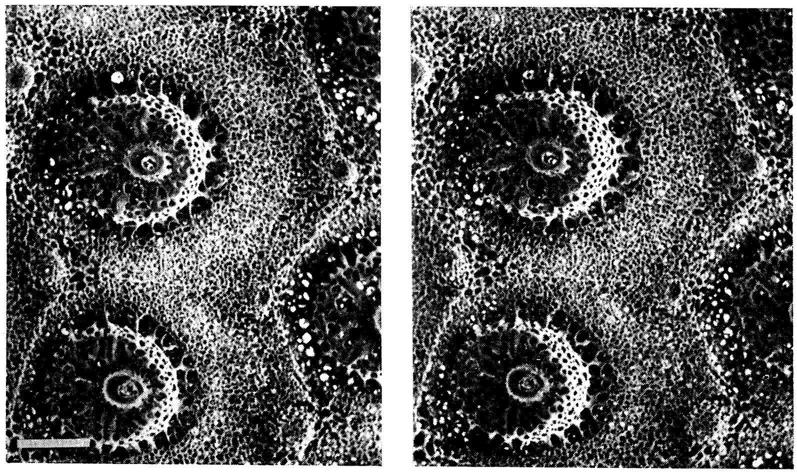

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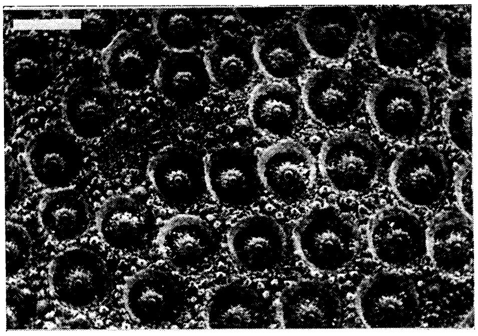

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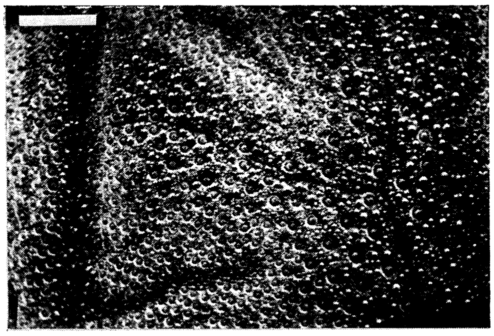

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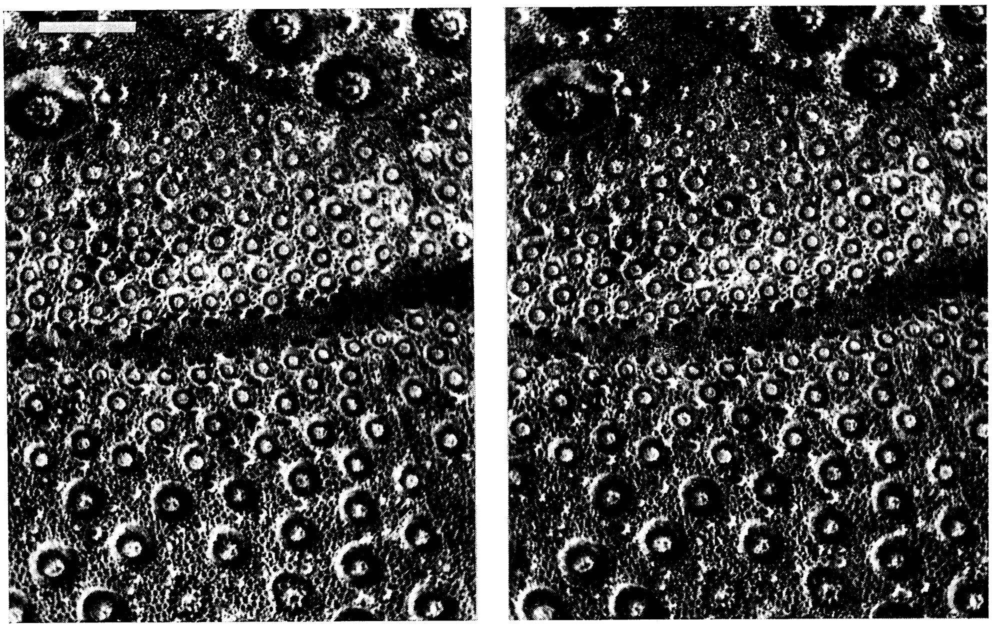

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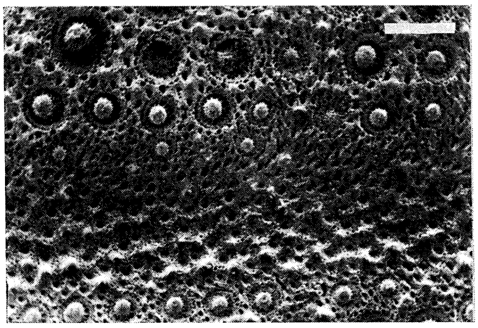

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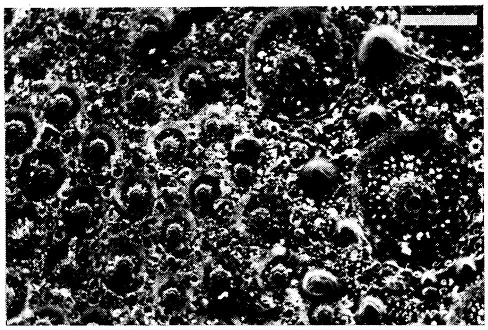

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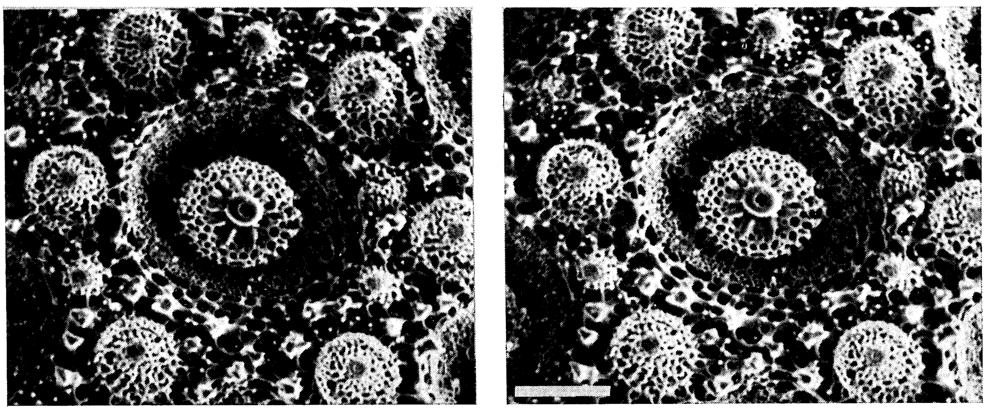

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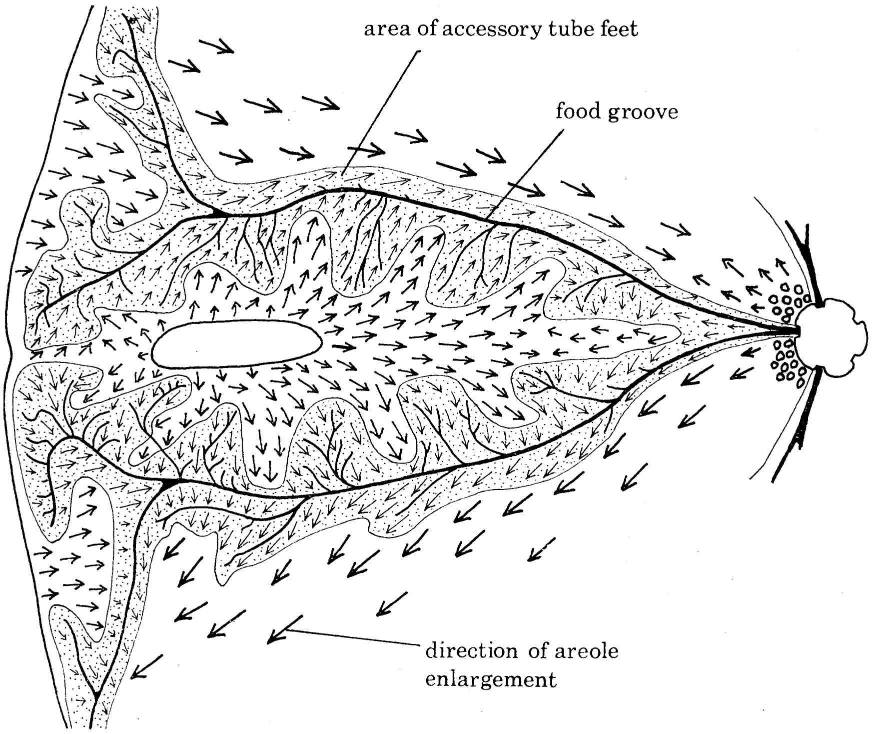

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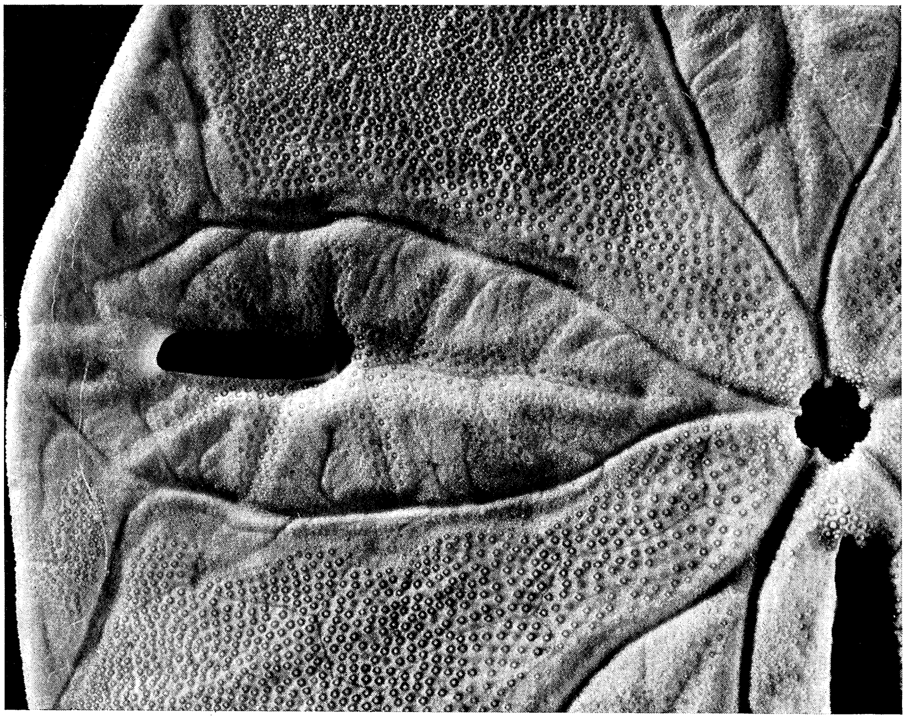

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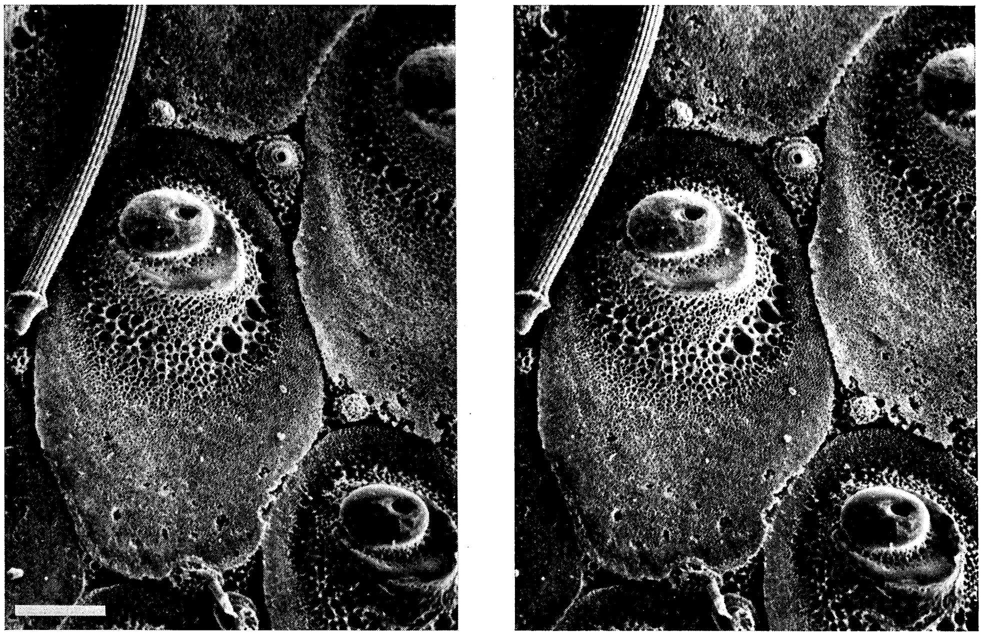

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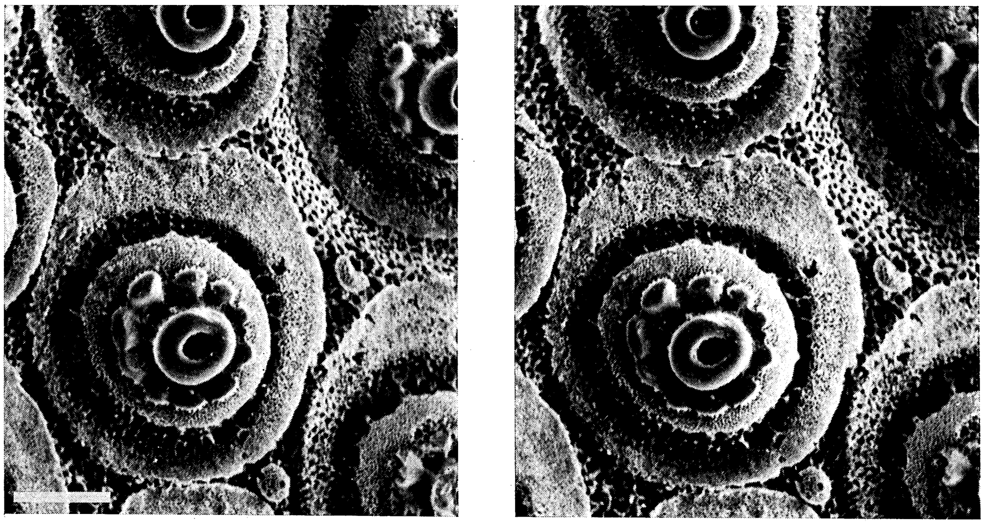

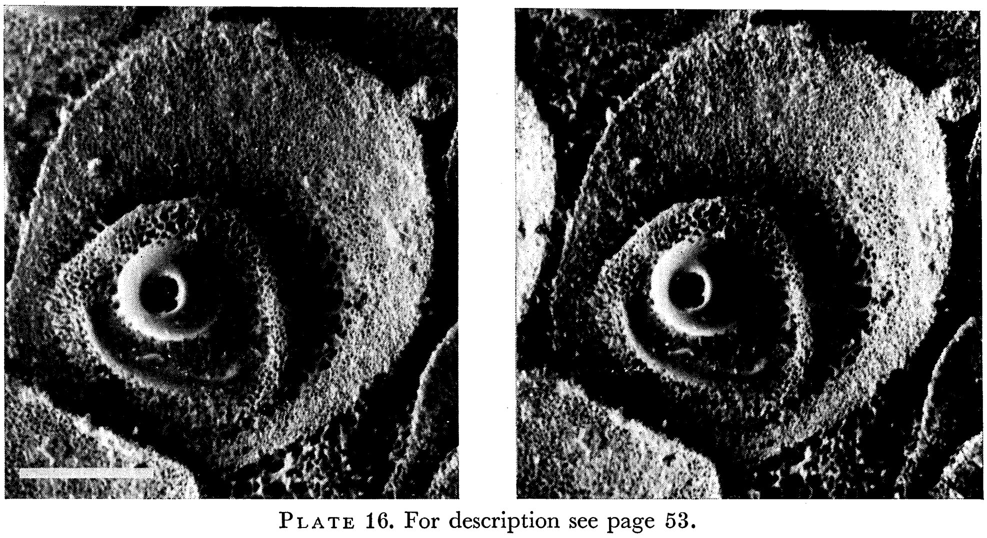

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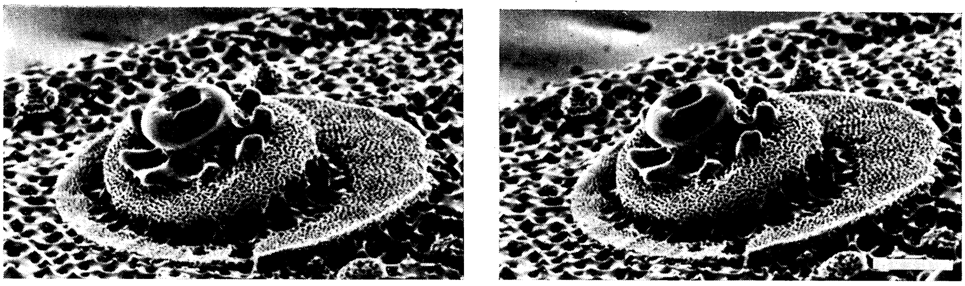

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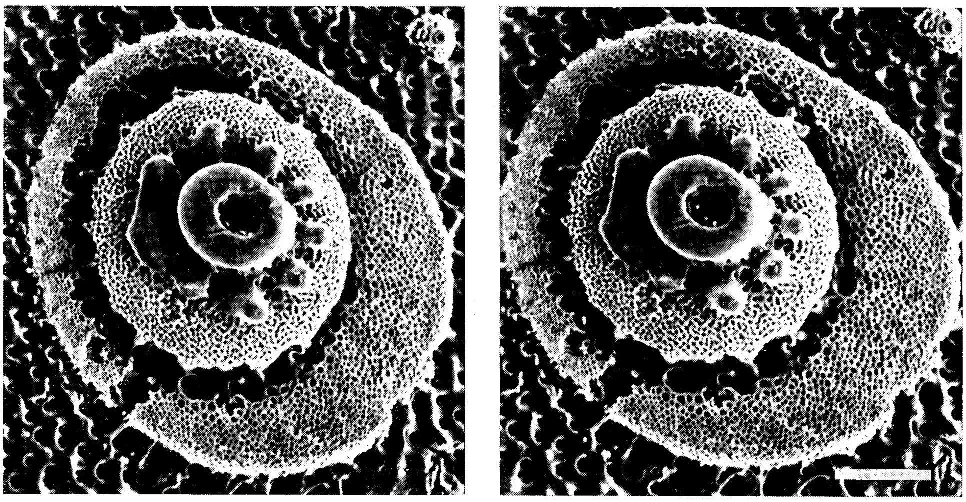

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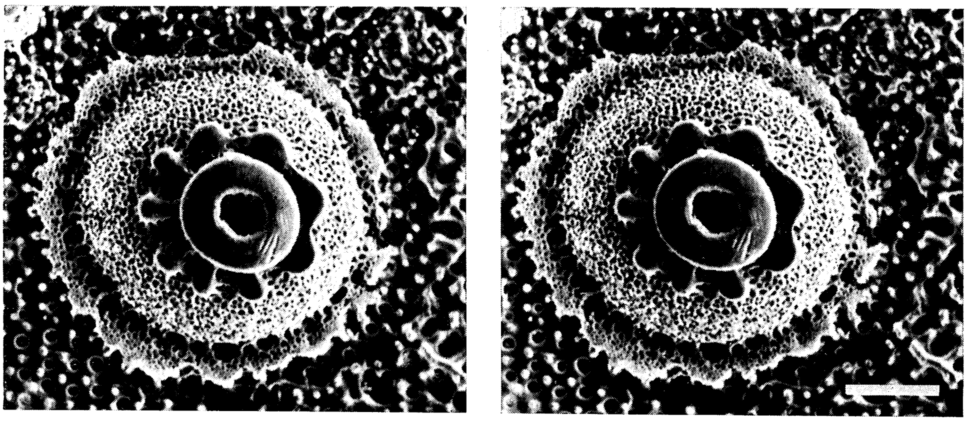

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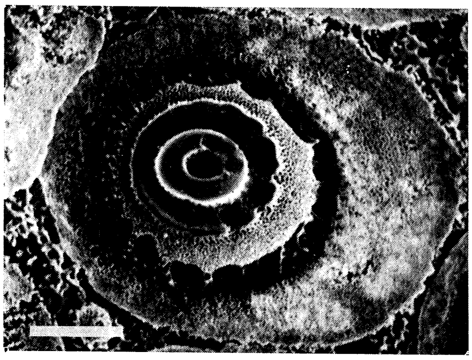

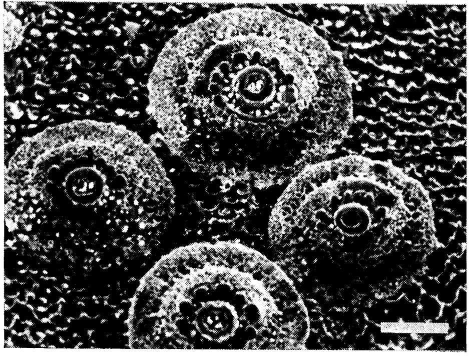

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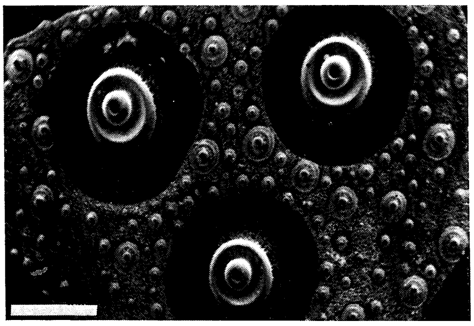
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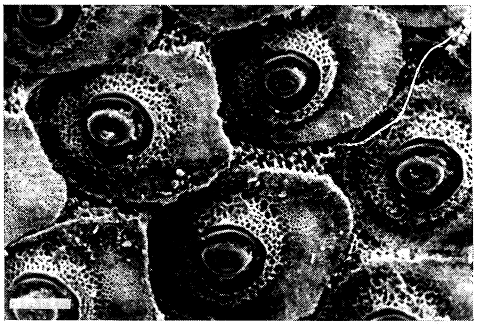
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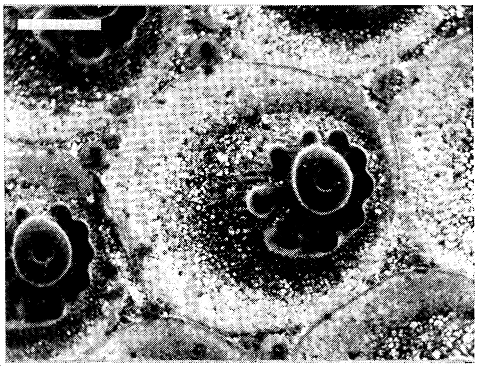
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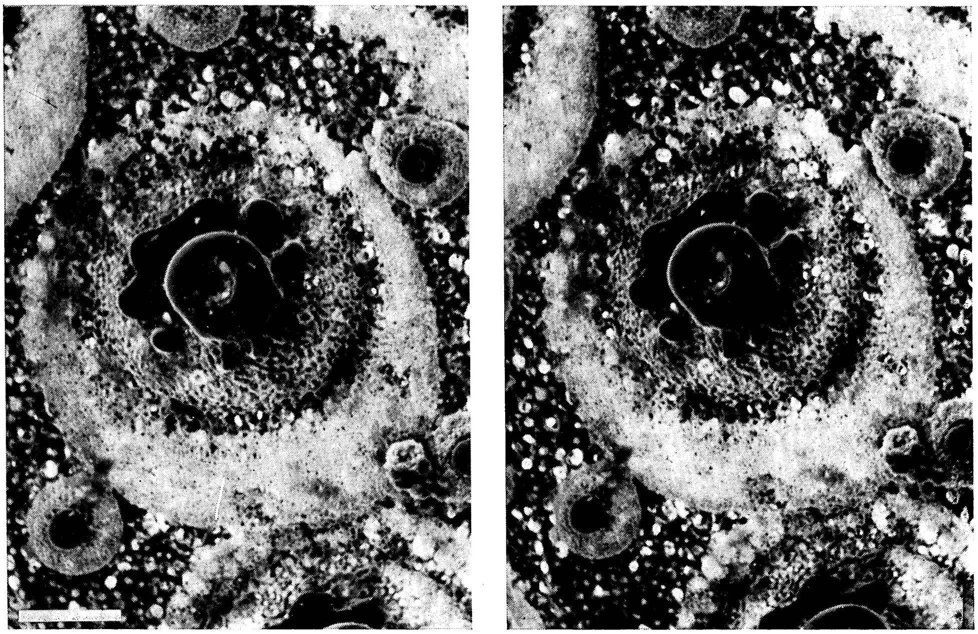
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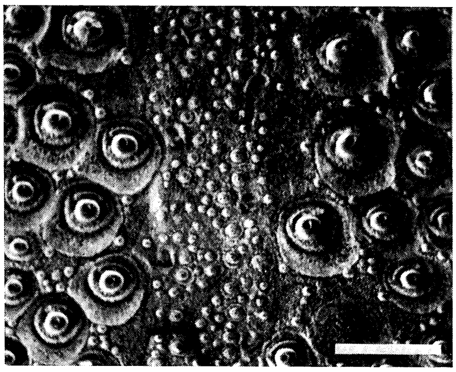
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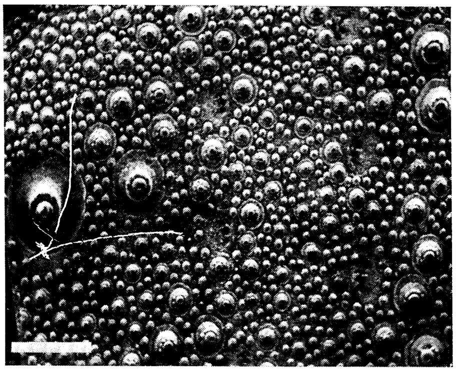
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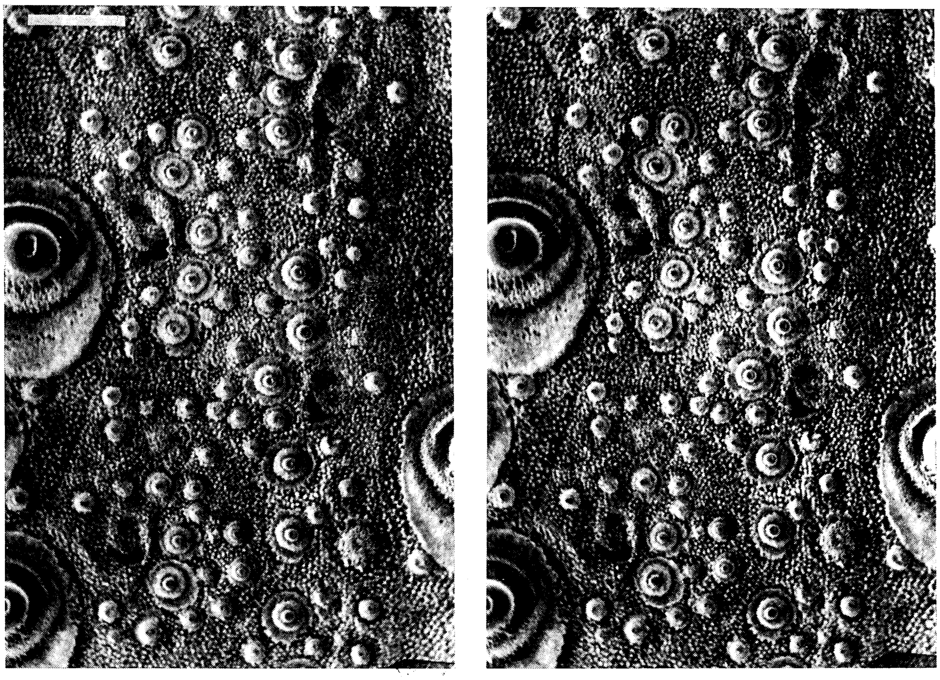
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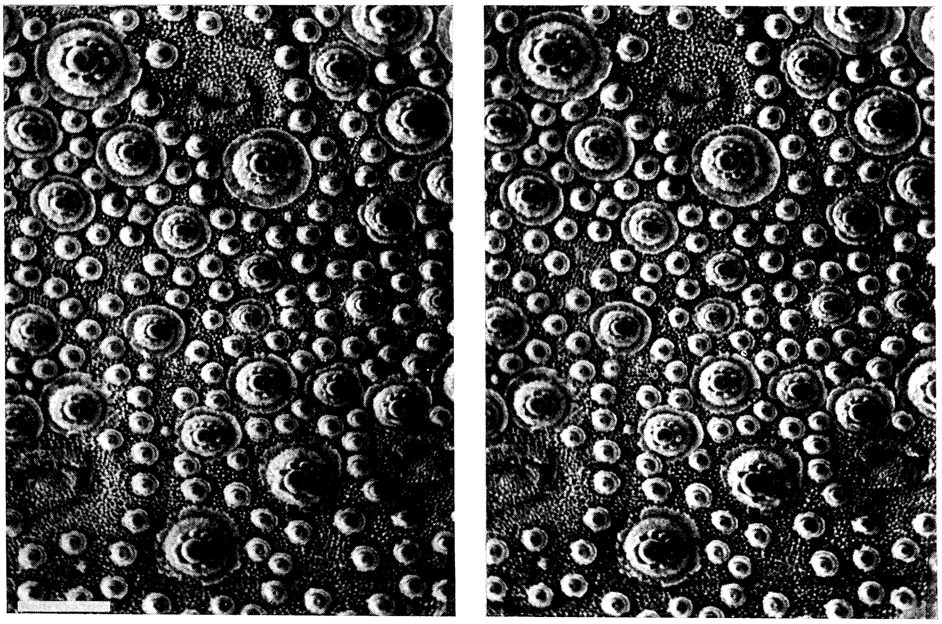
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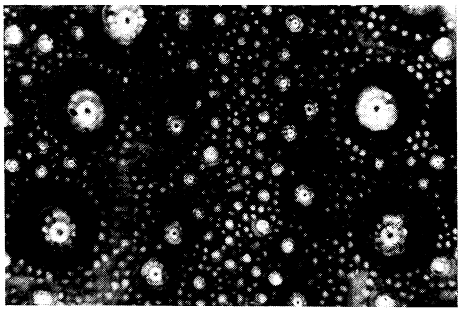

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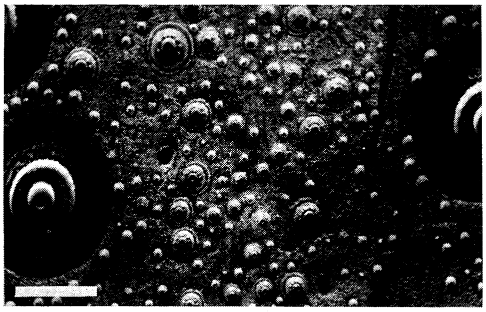

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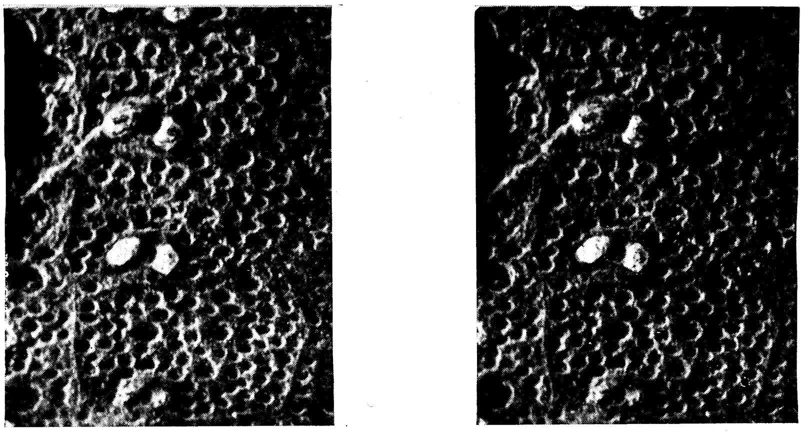

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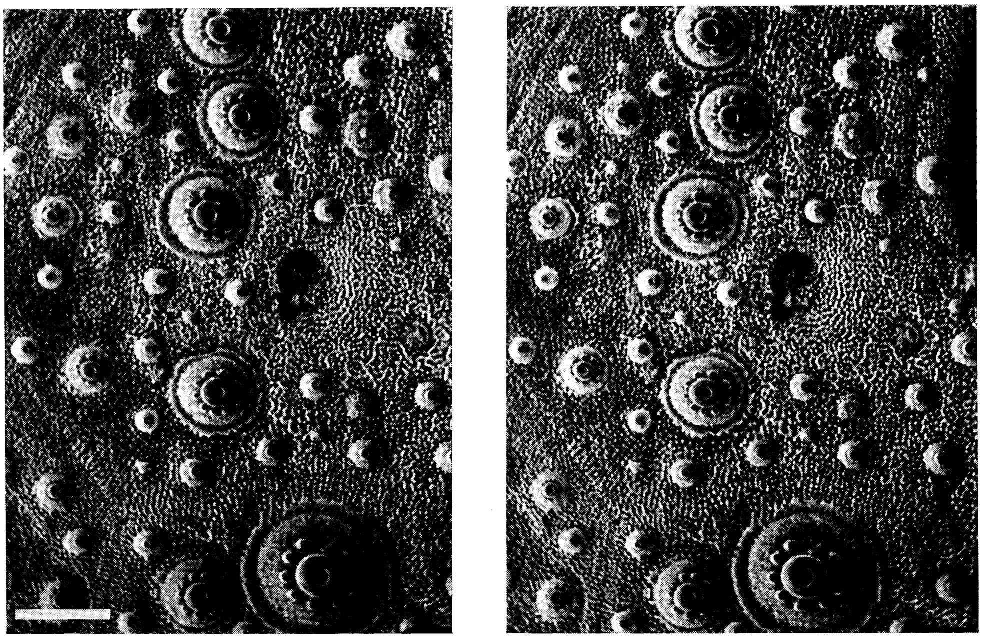

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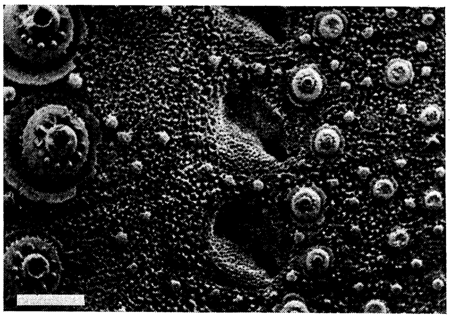
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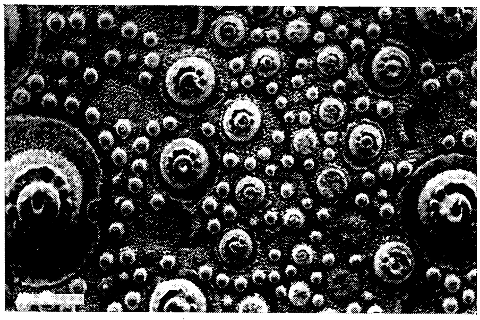
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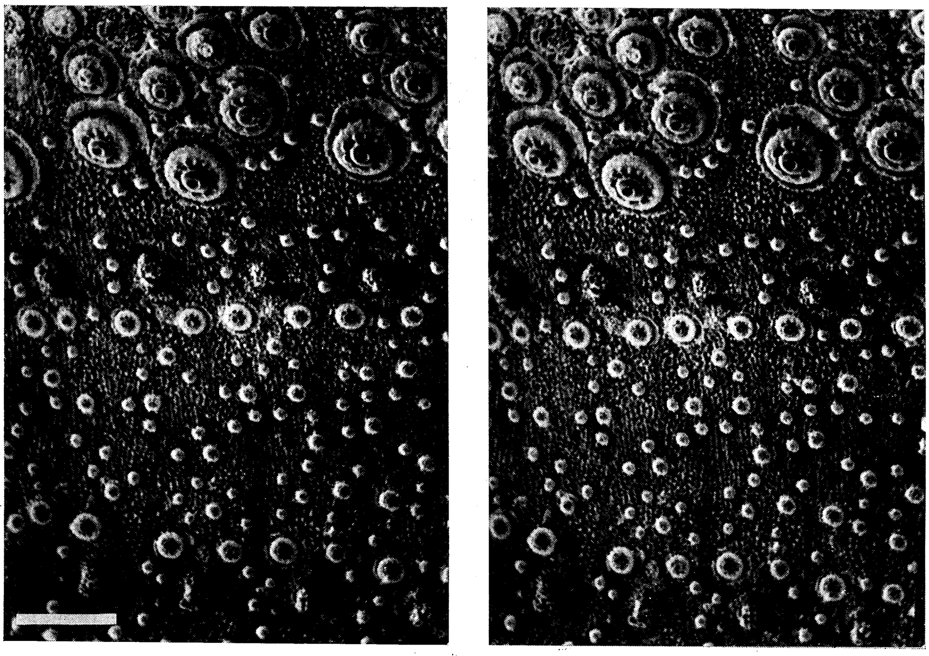
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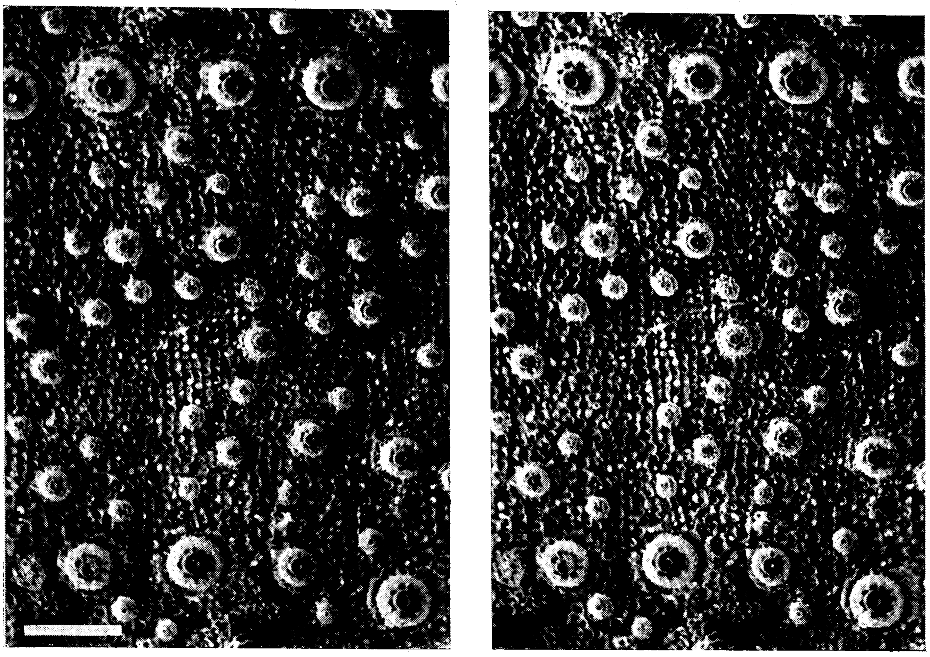
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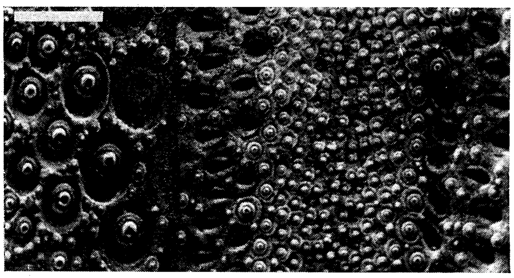
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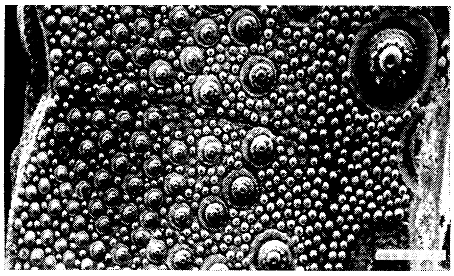
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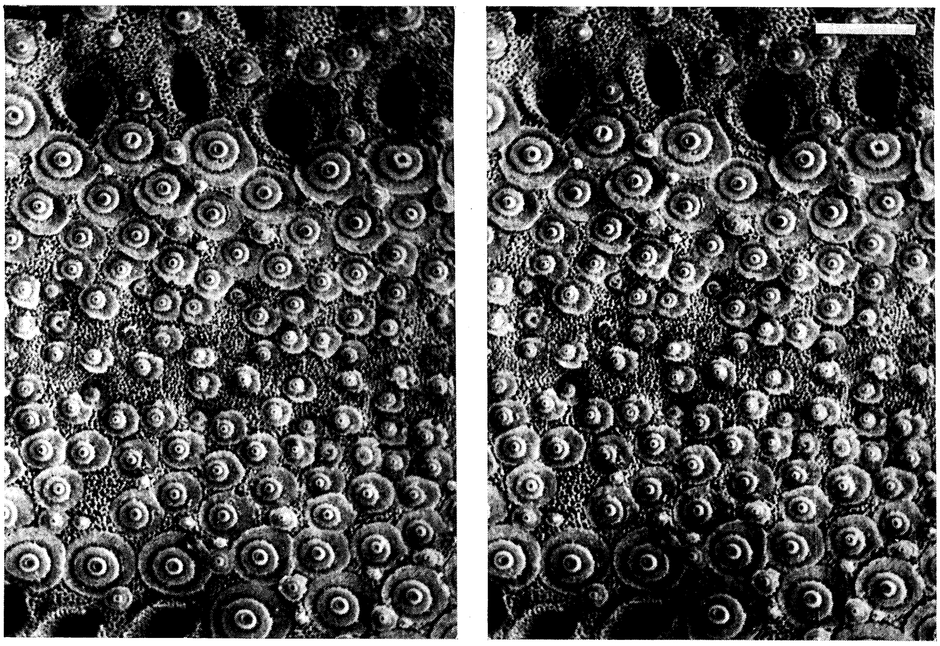
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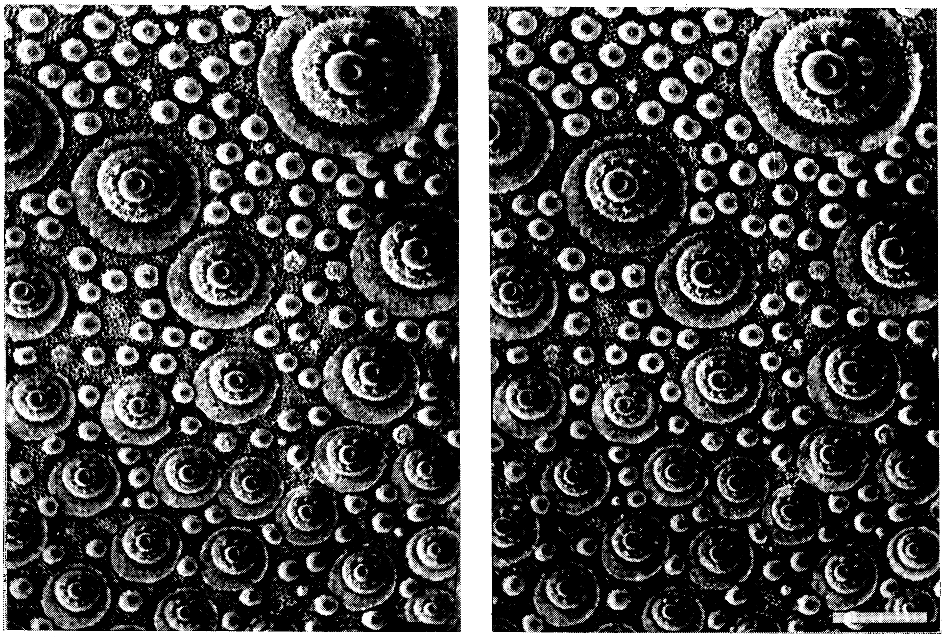
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PLATE 22. For description see page 54.

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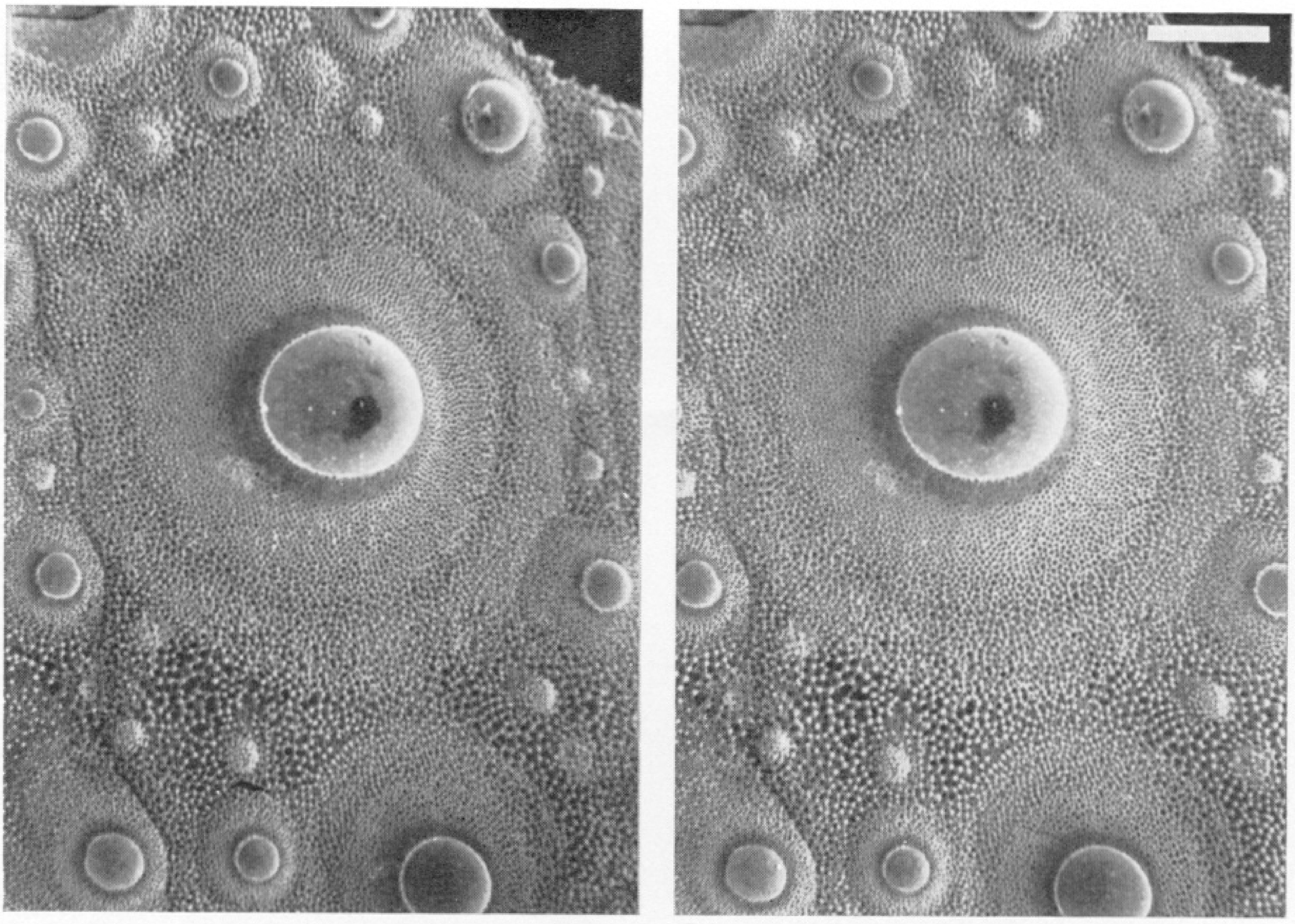

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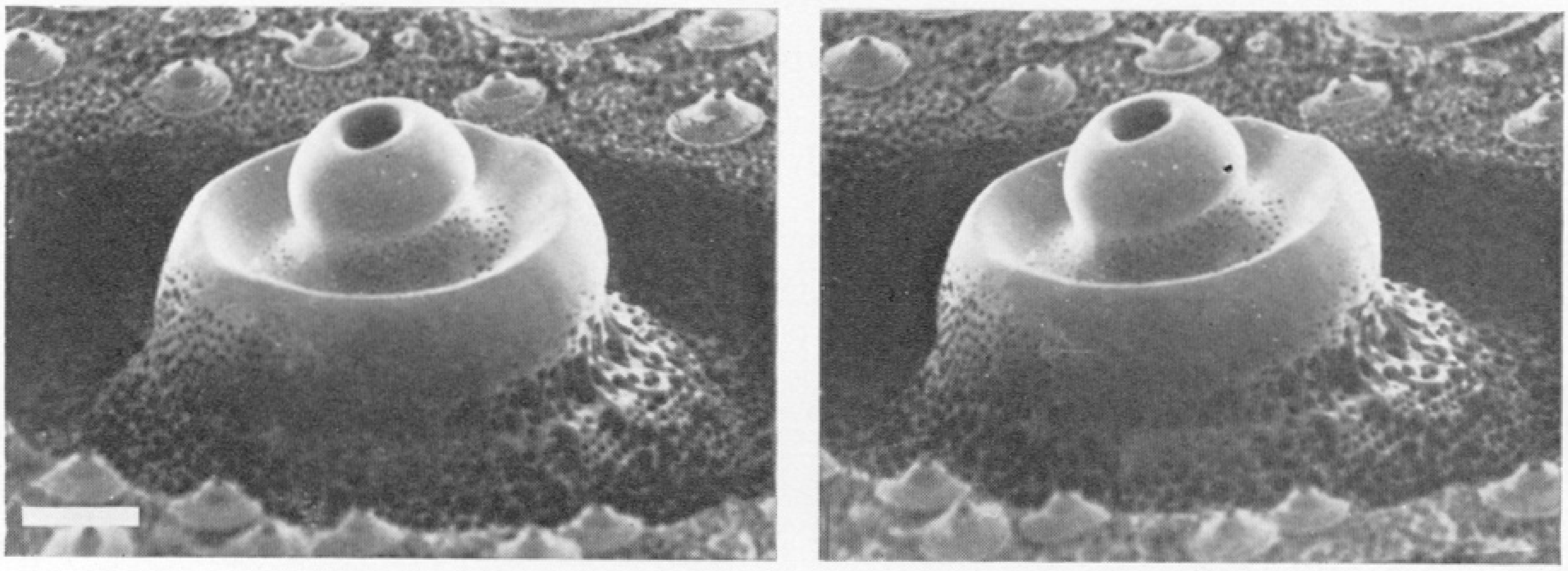

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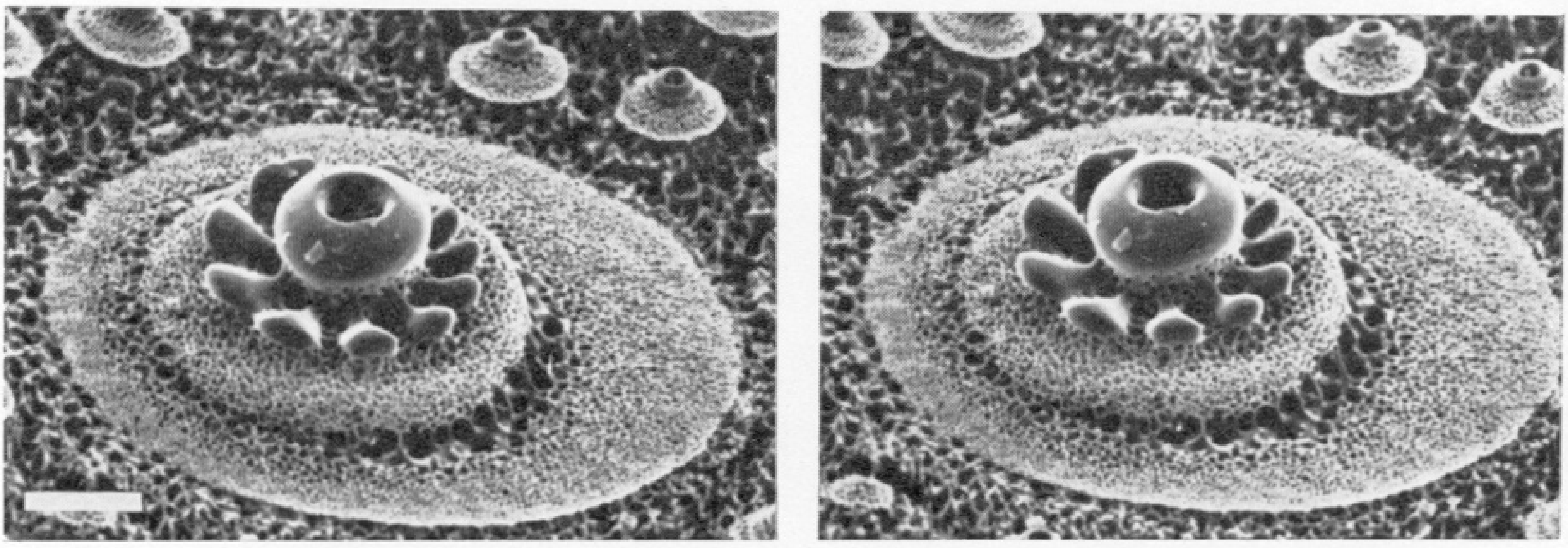

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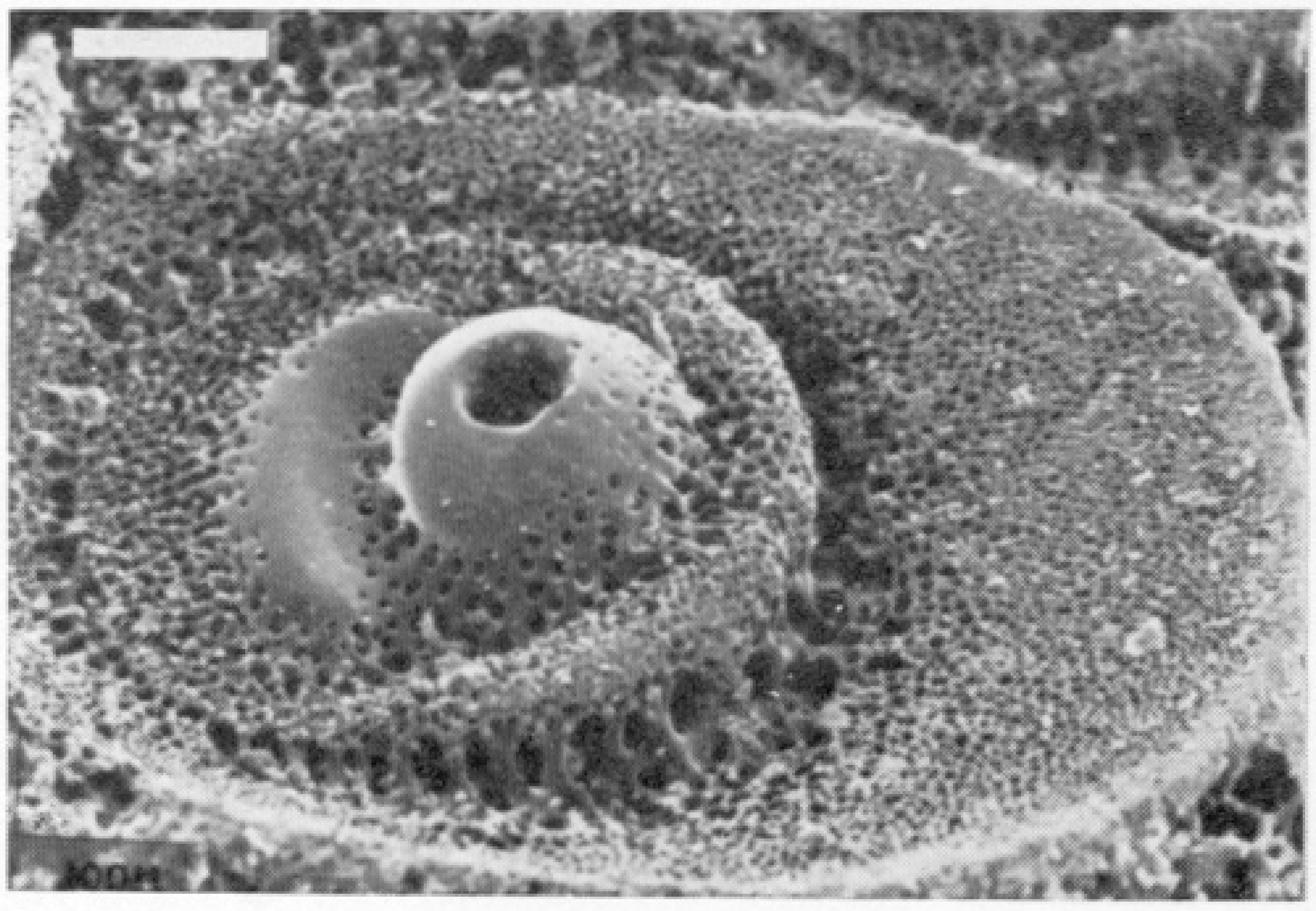


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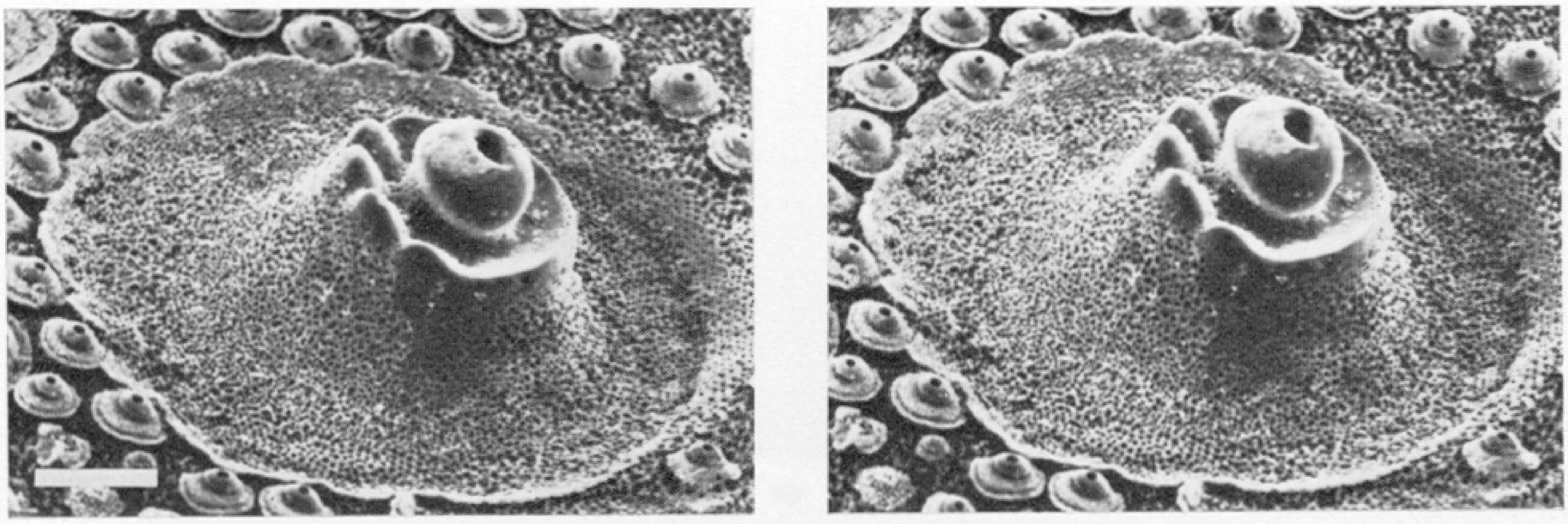

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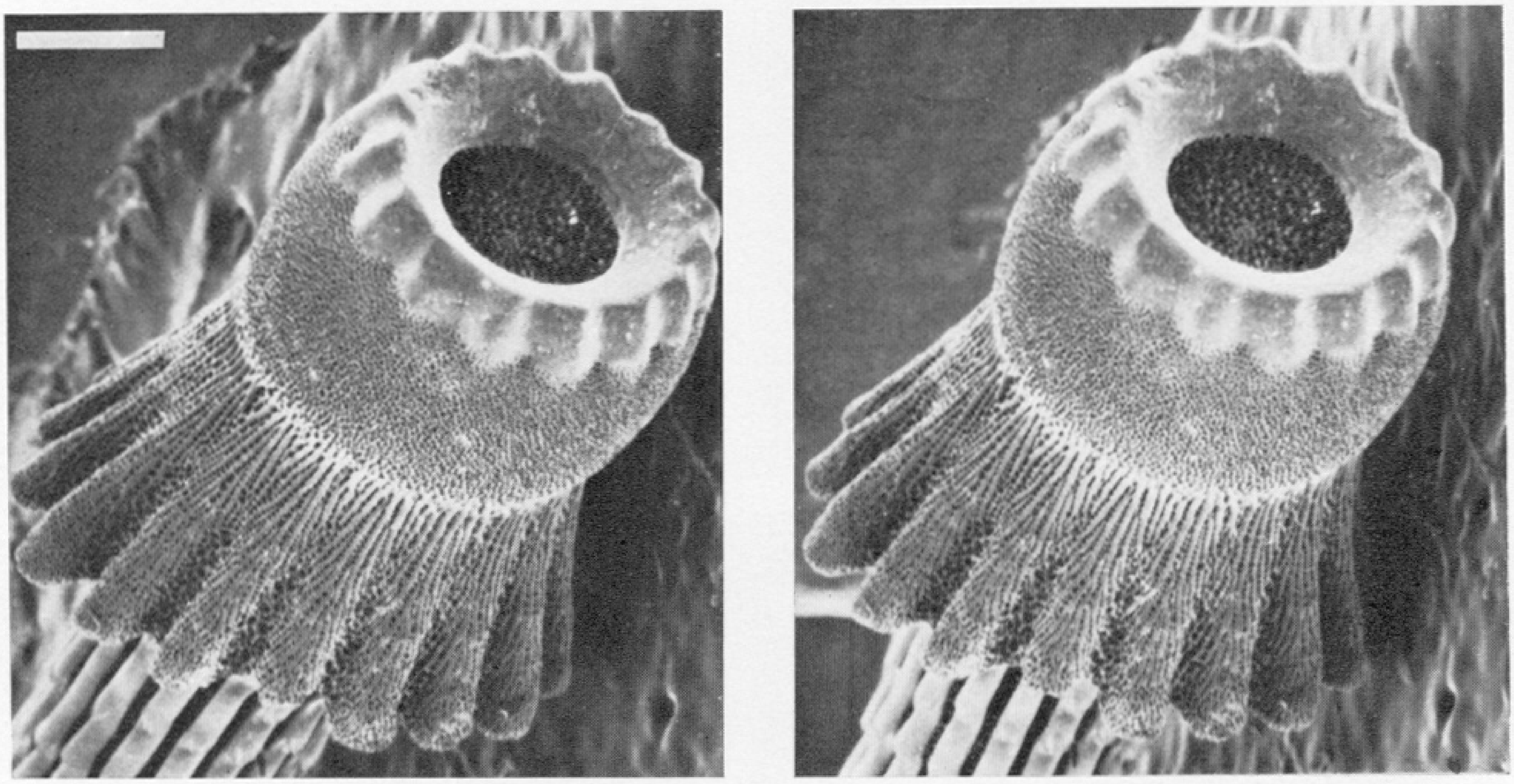

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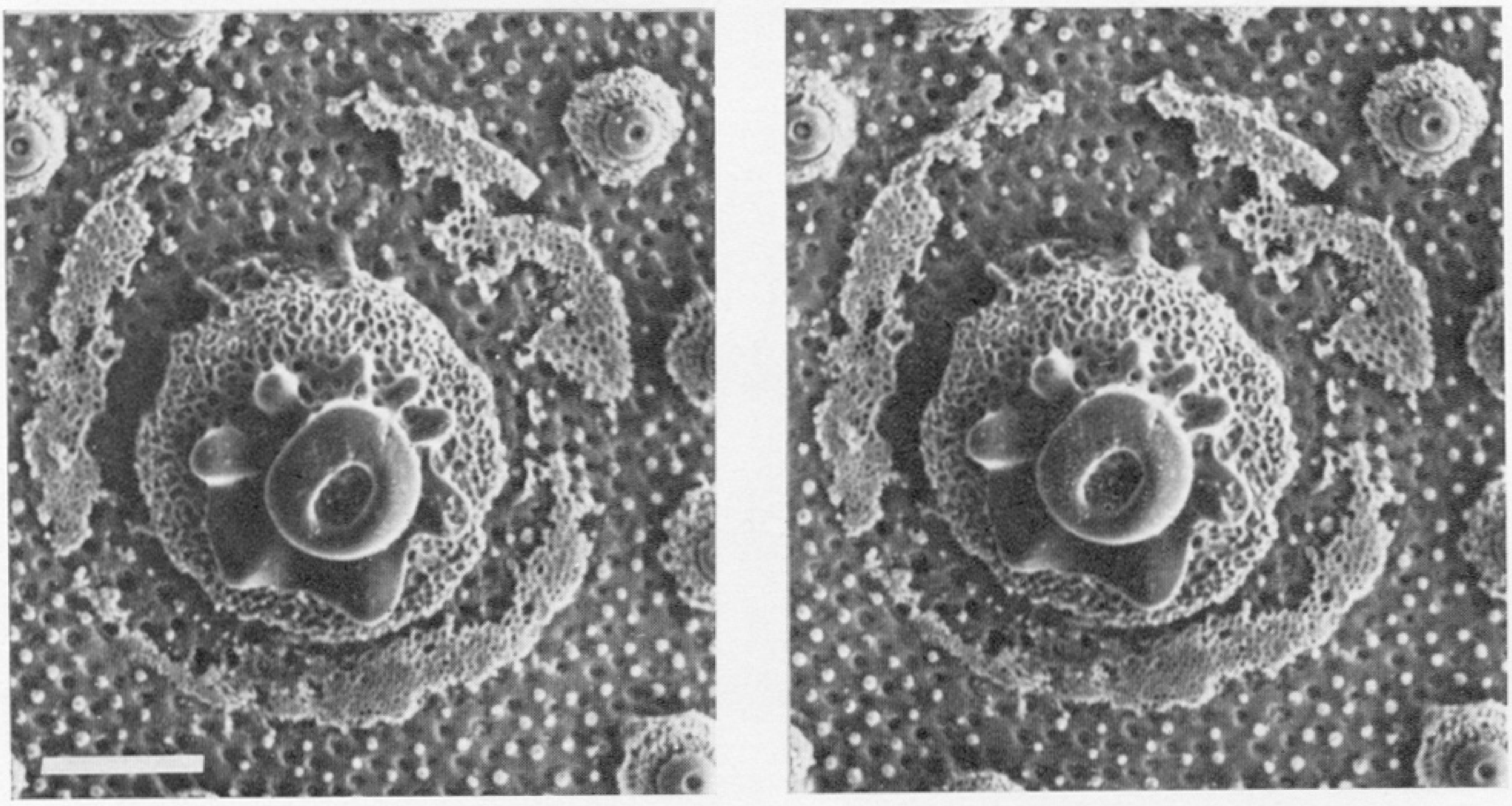

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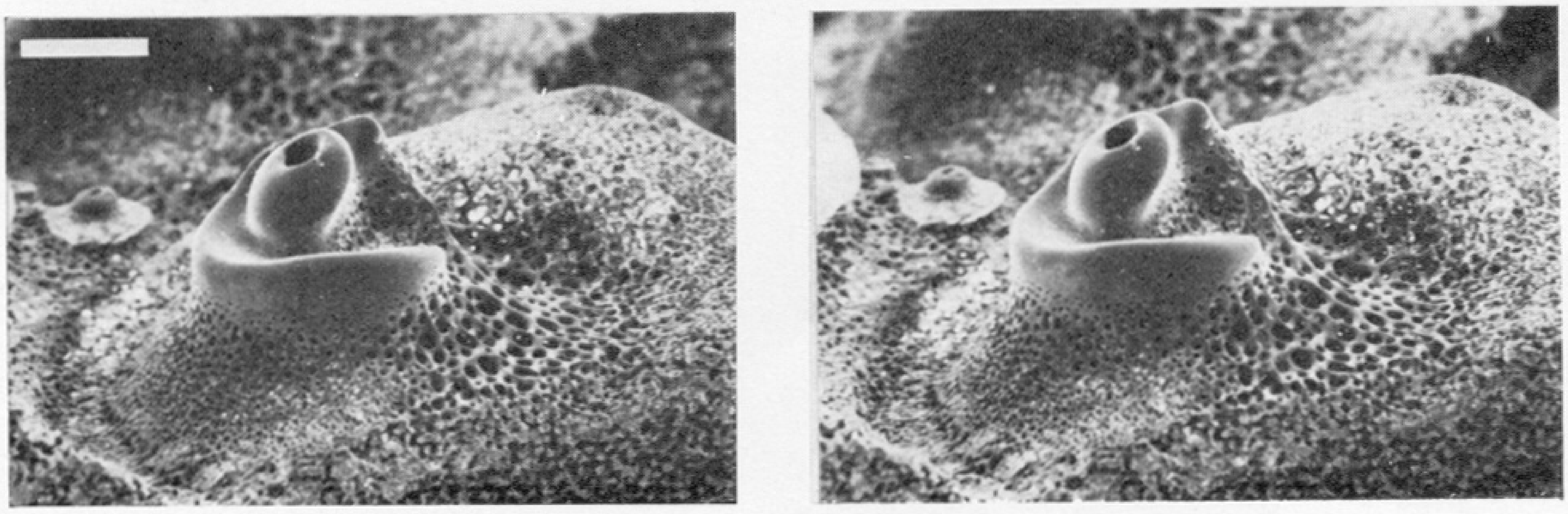

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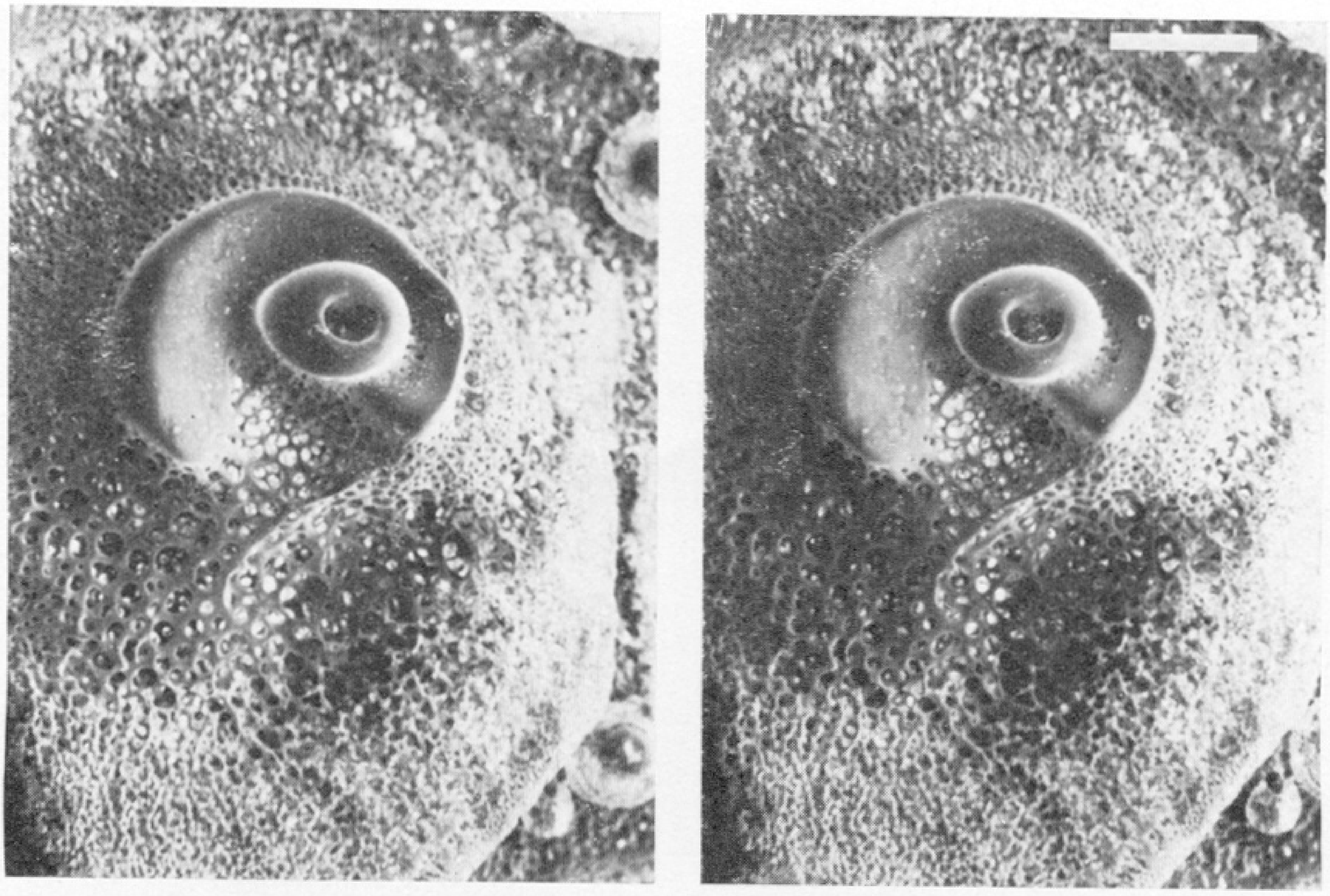

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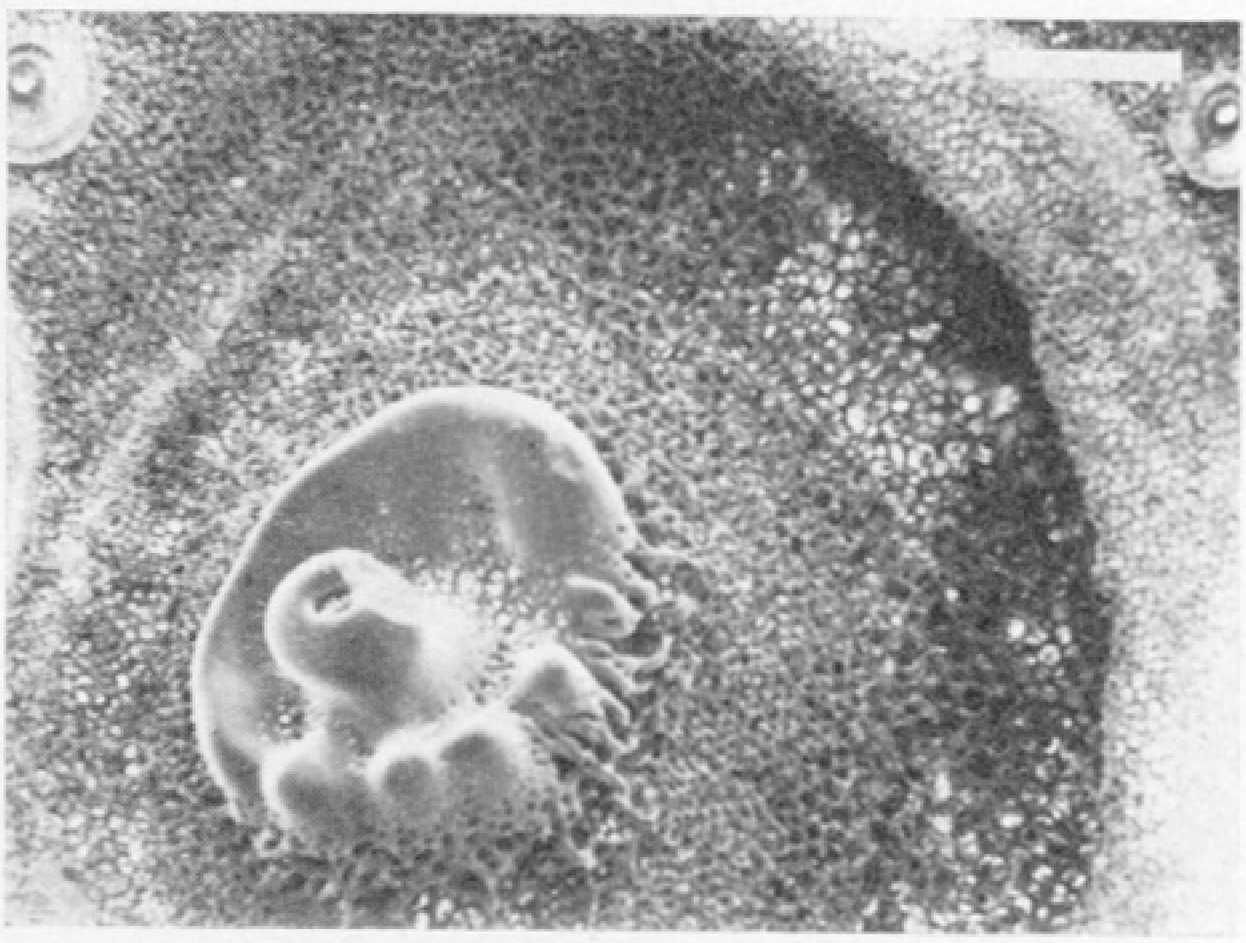

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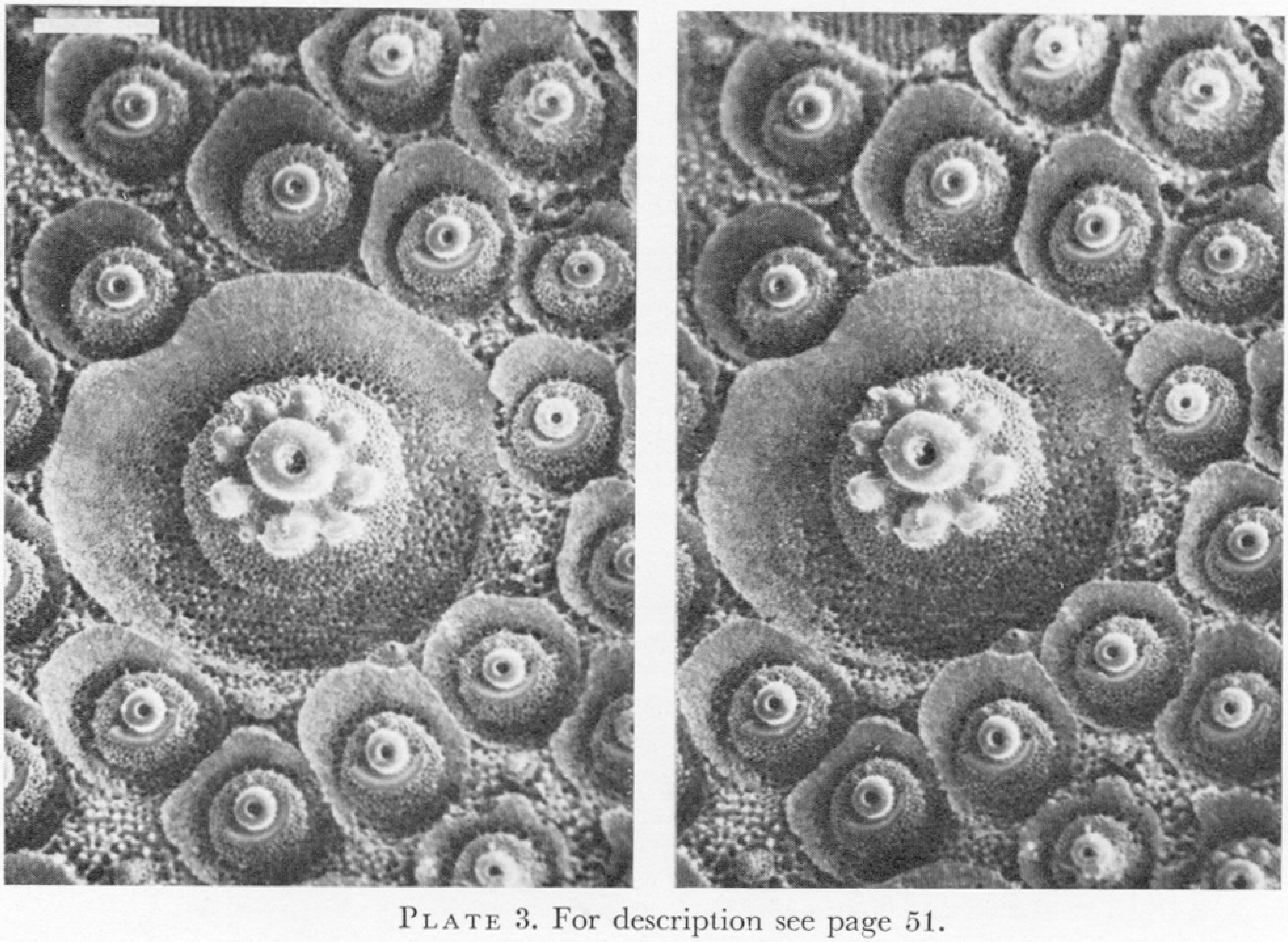

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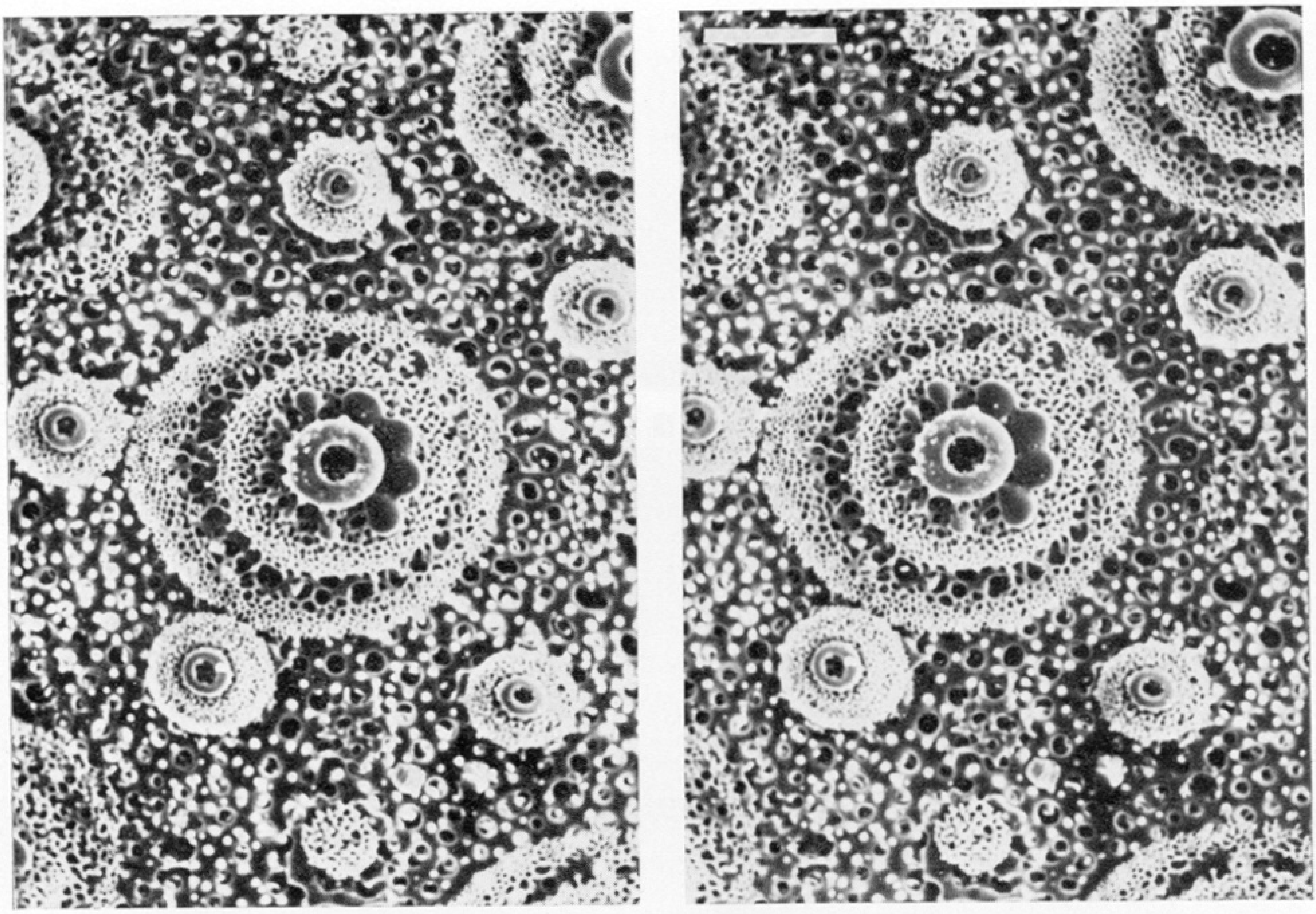

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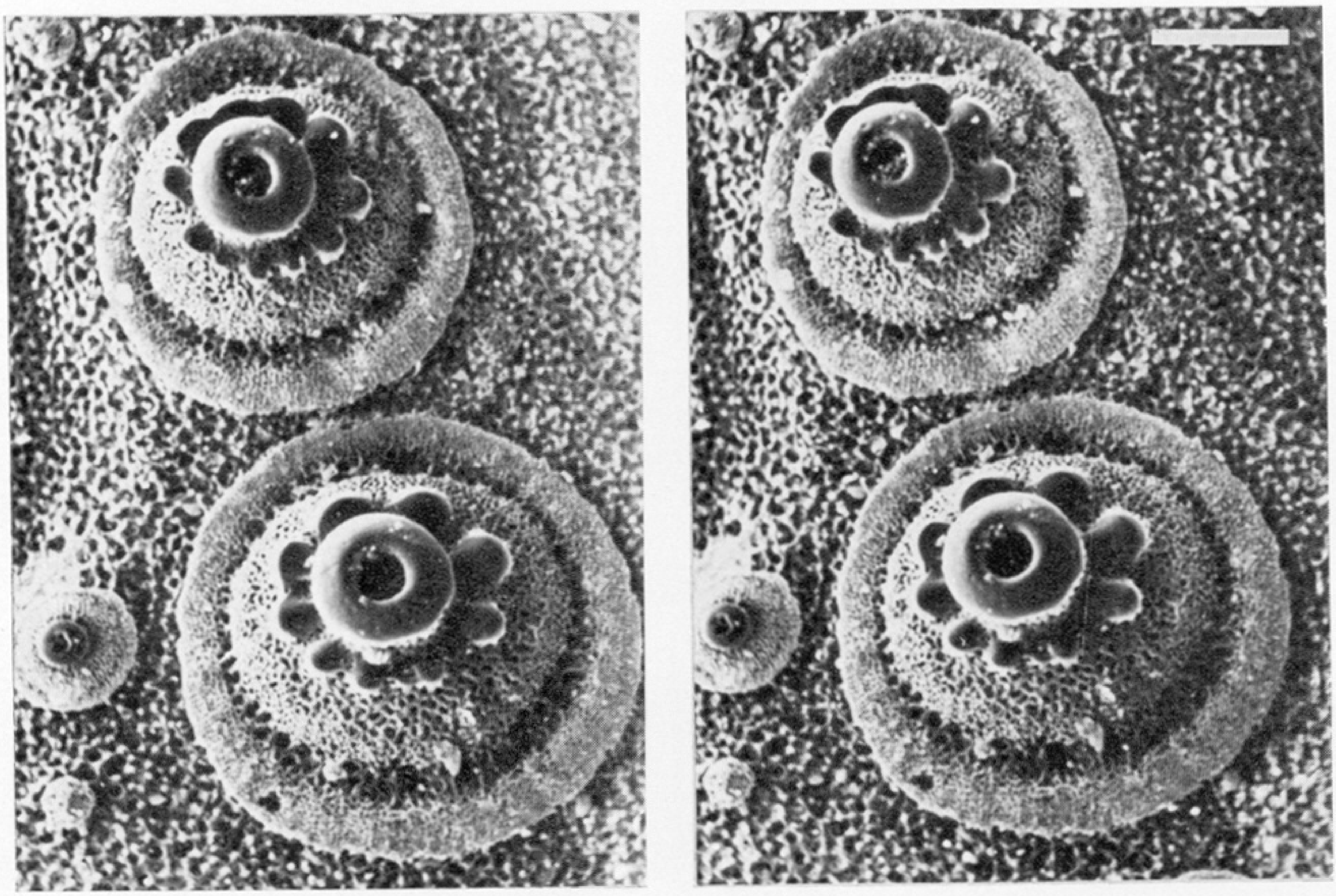

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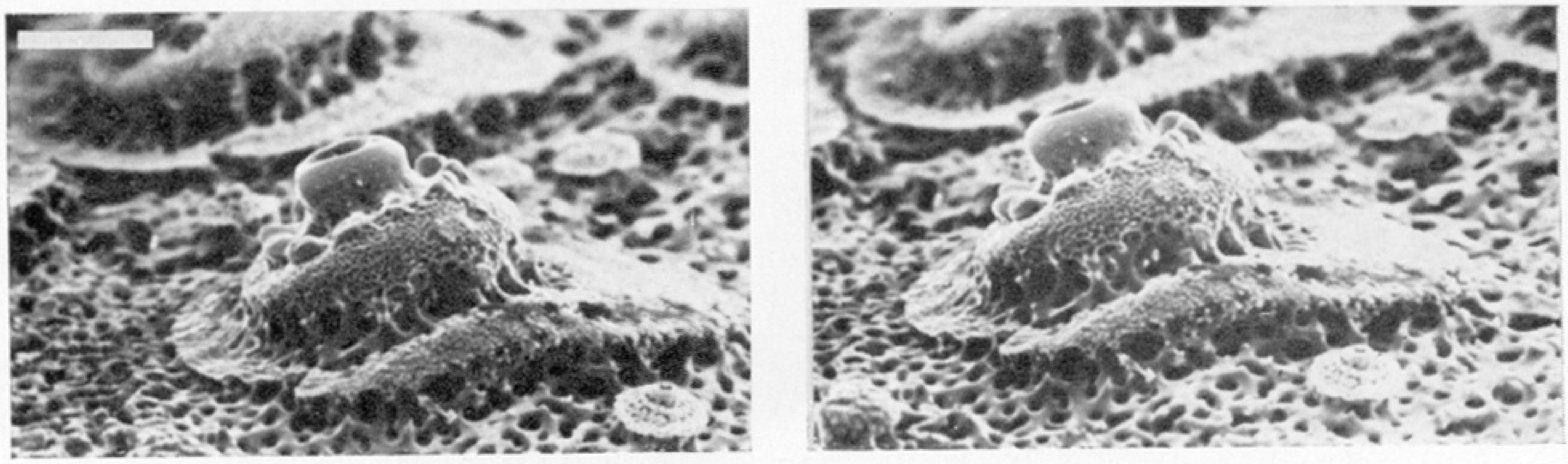

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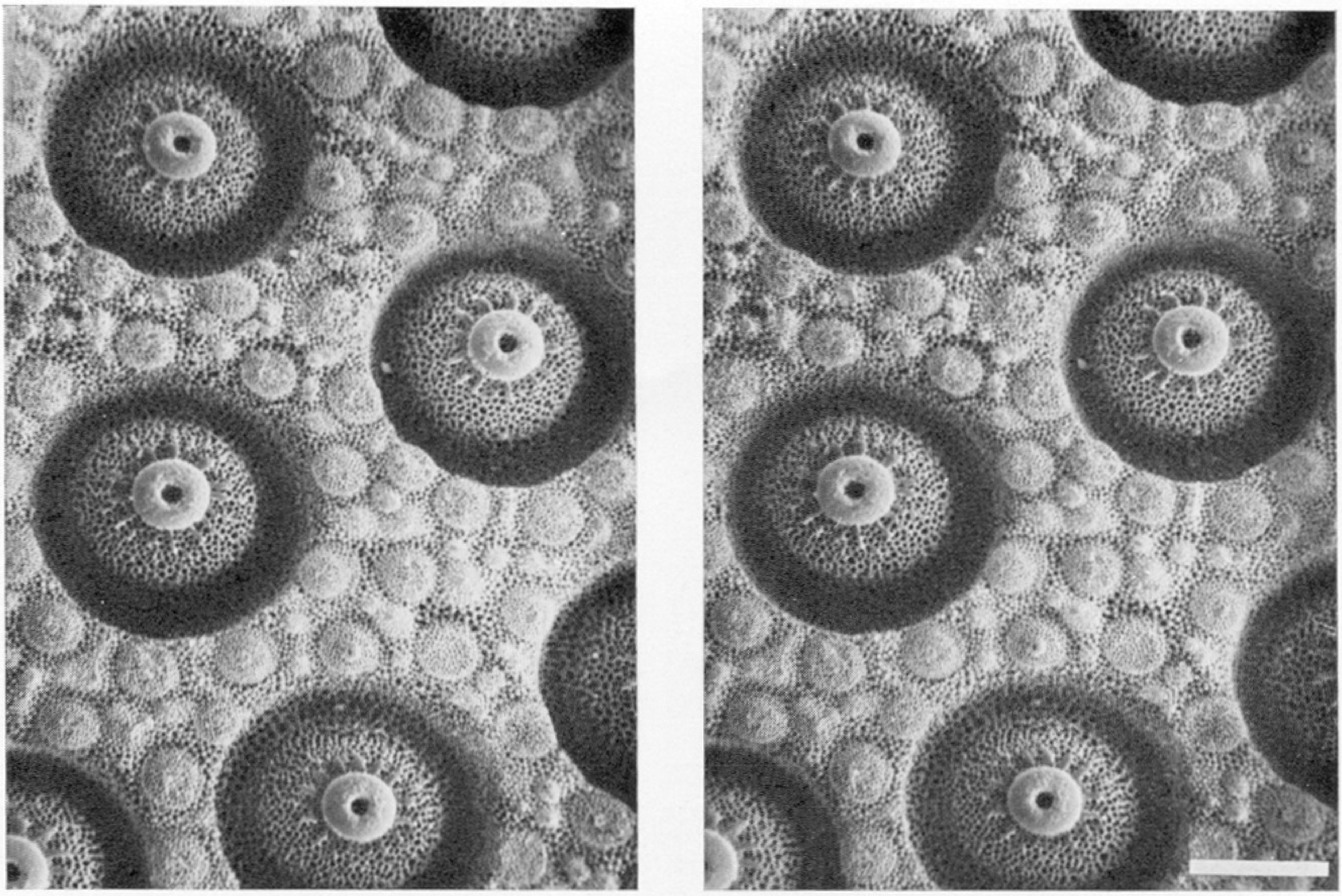
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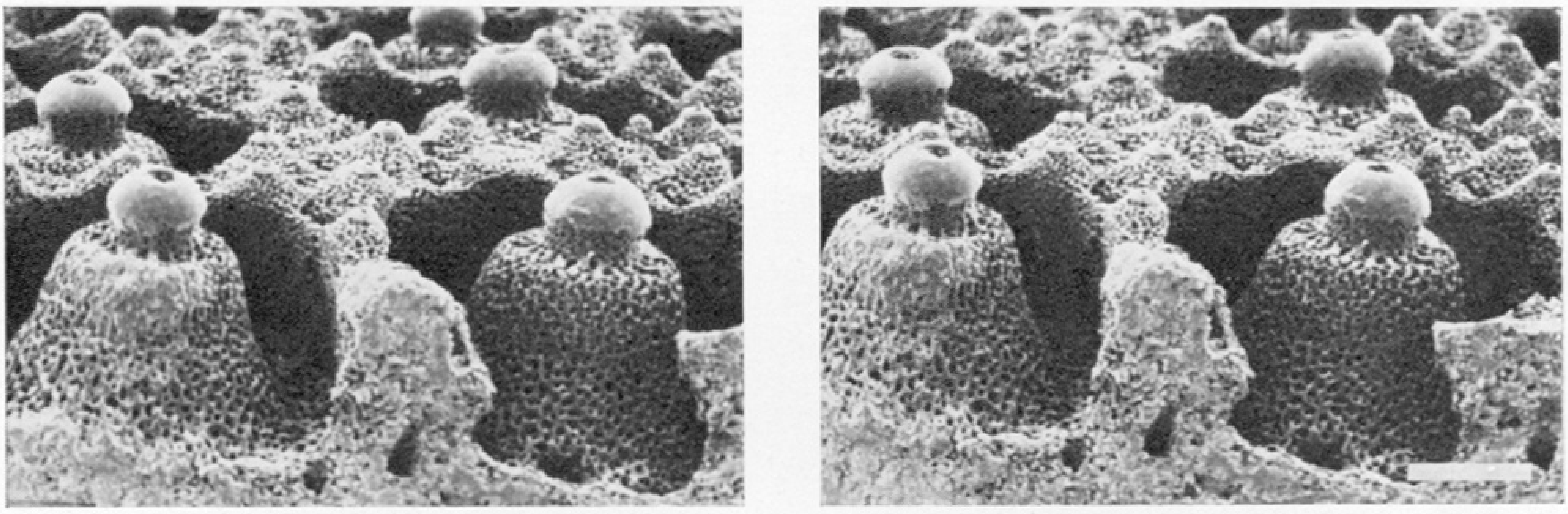
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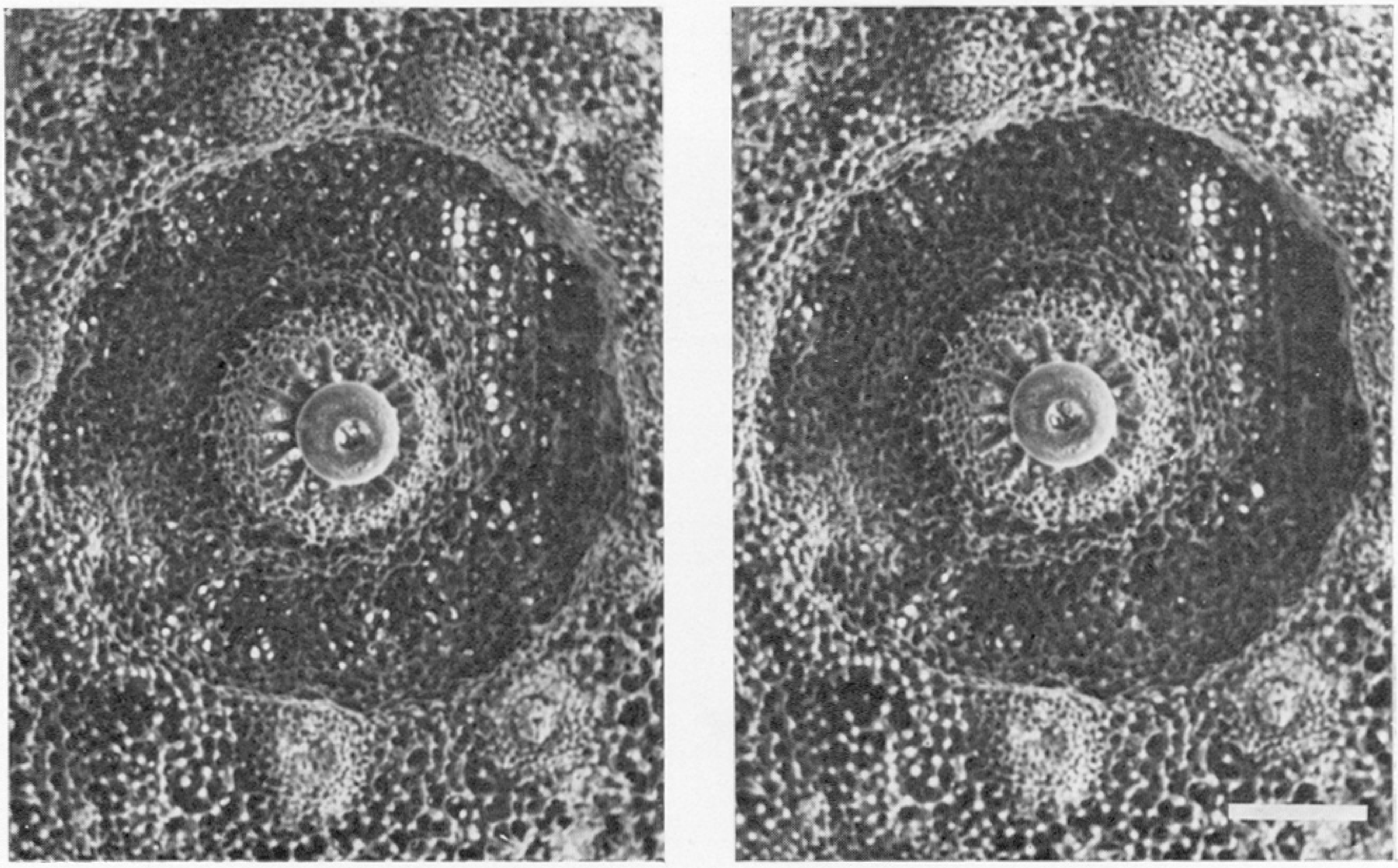
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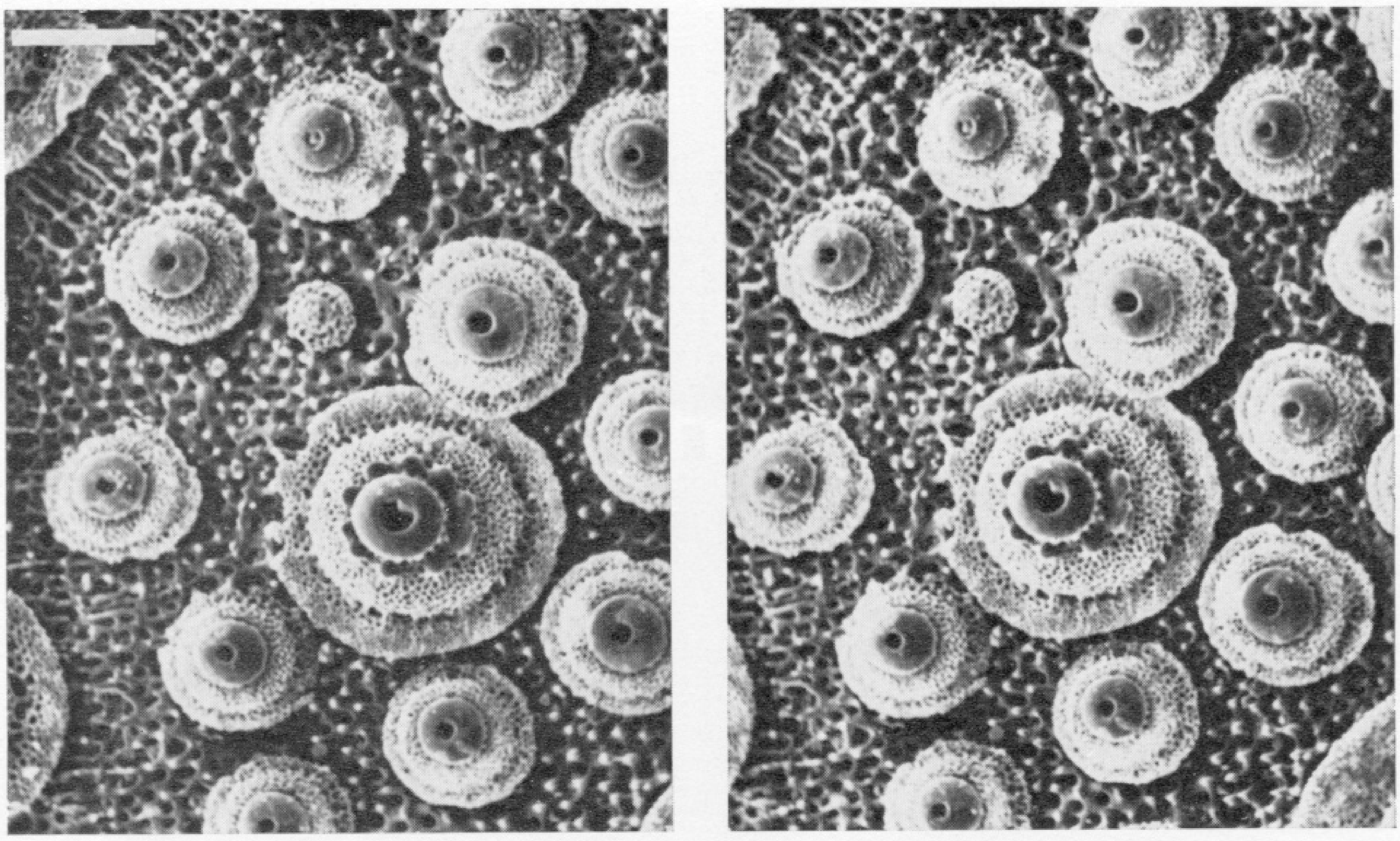

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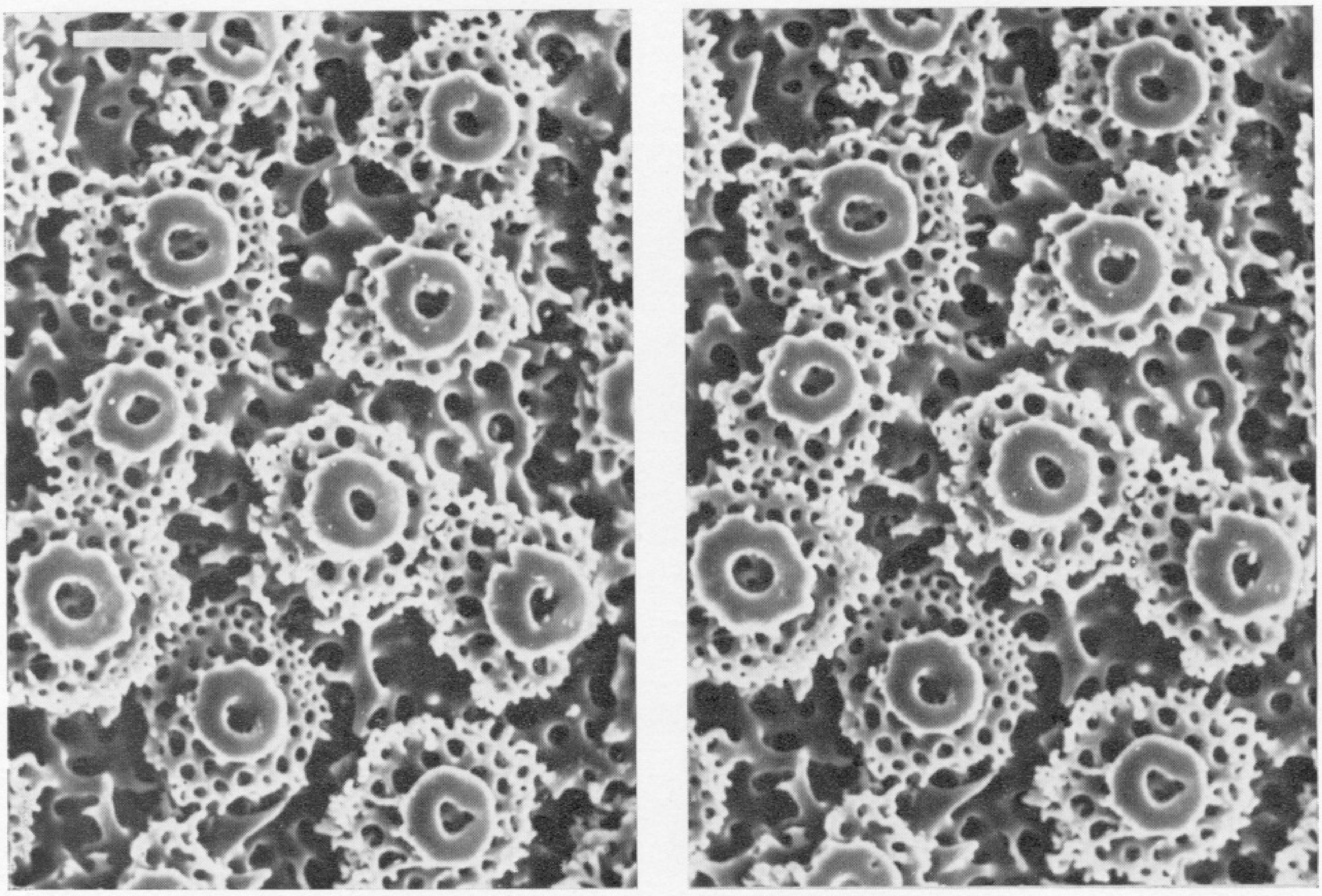

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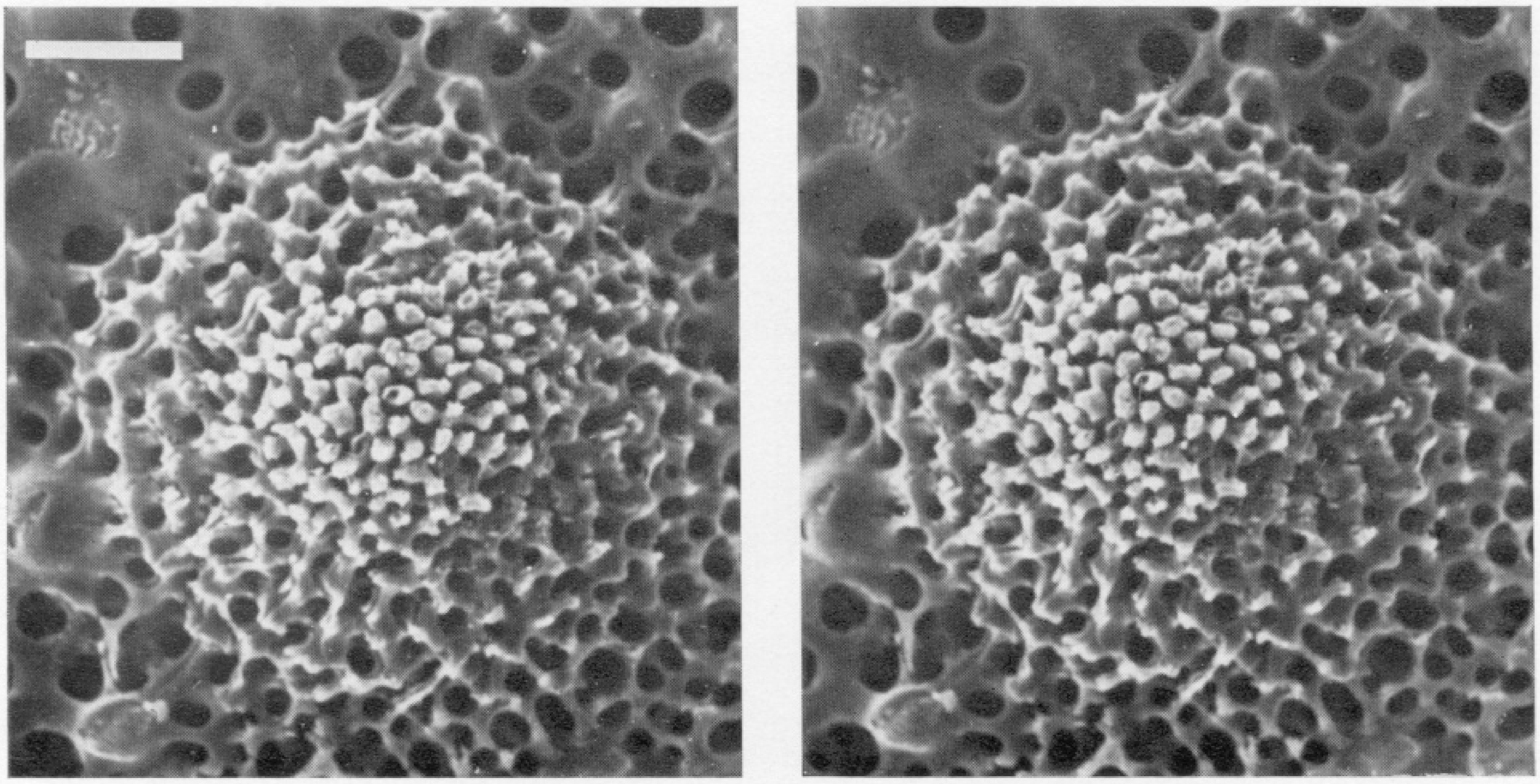

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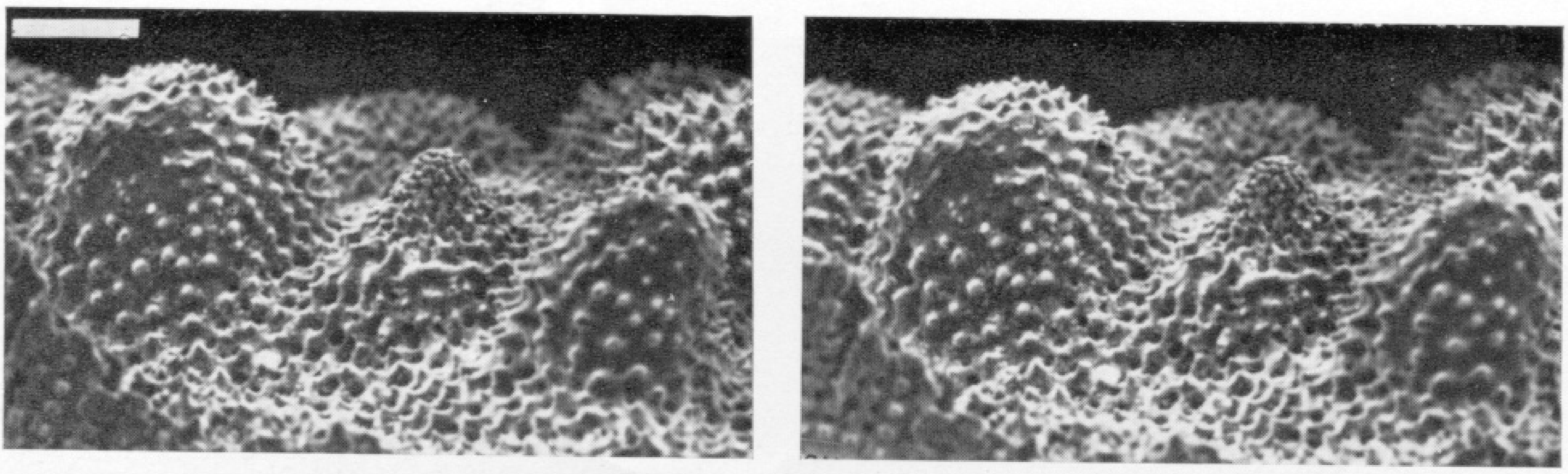

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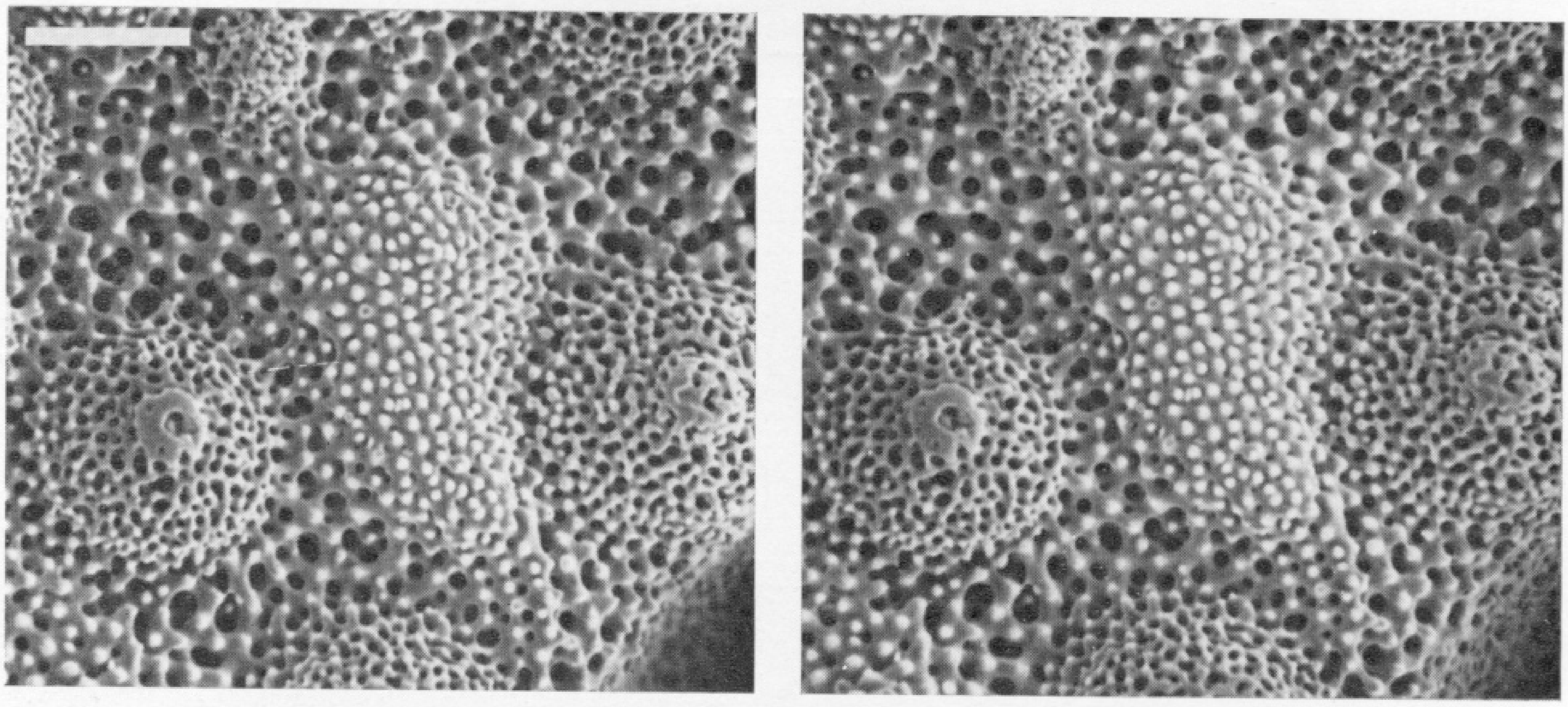

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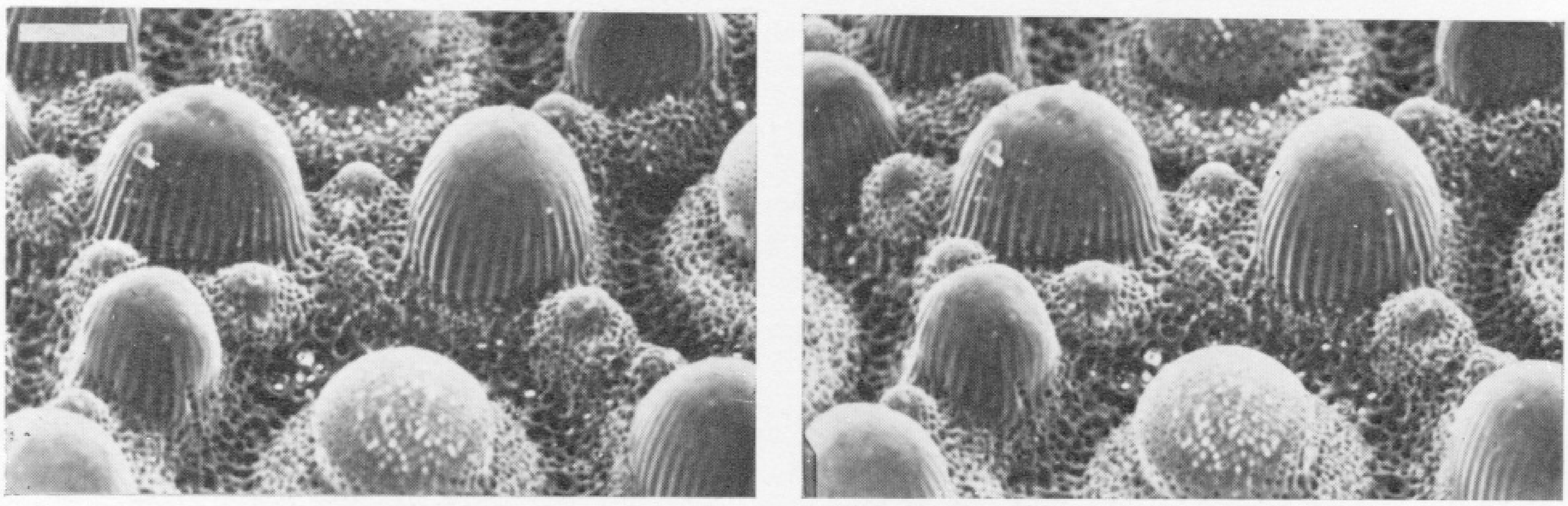

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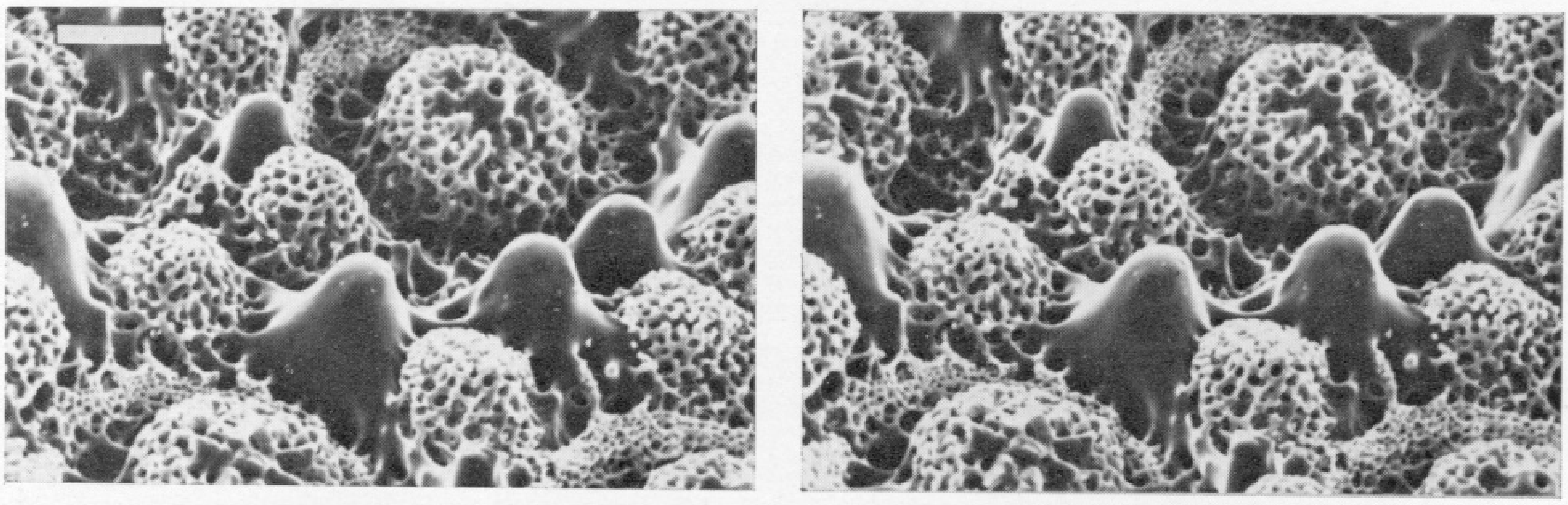

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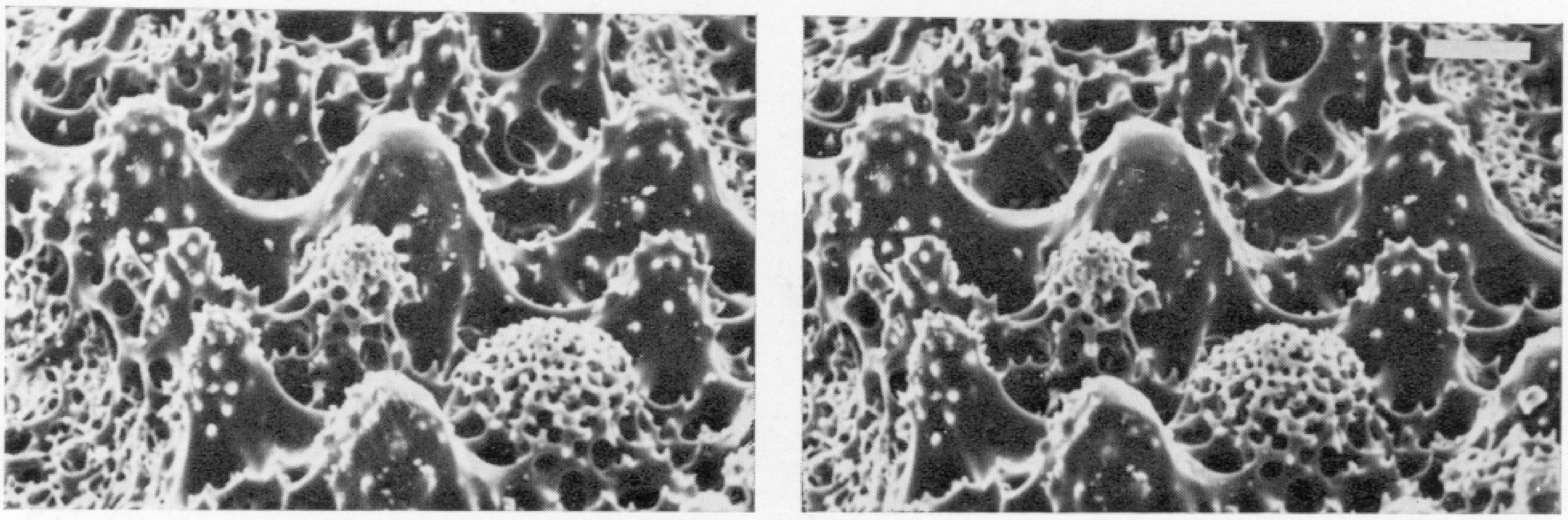

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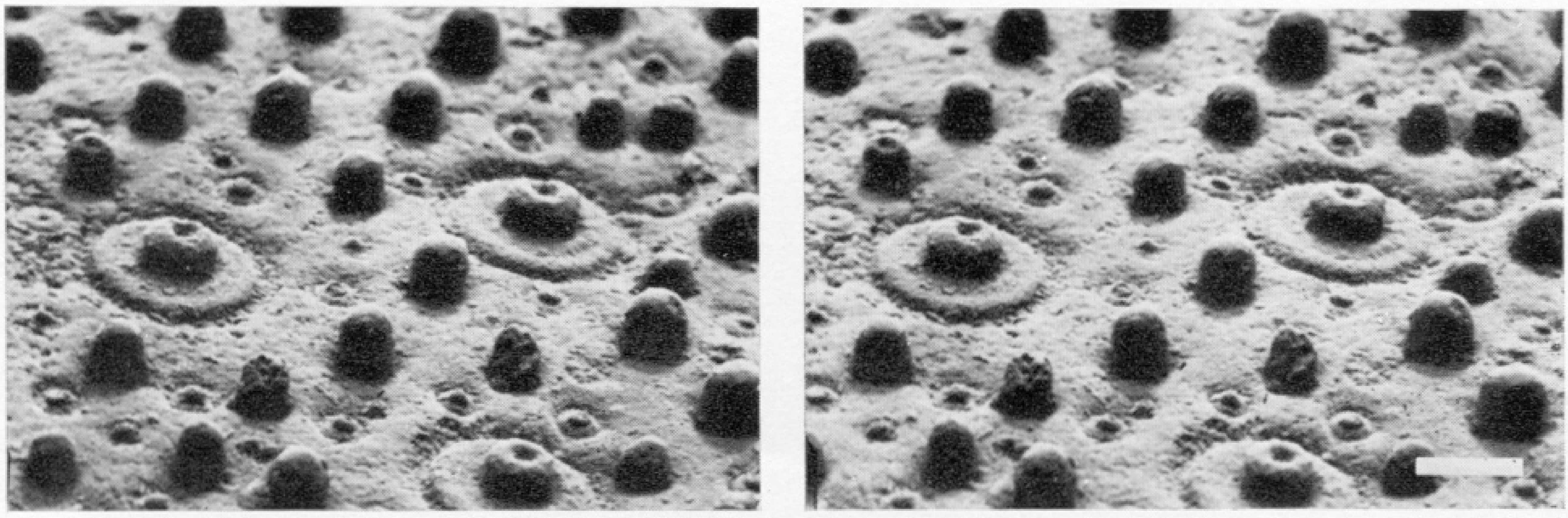
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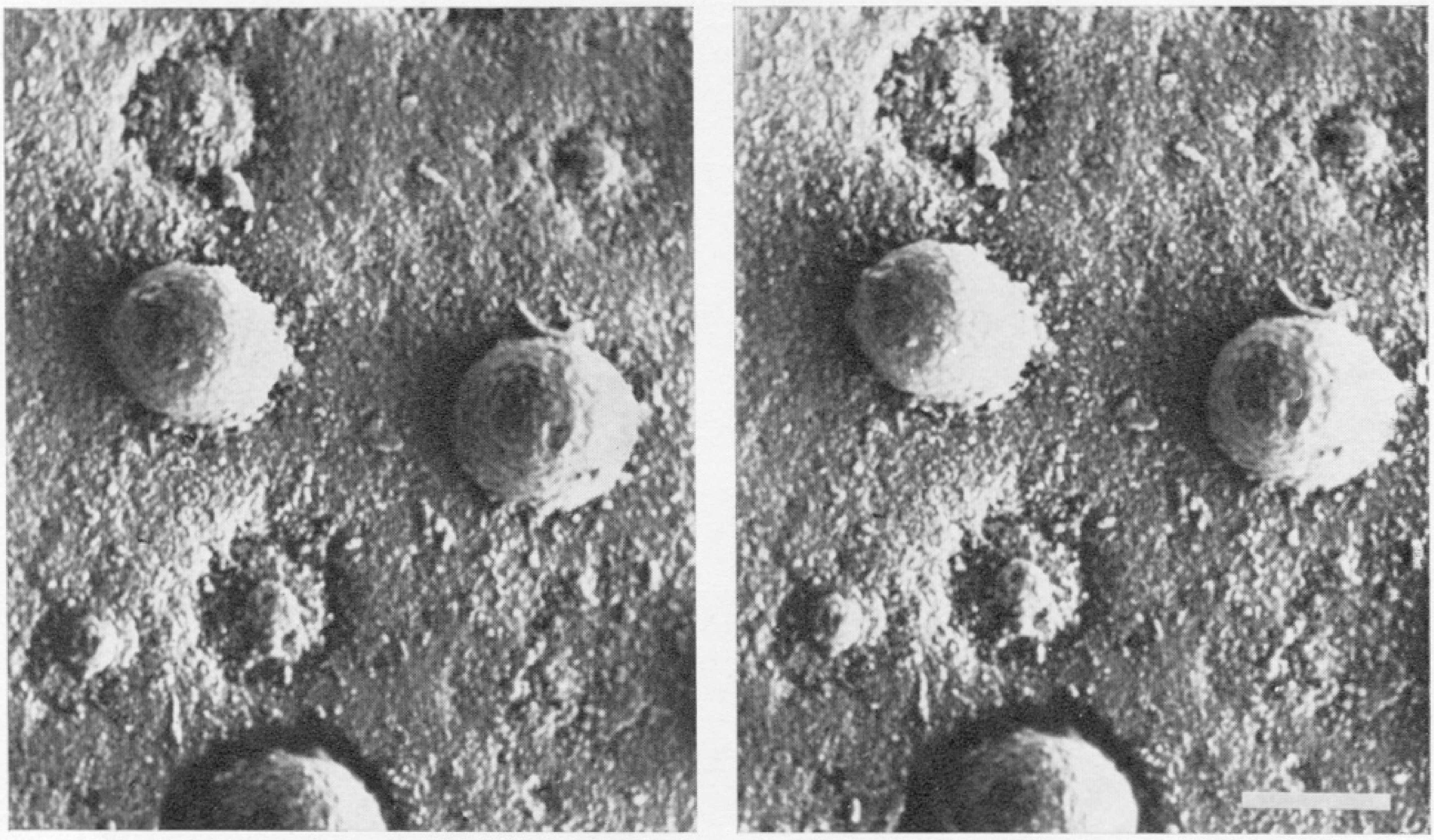
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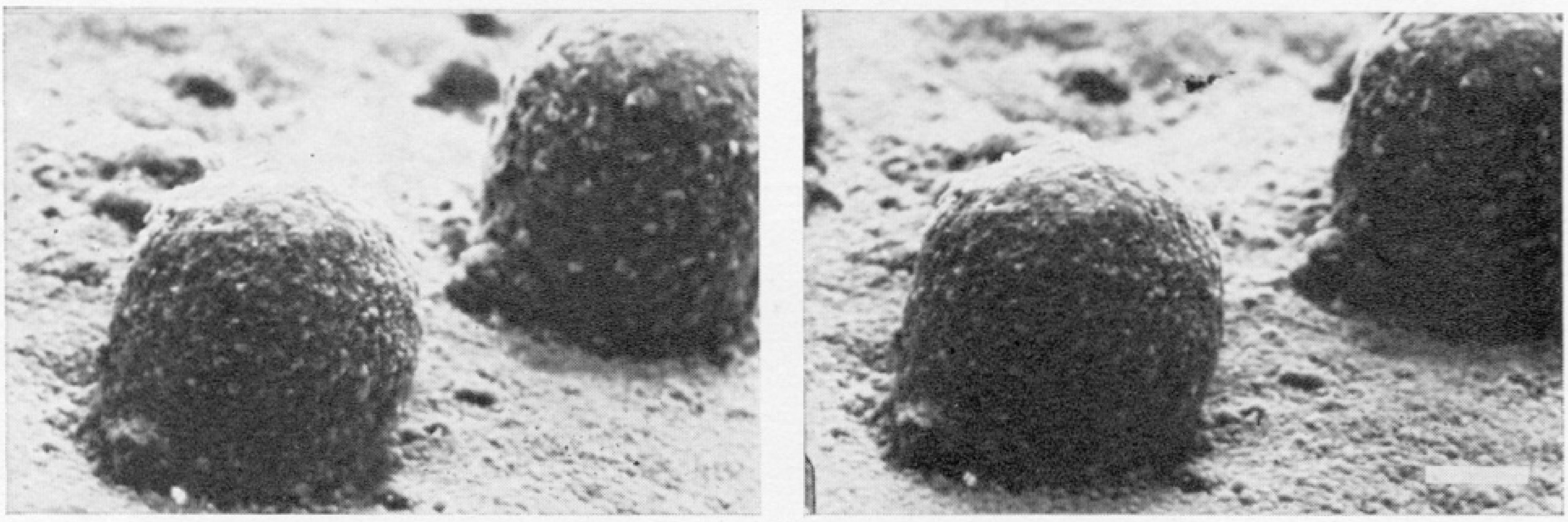
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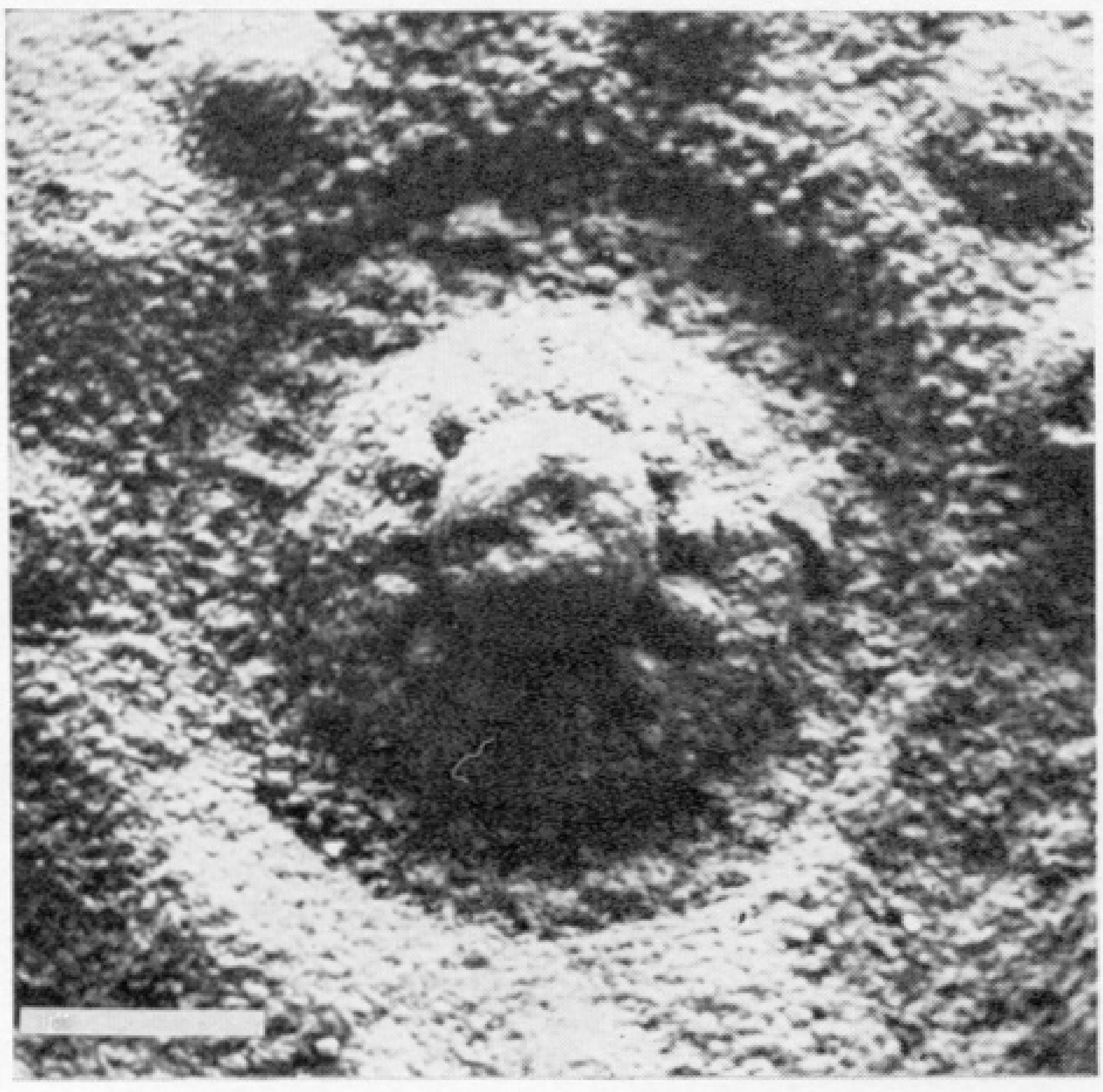
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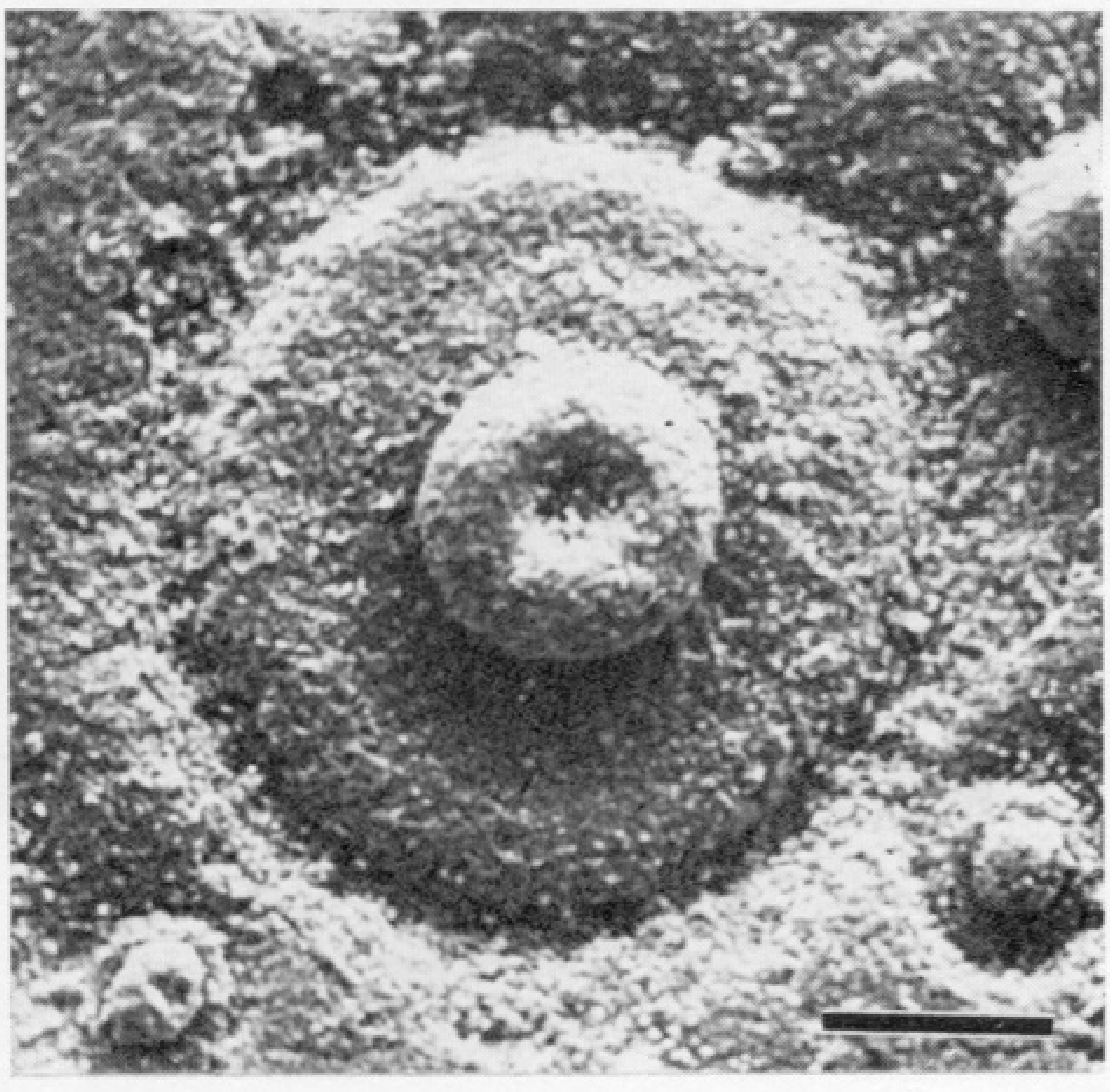
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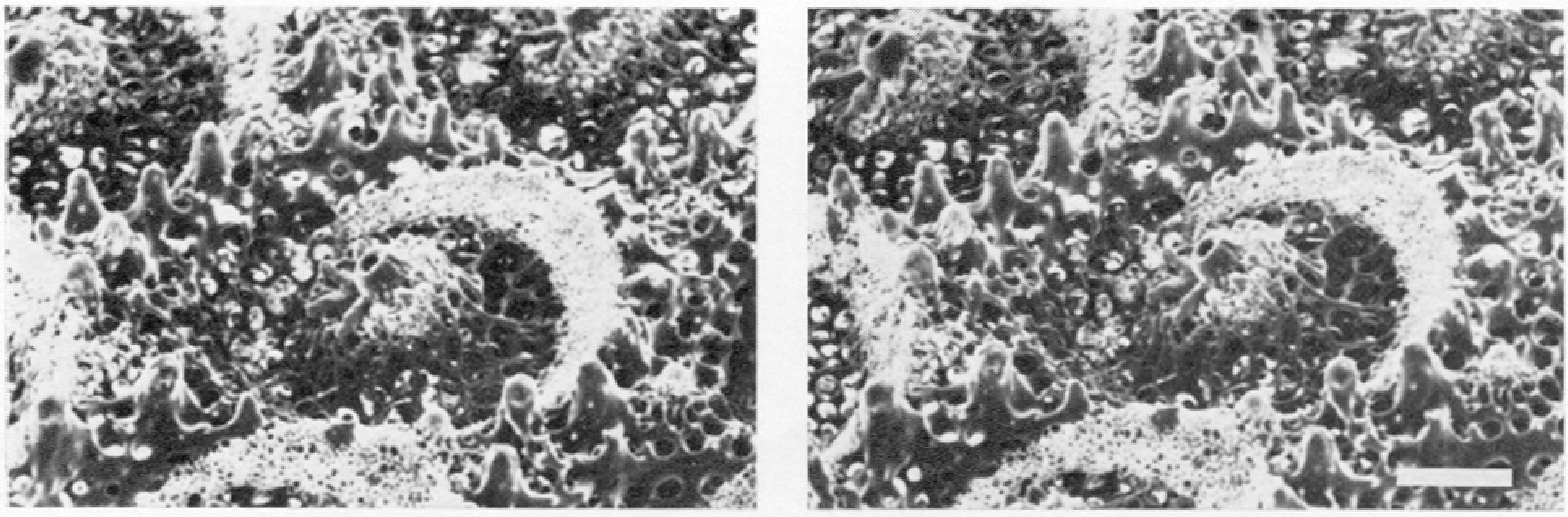

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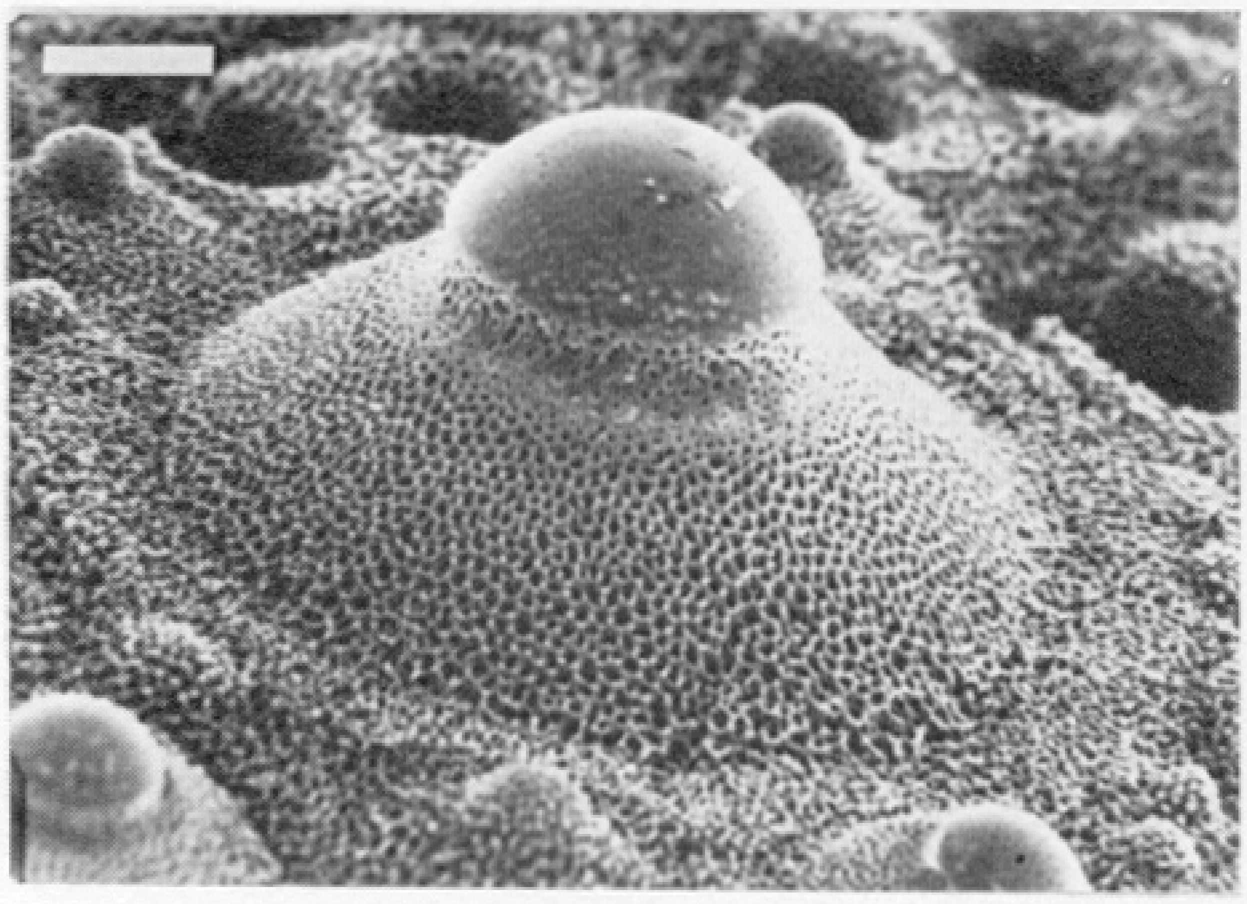

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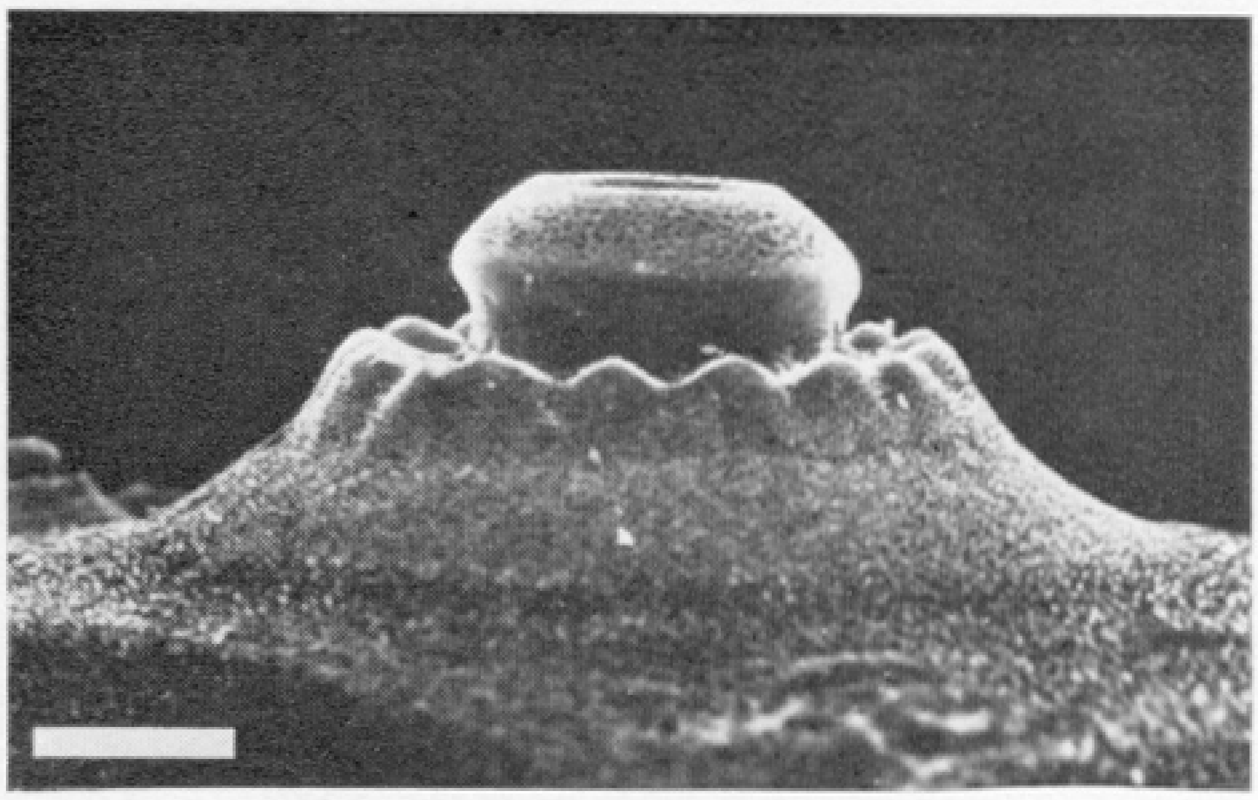

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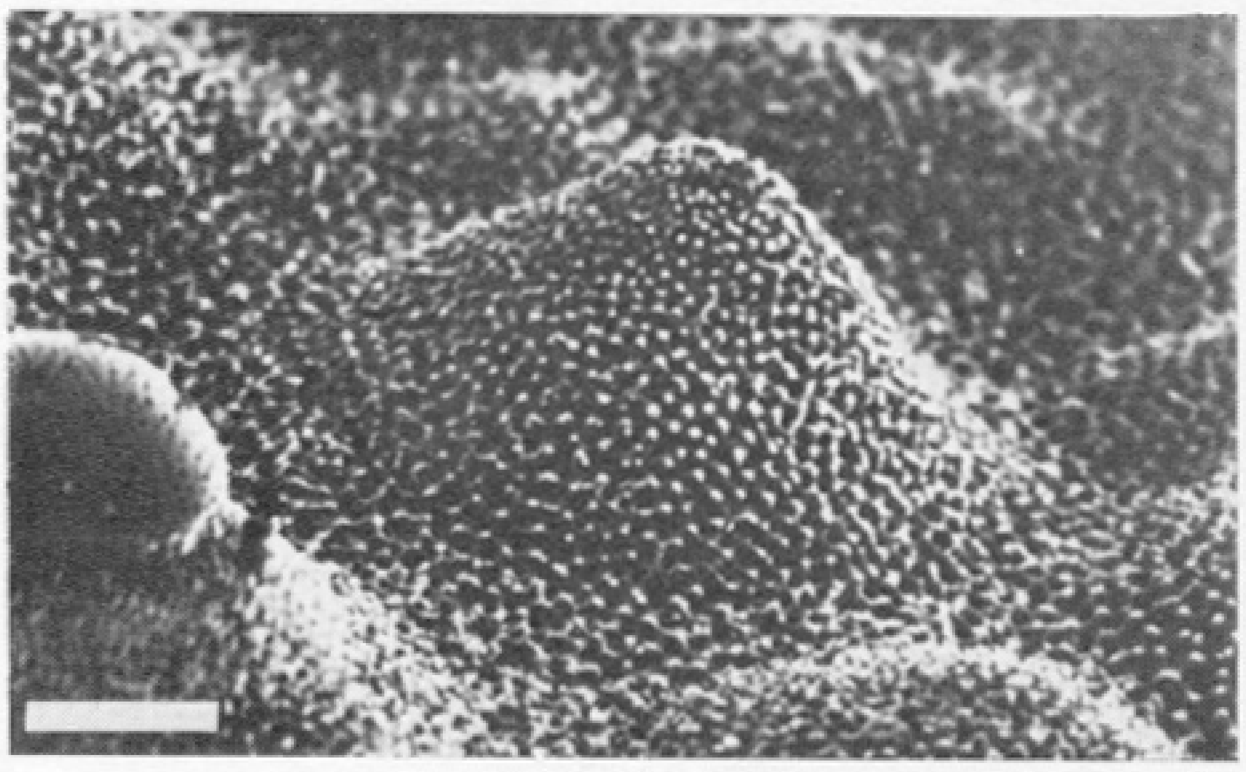

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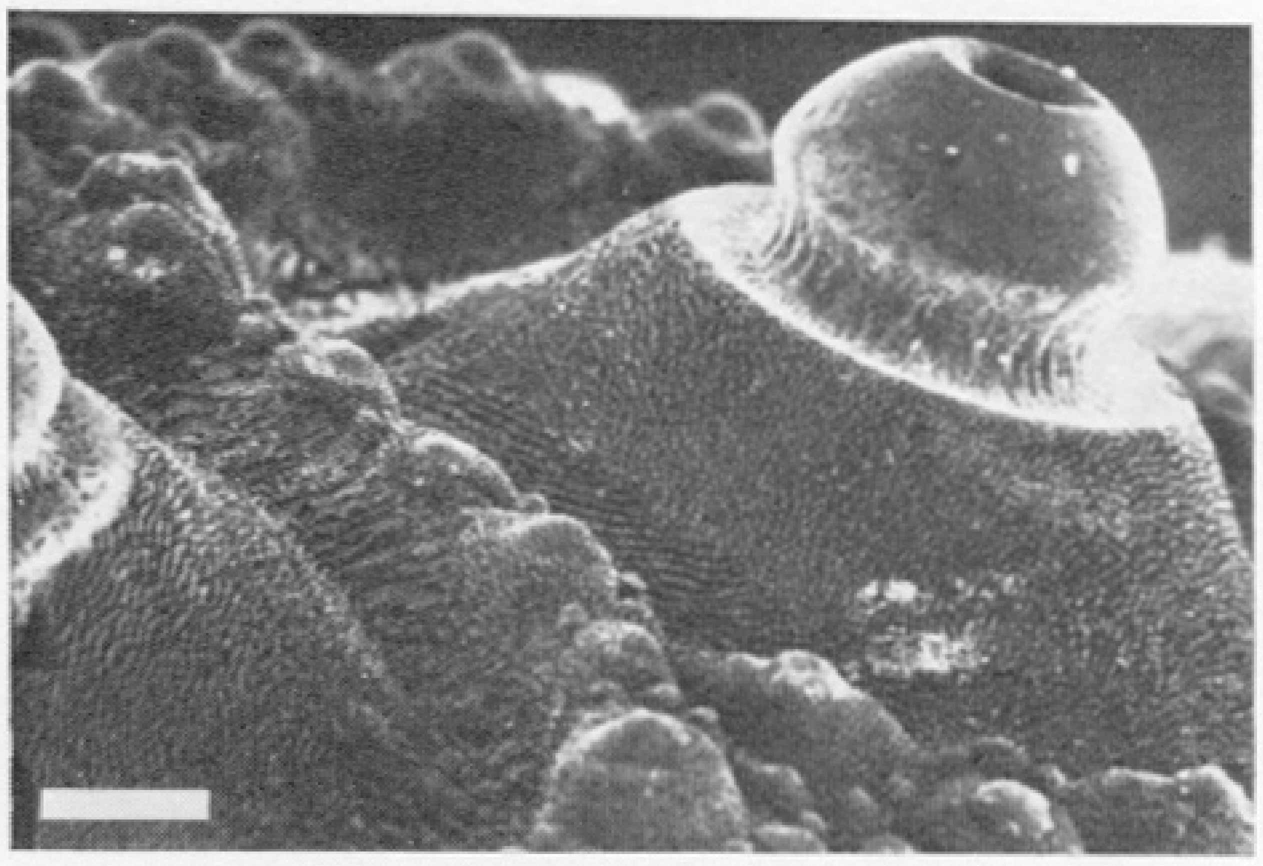

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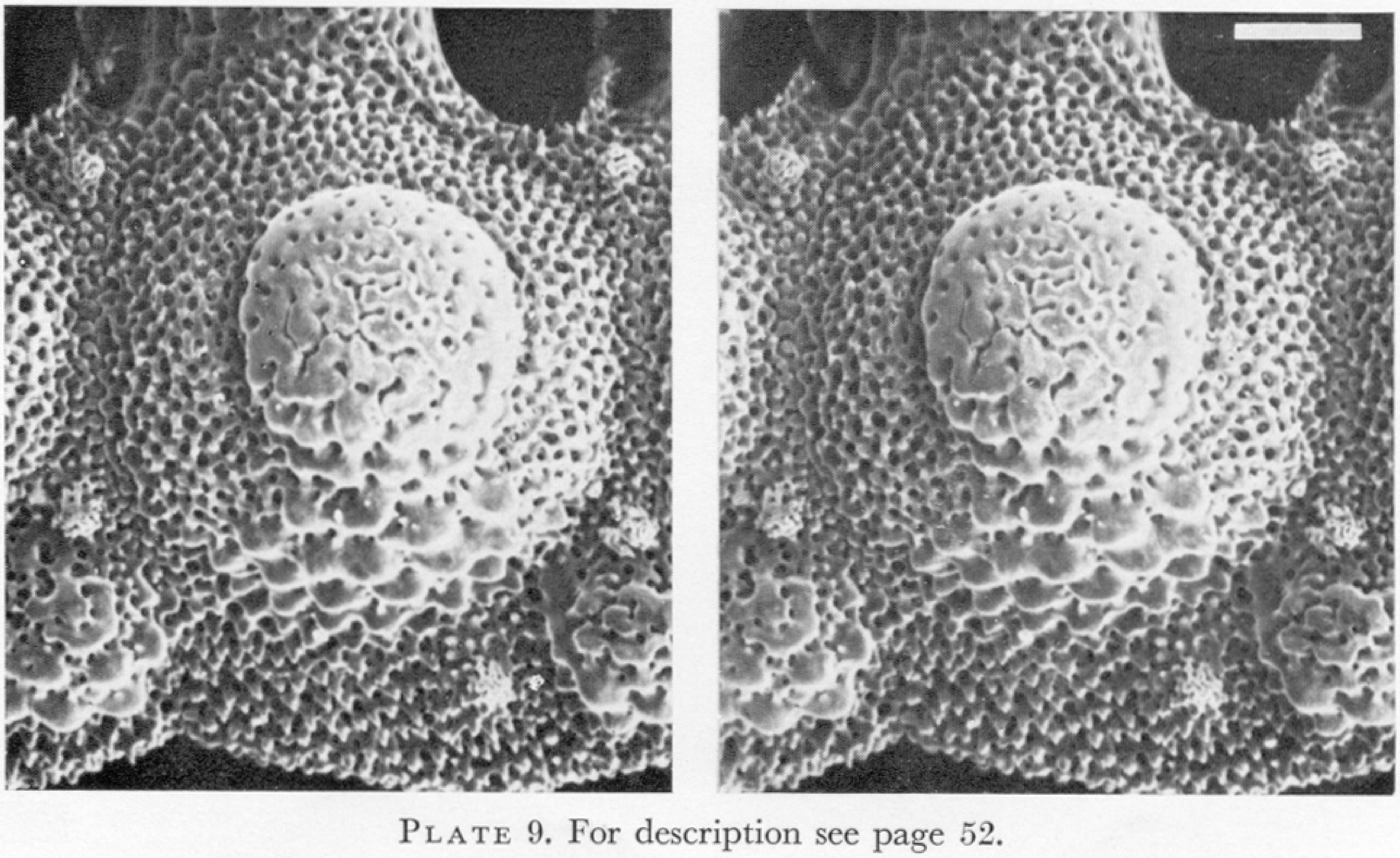

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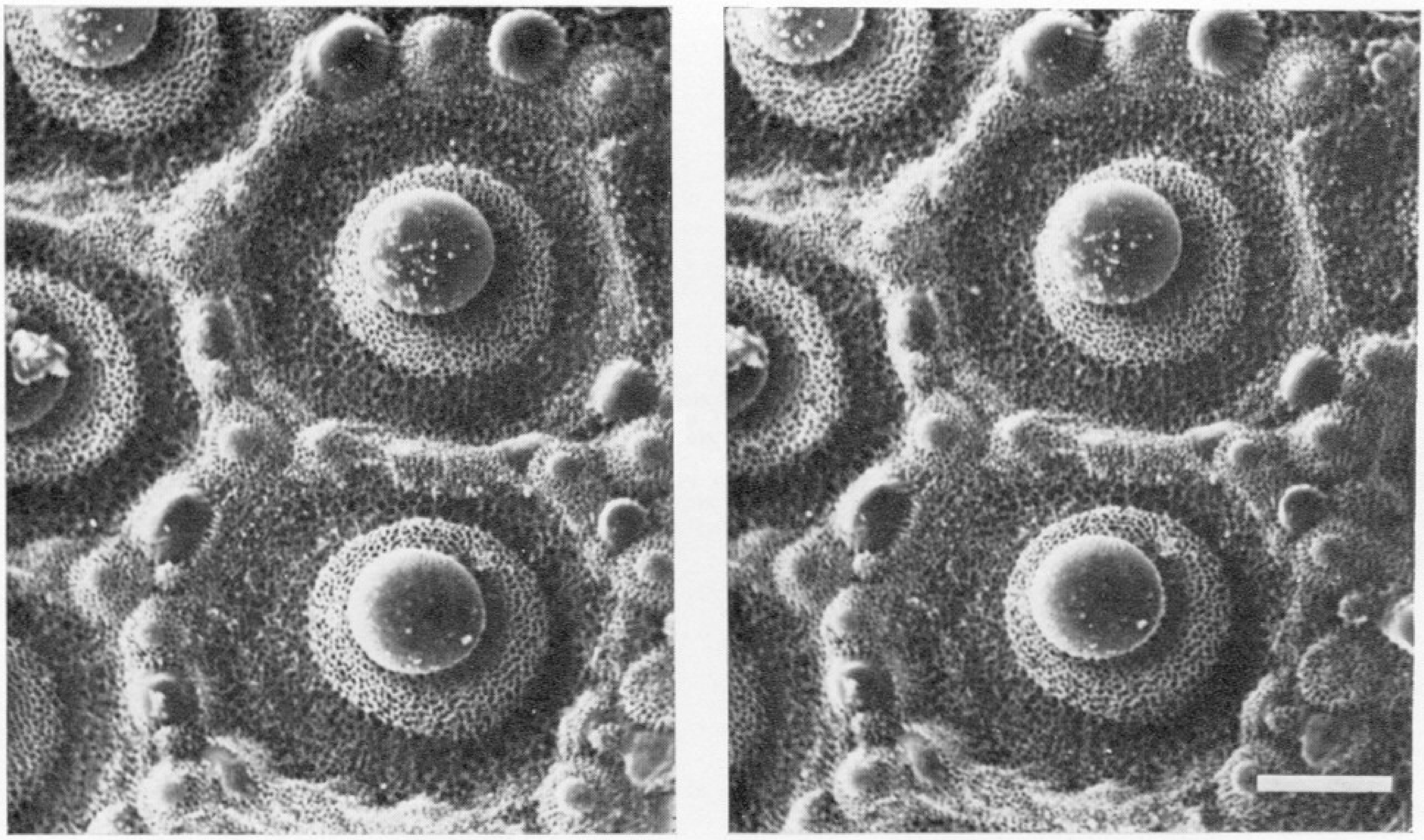

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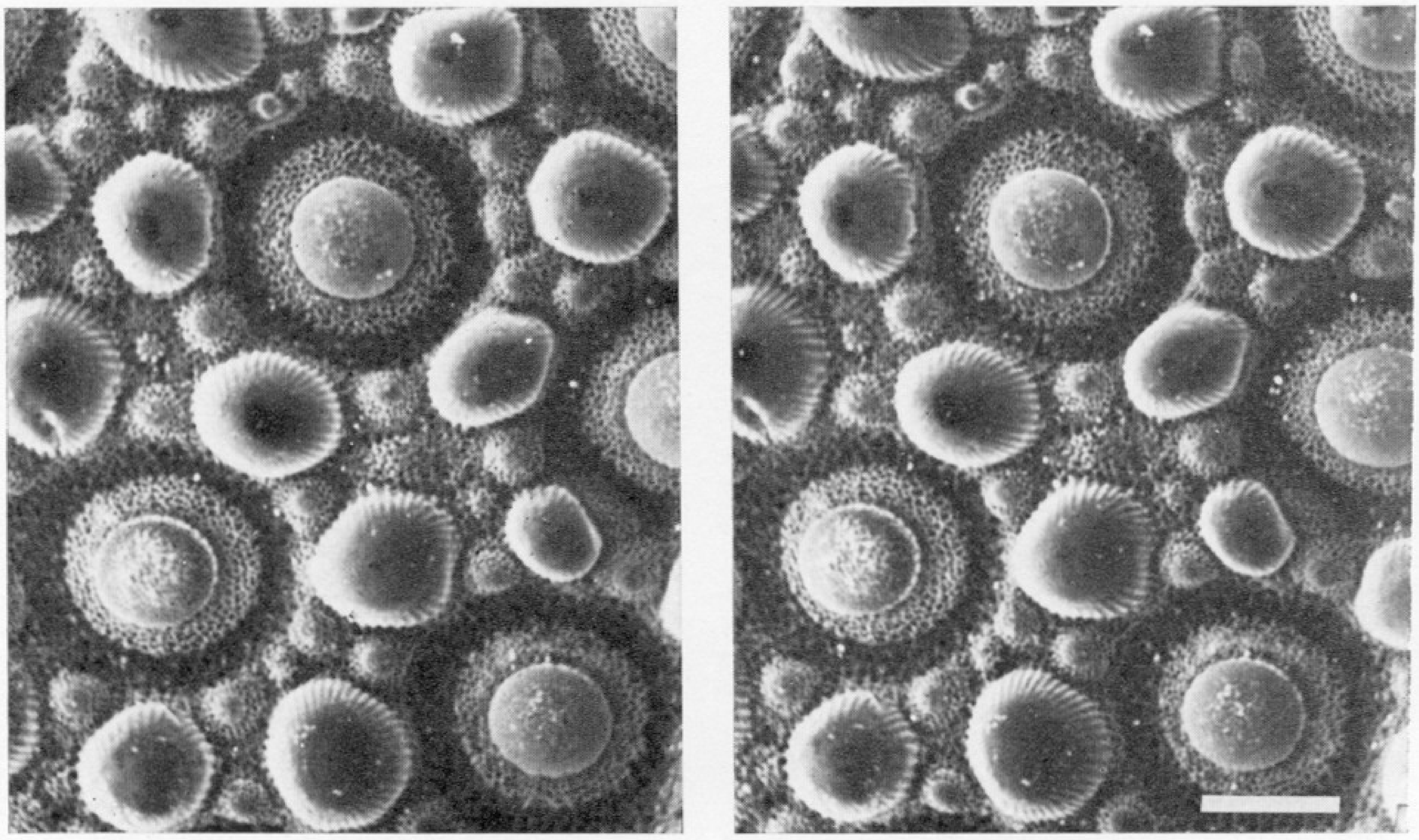

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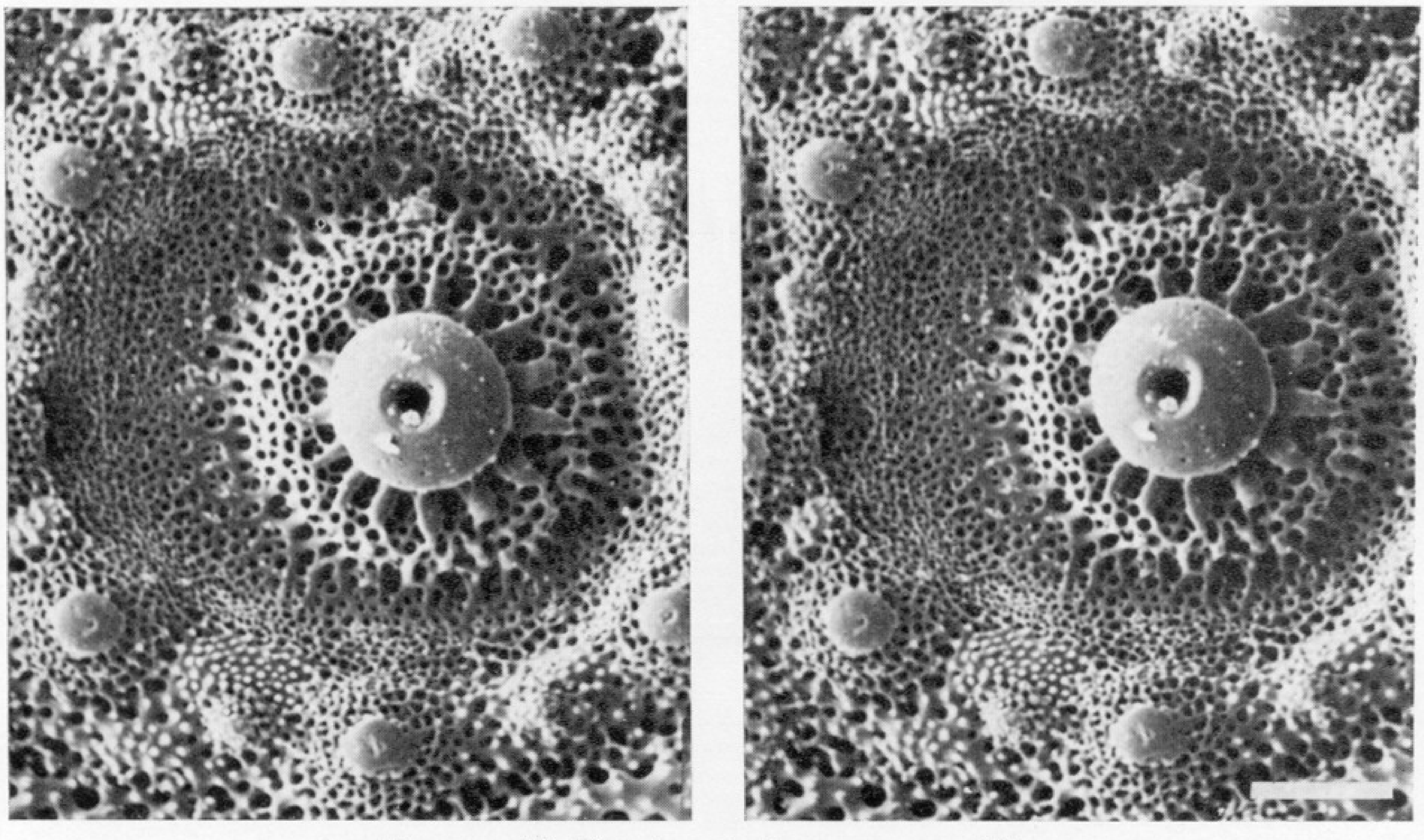

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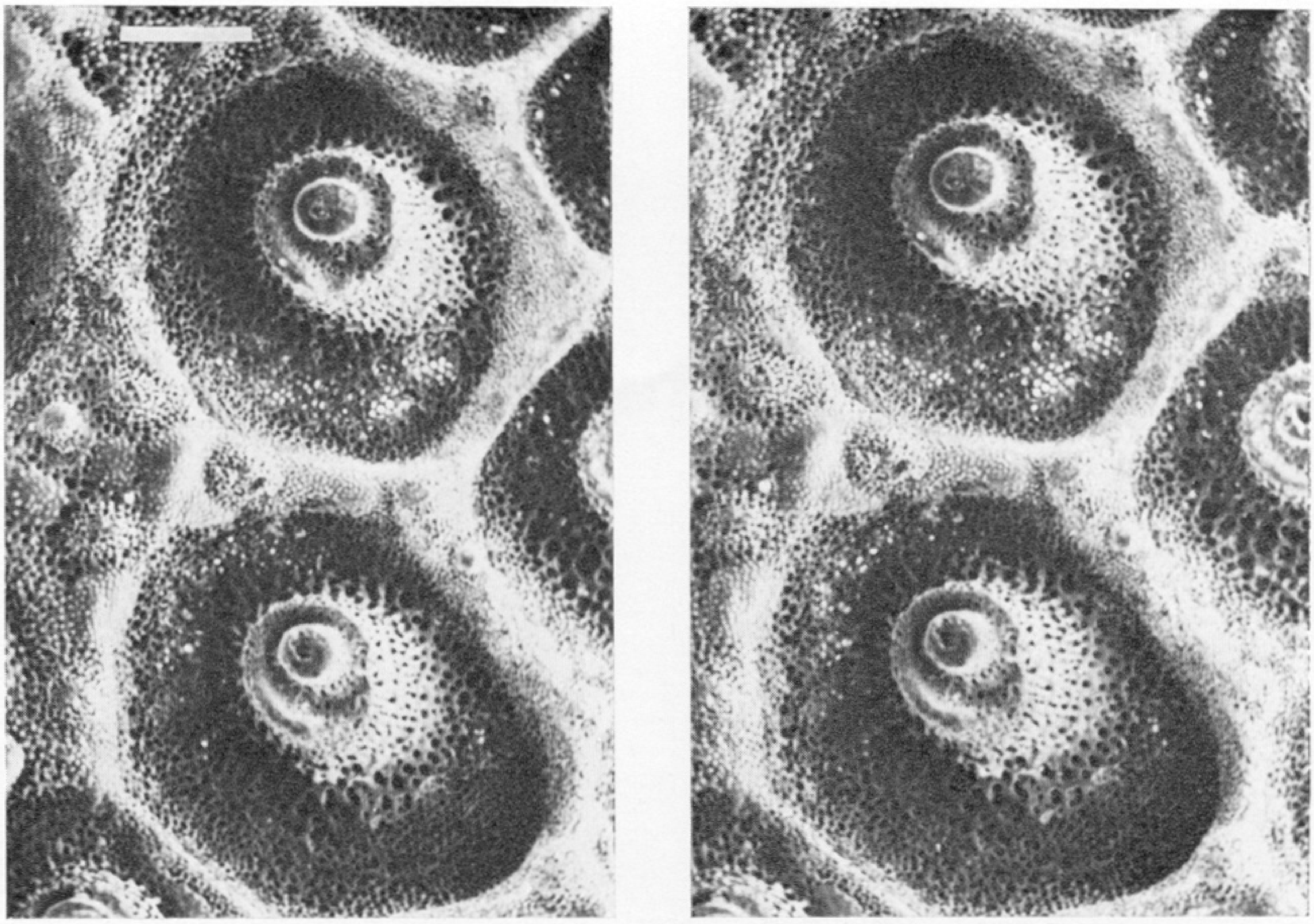

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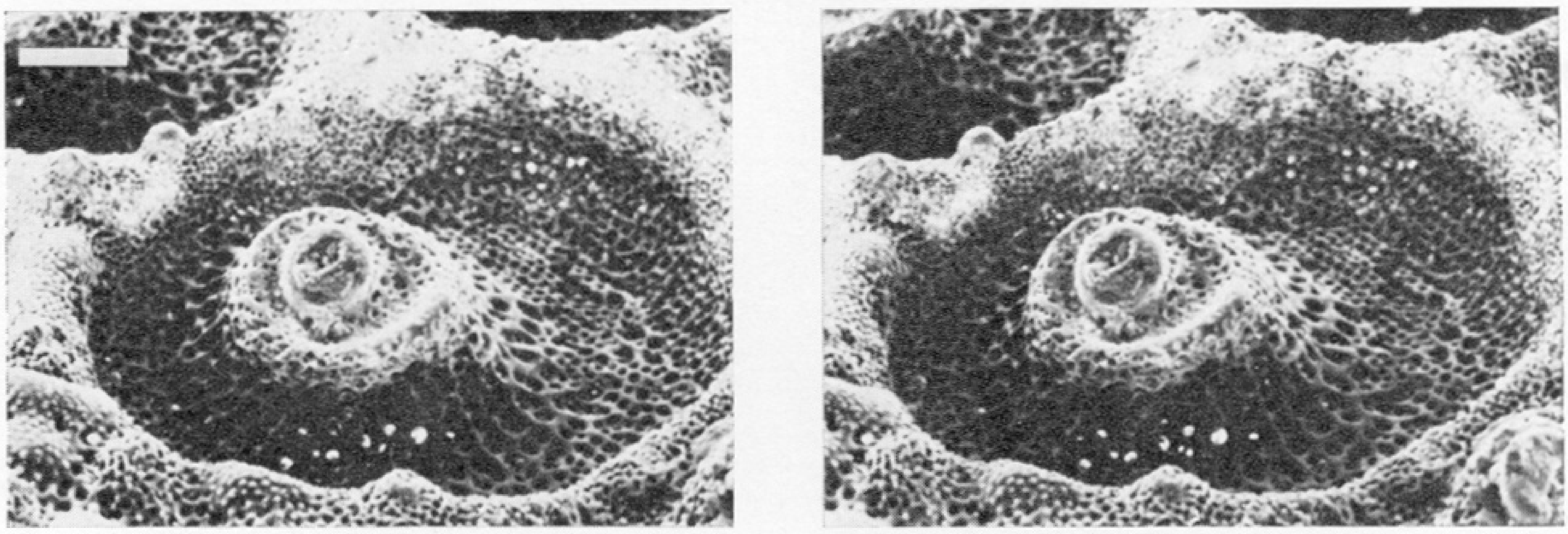

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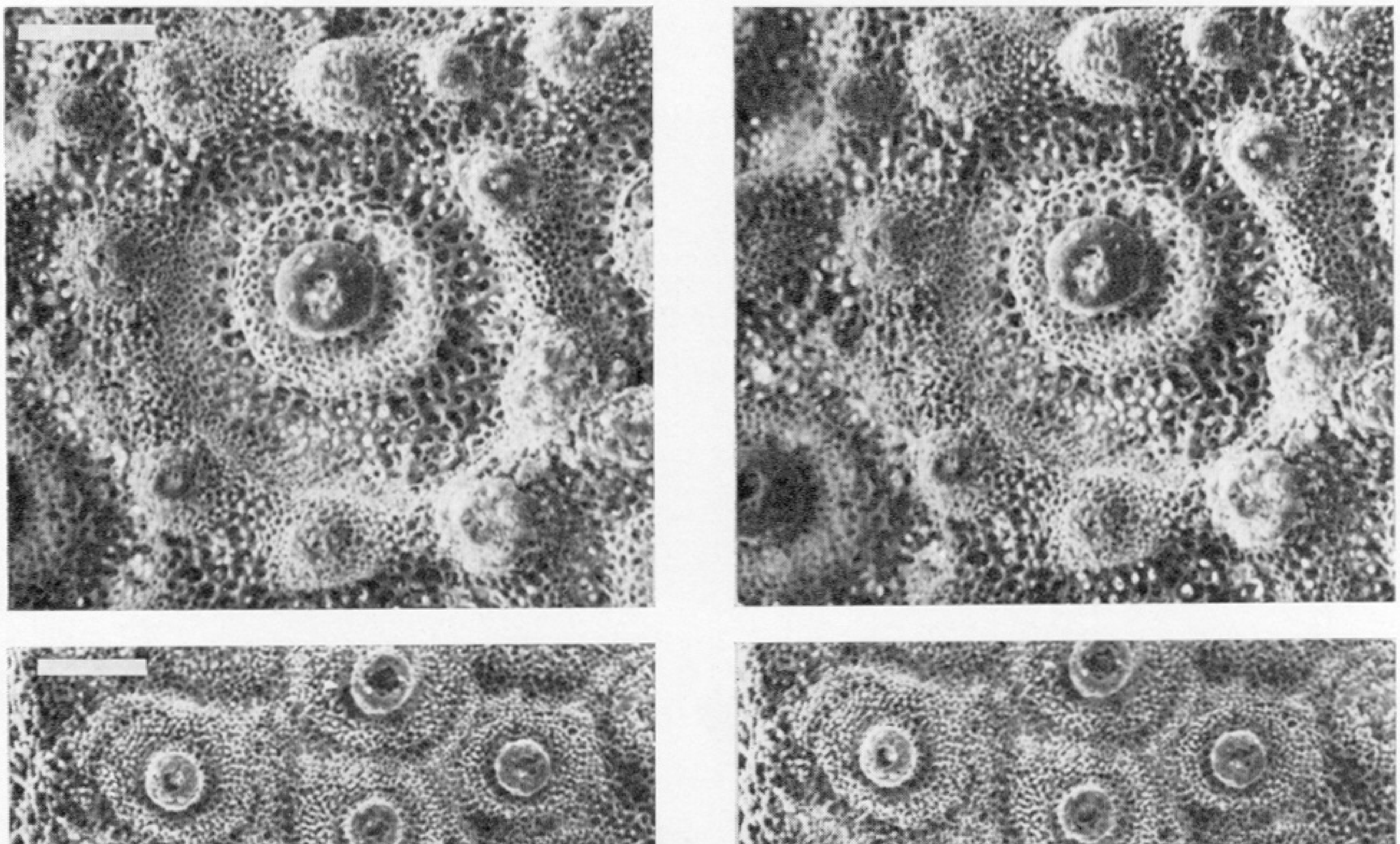

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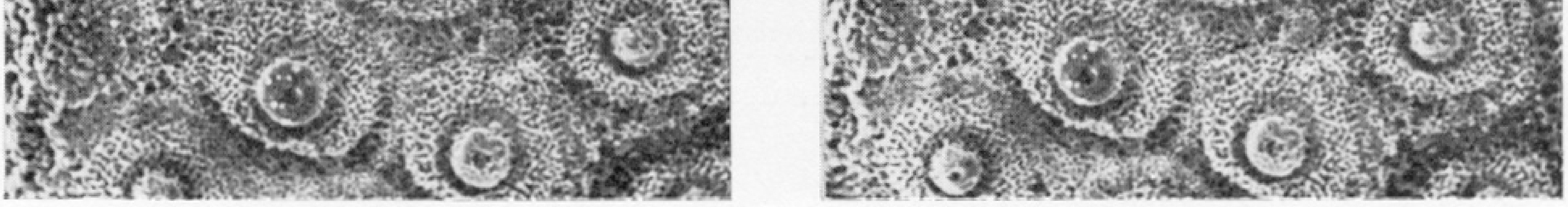

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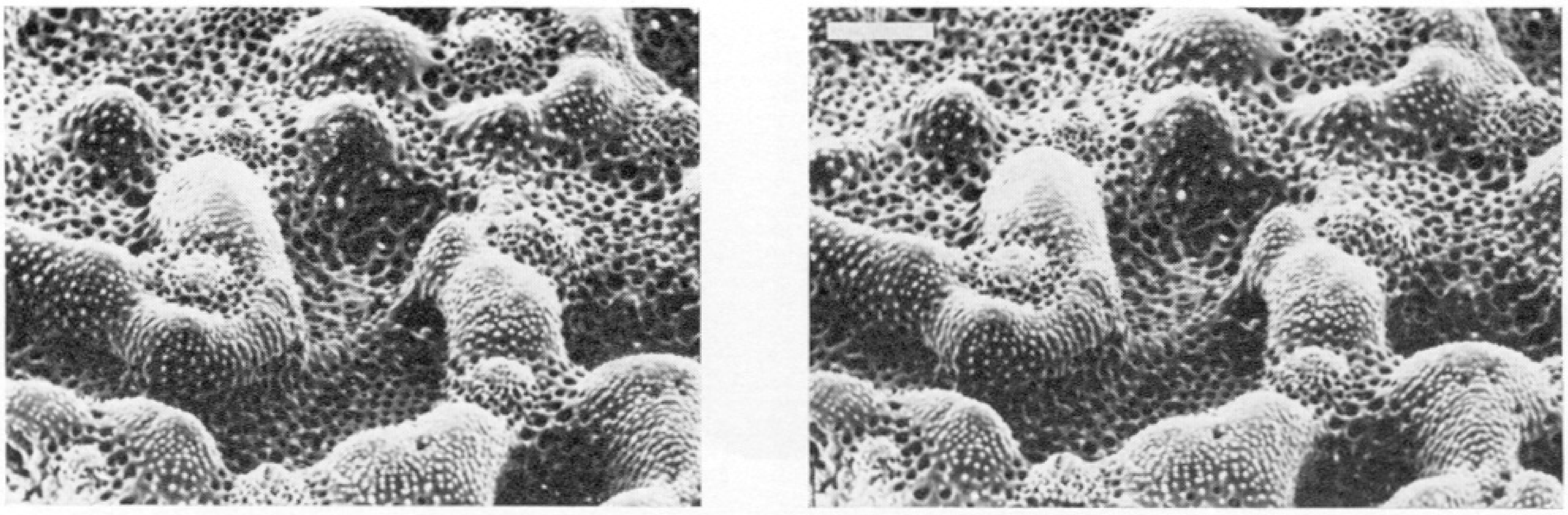
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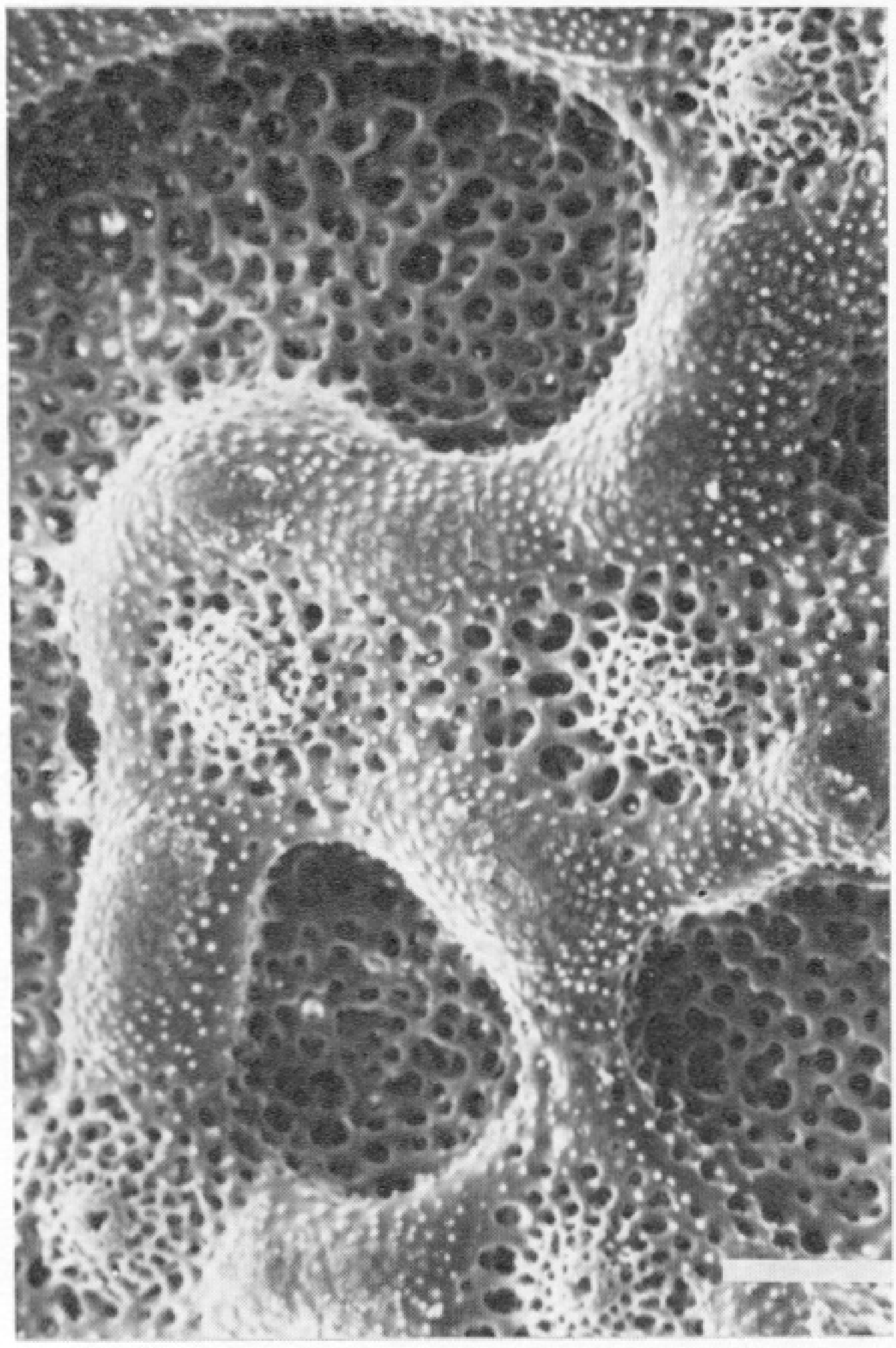
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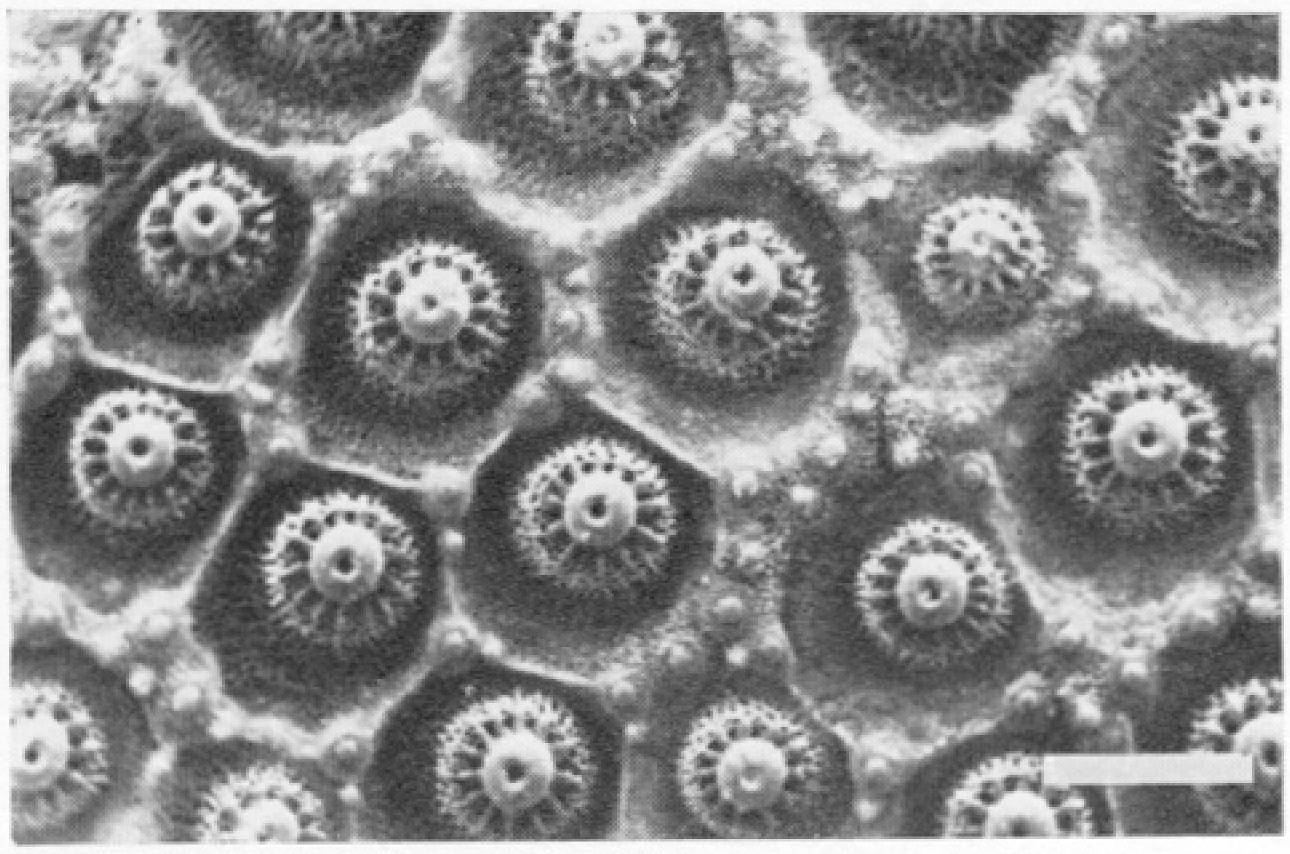
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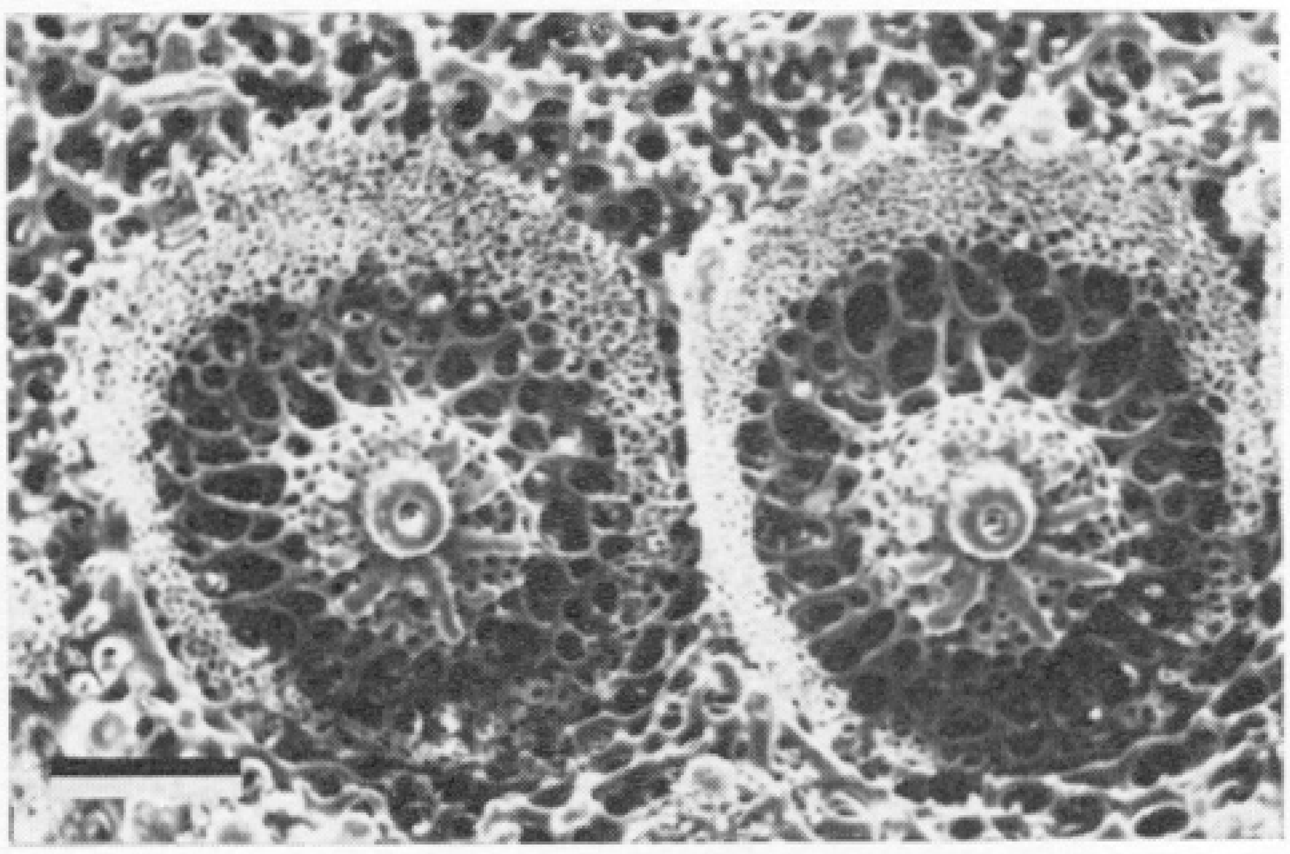
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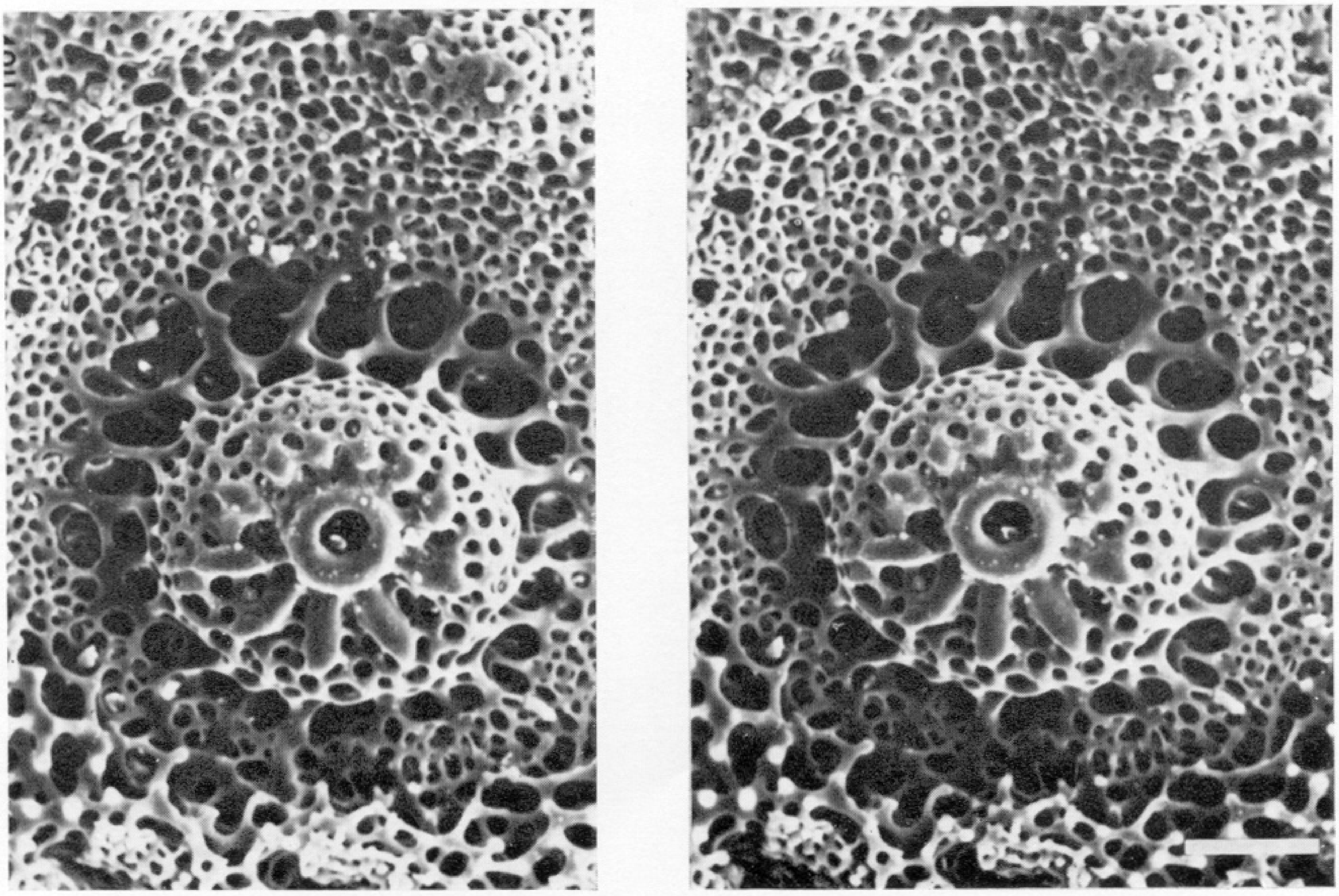
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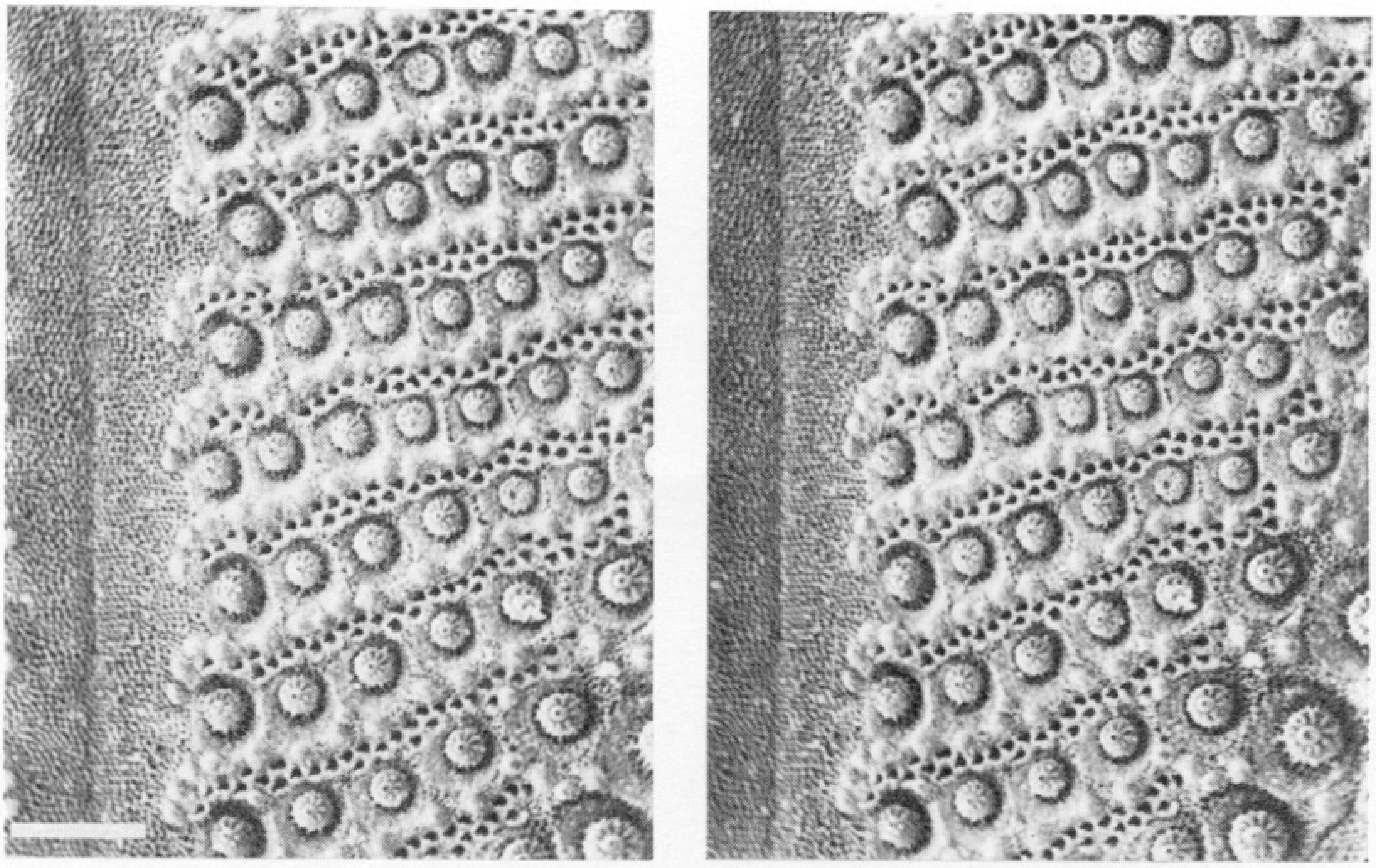
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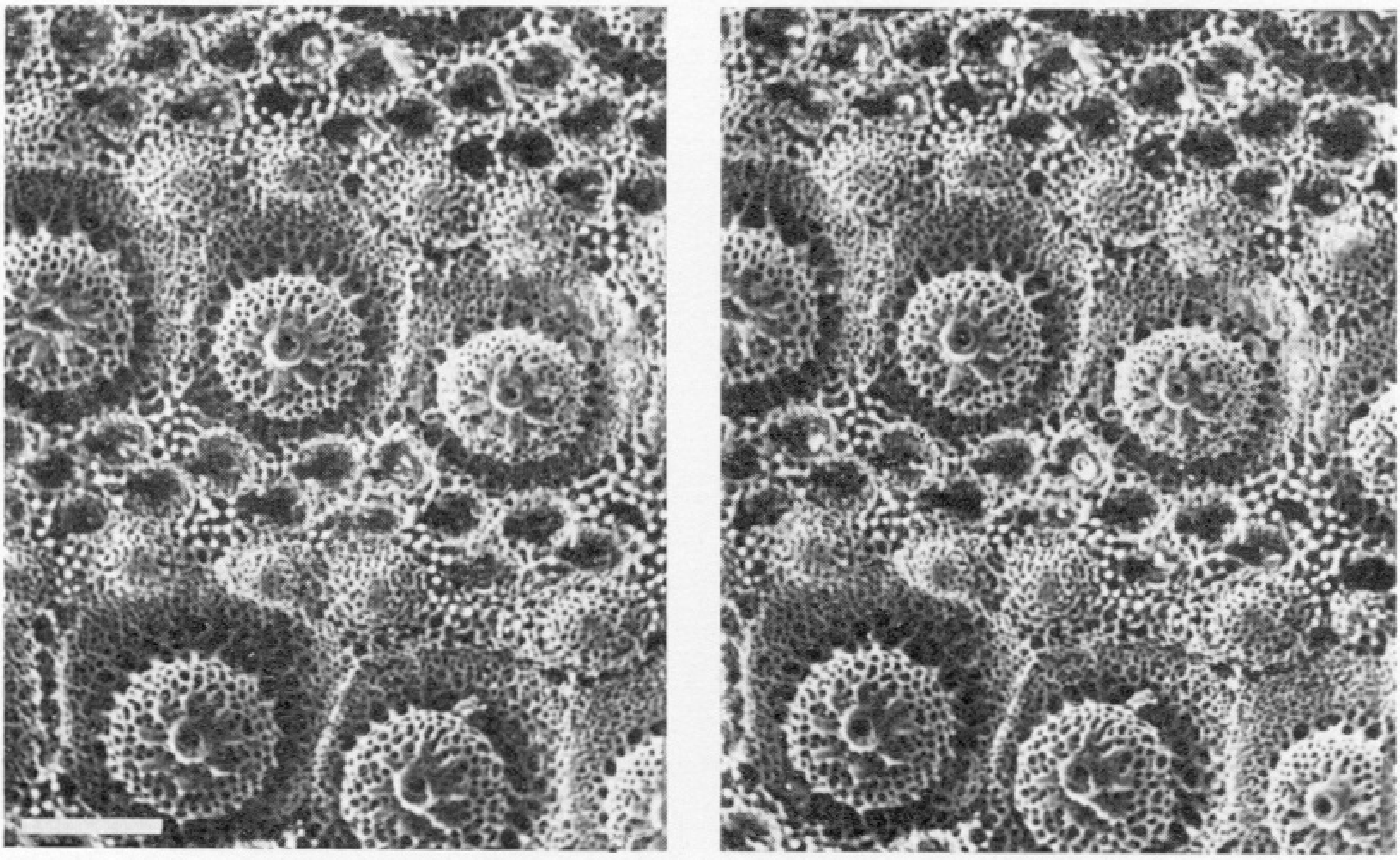
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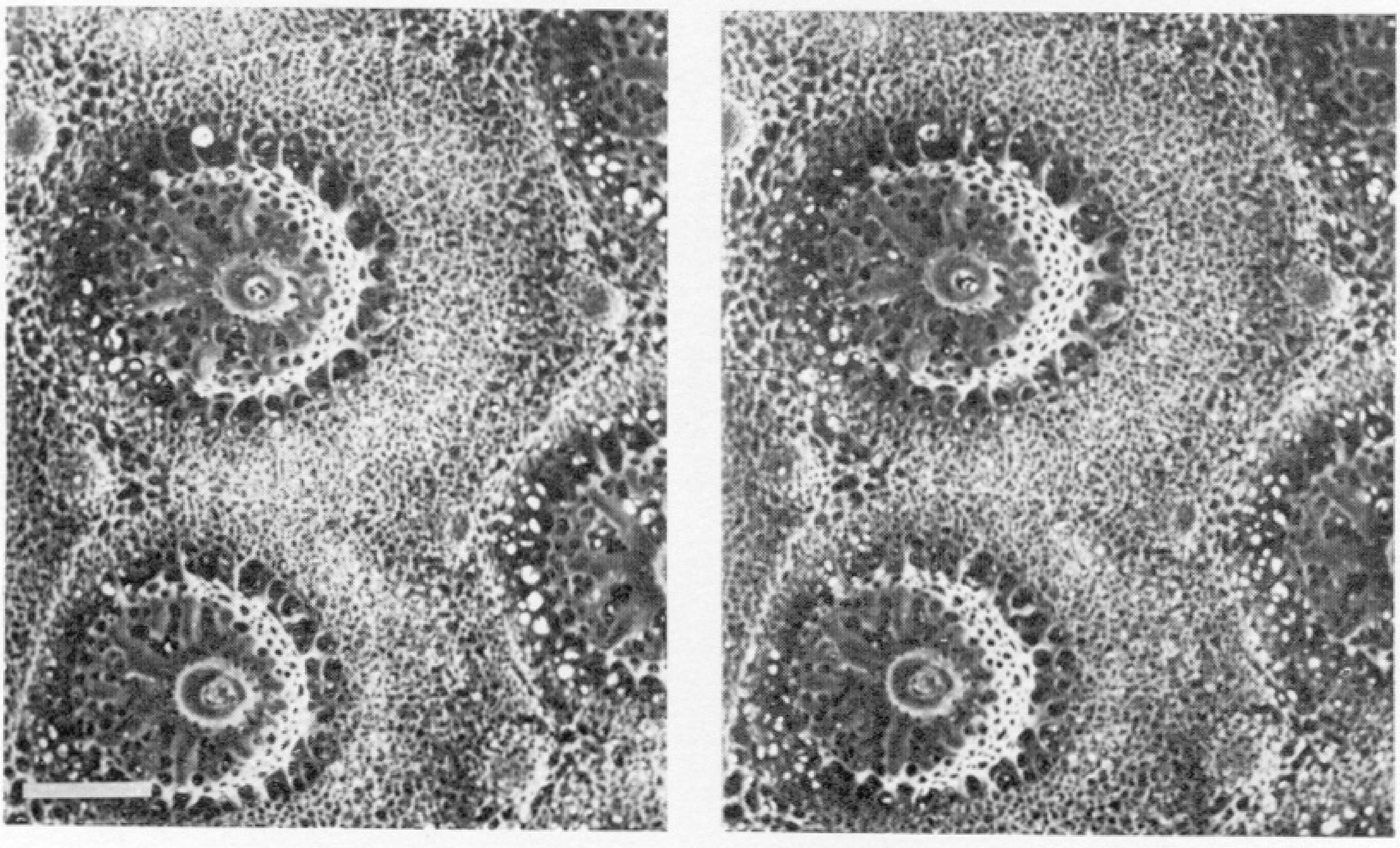
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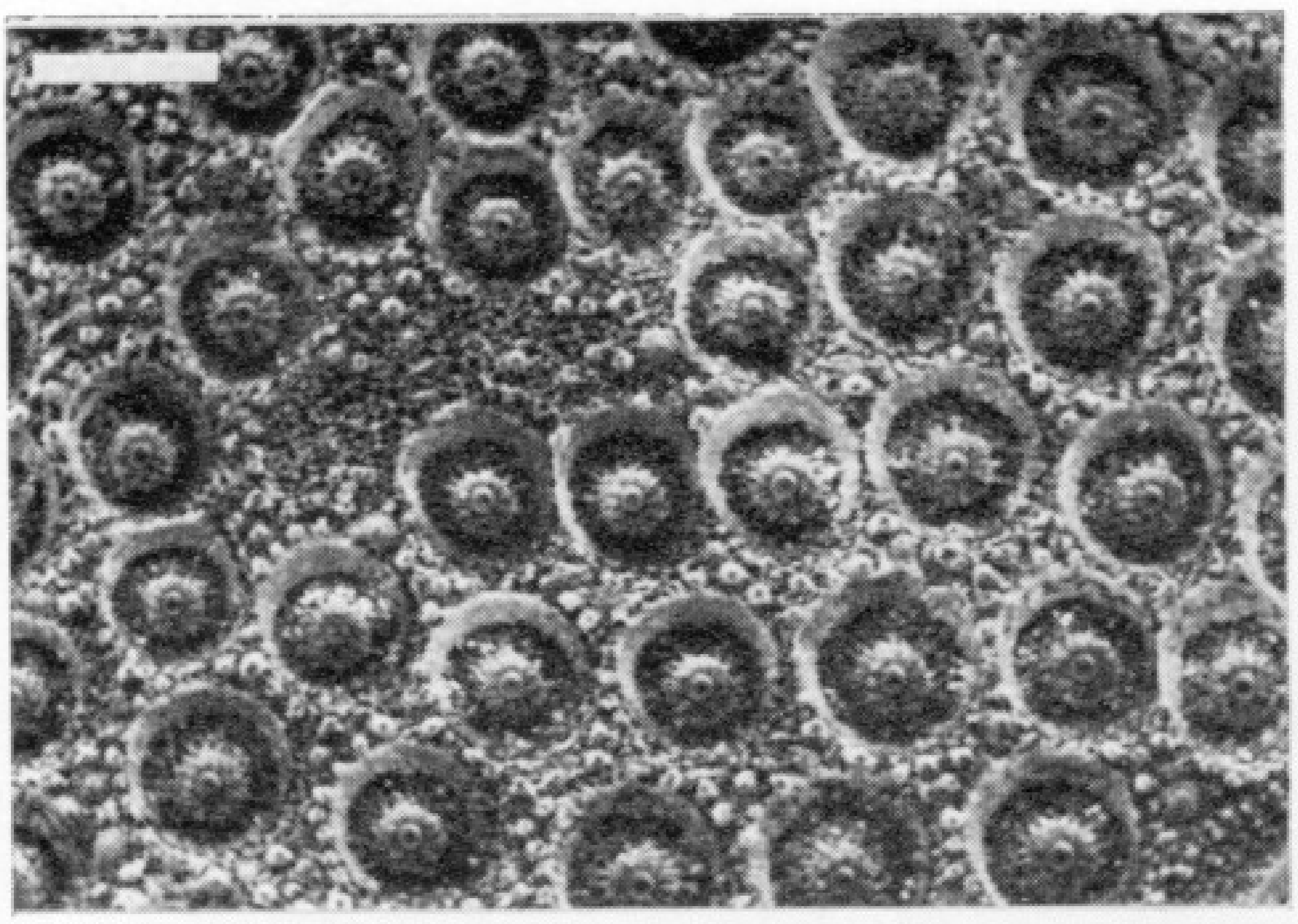

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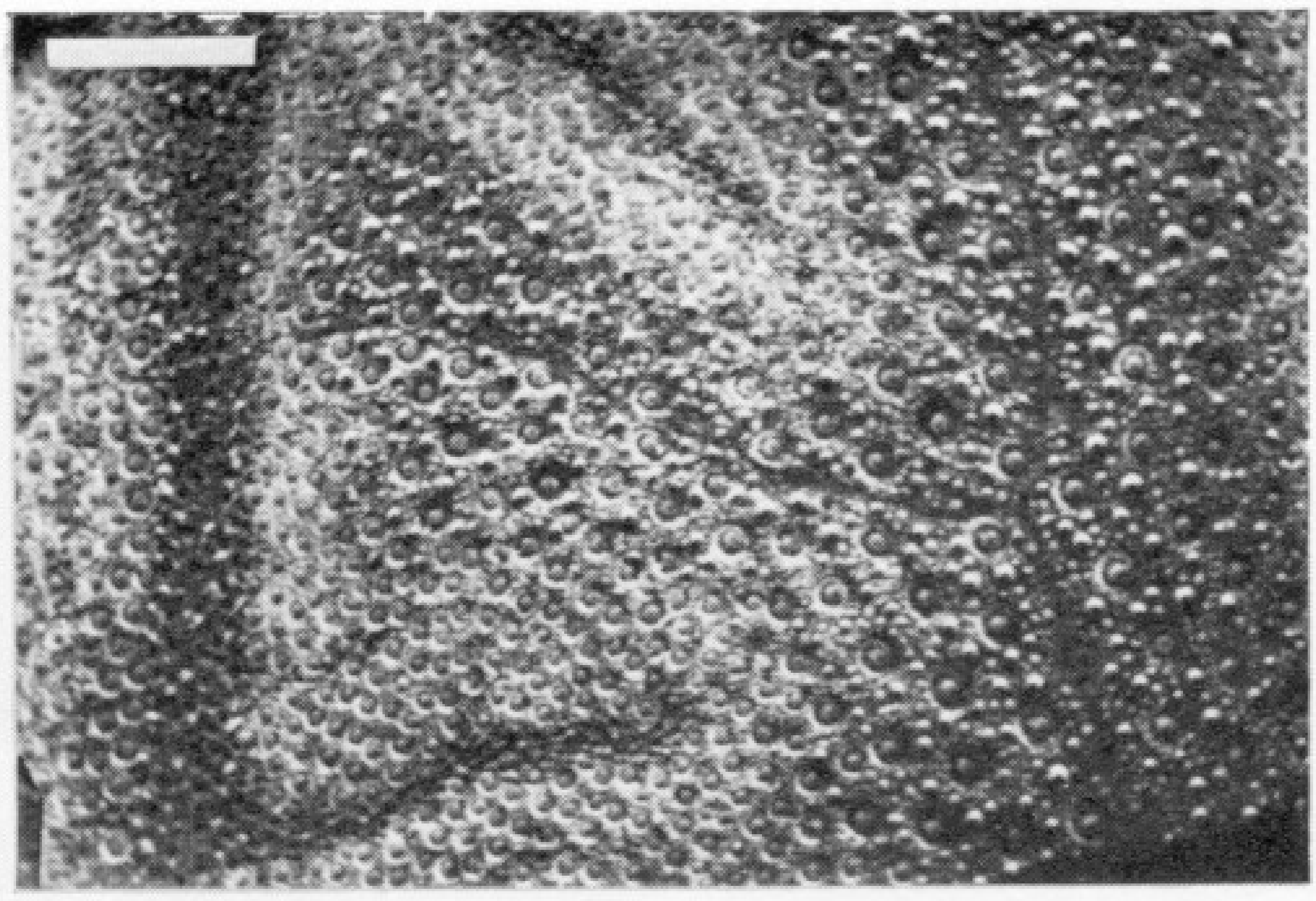

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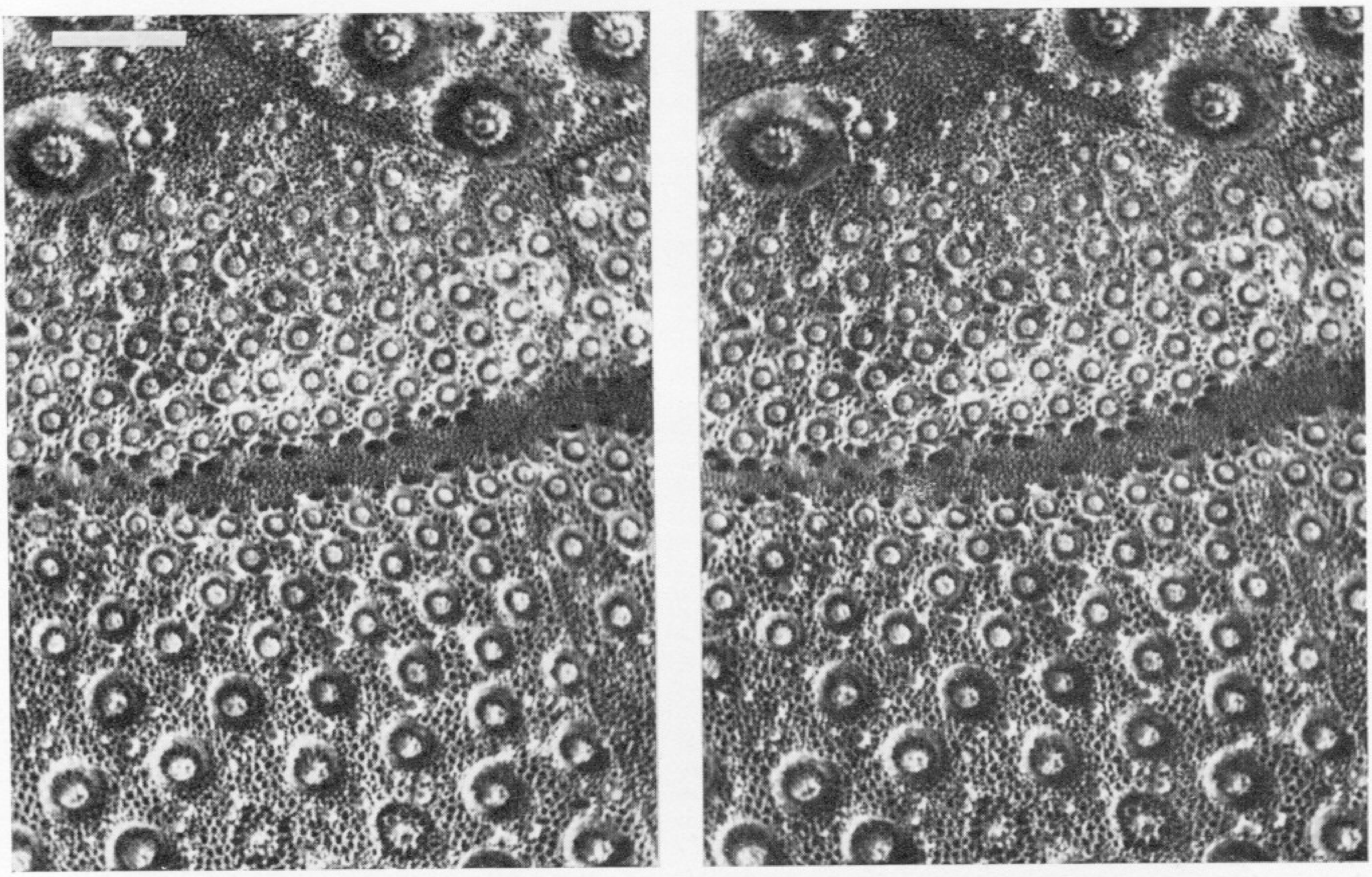

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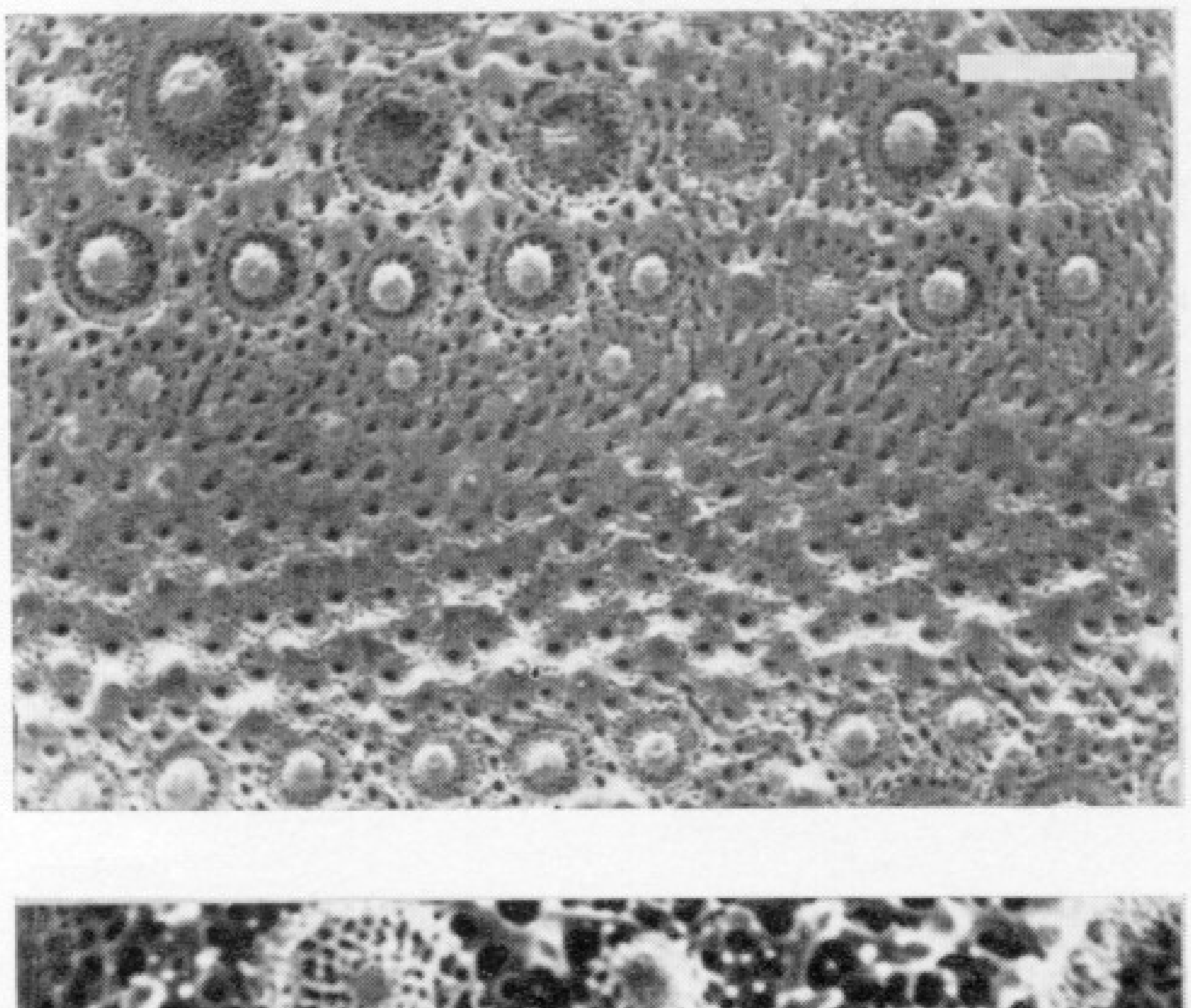

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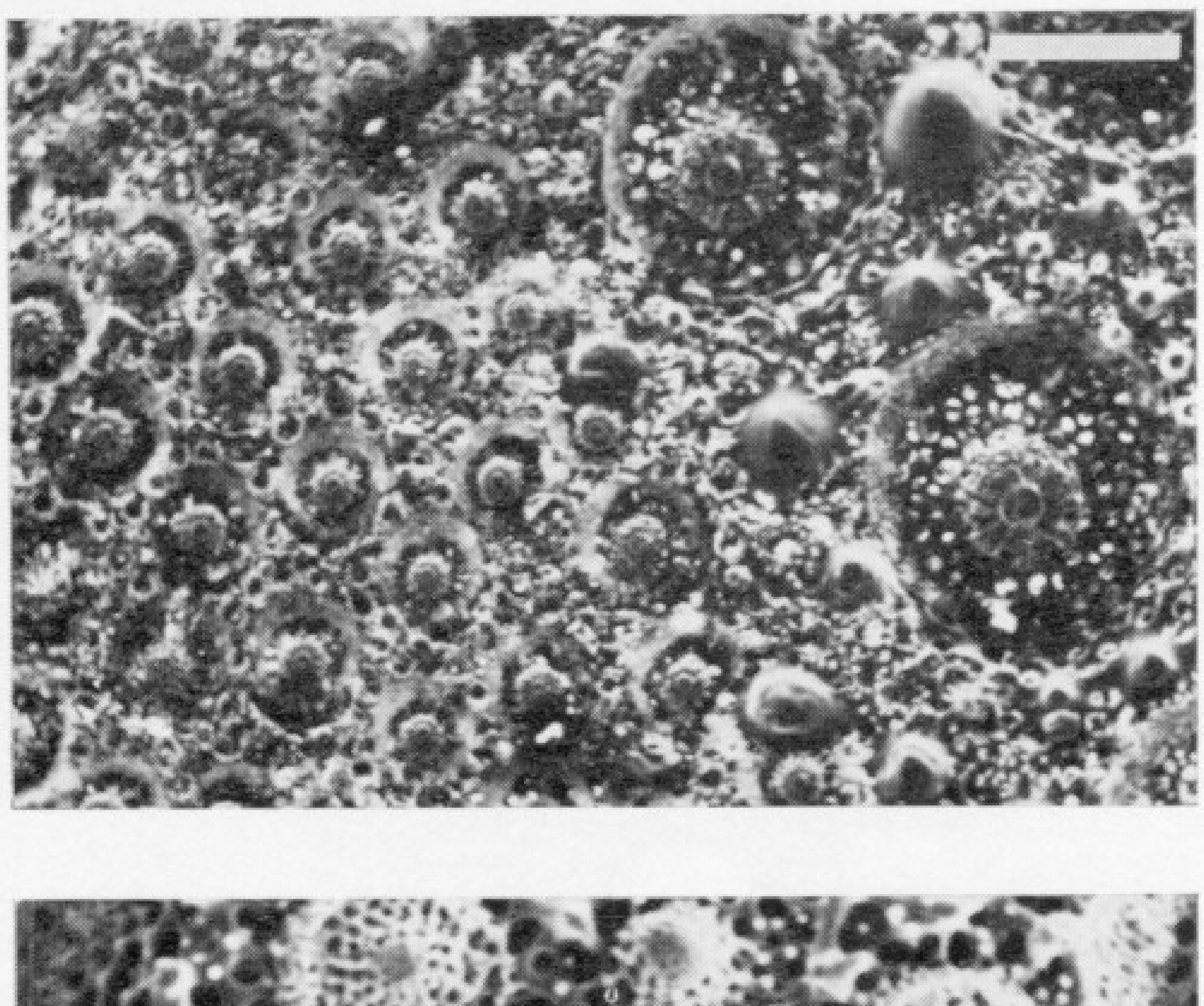

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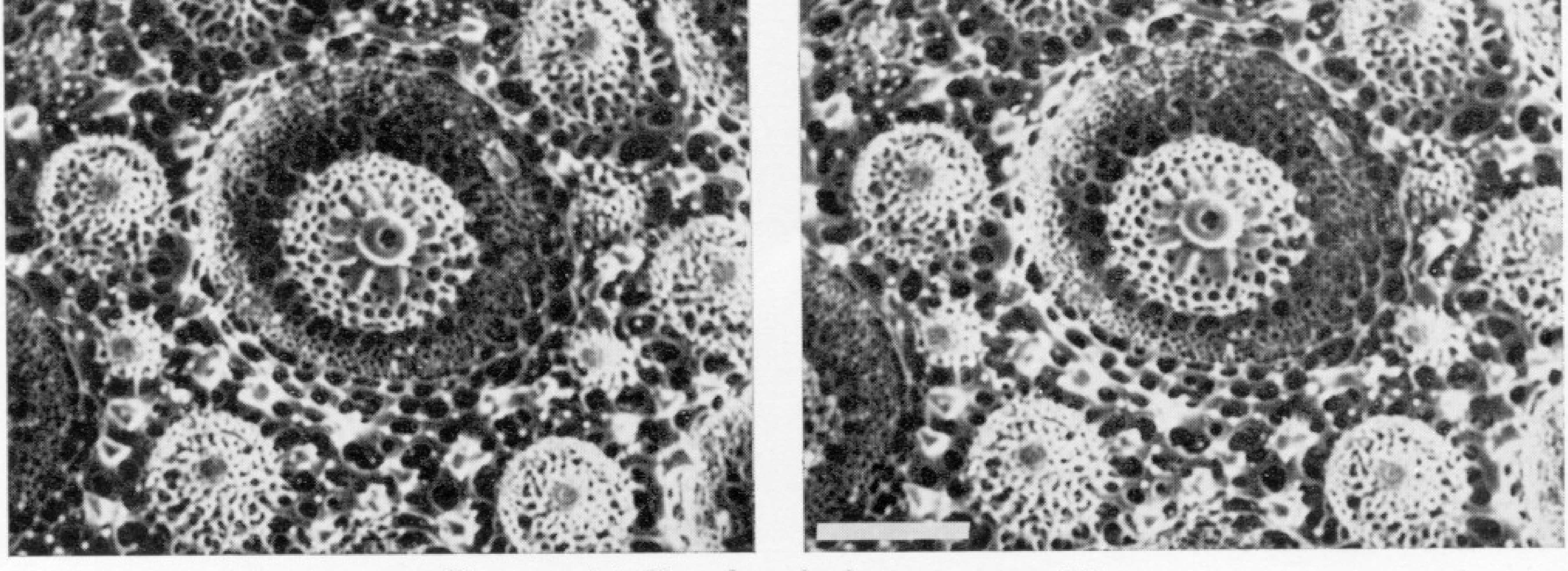

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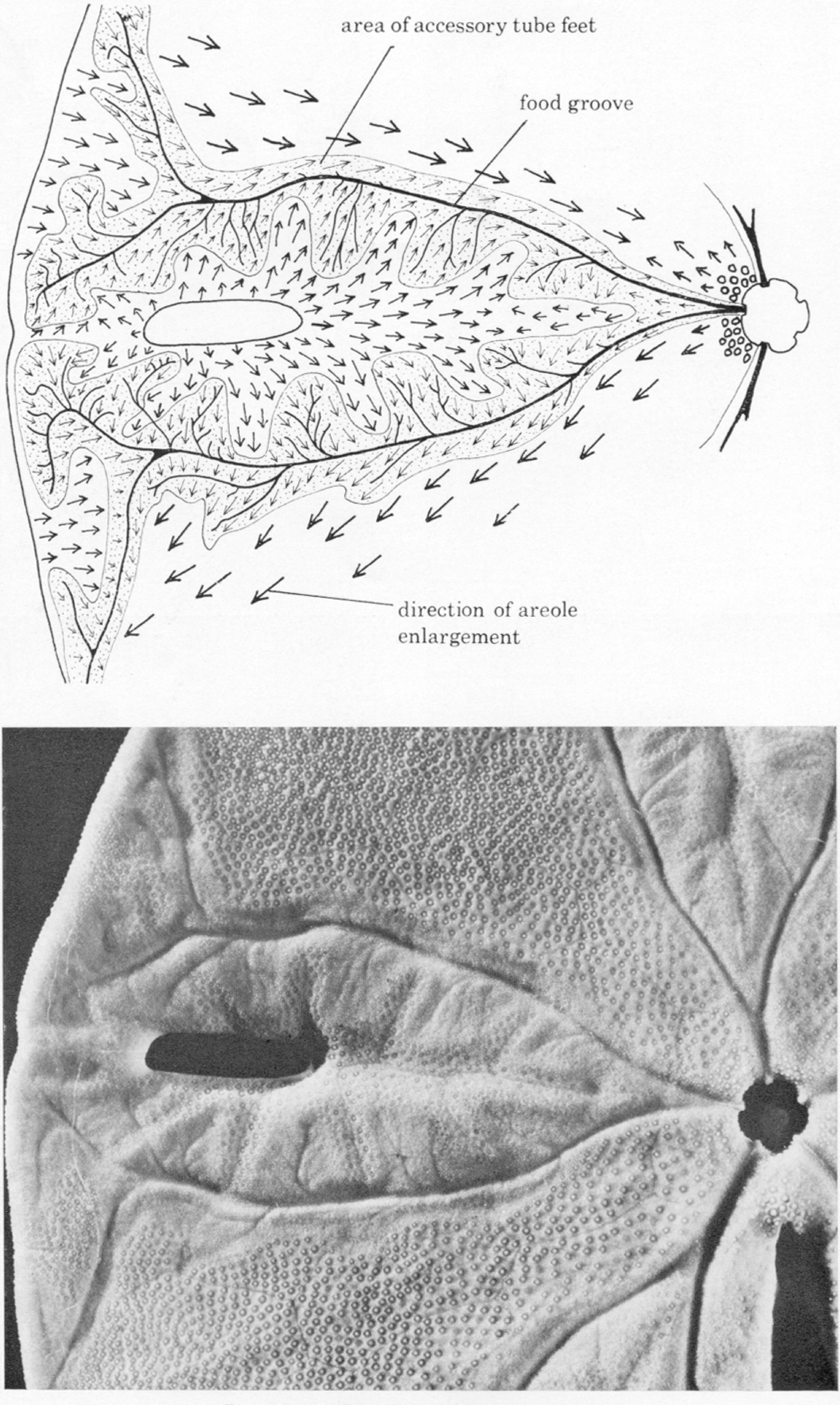

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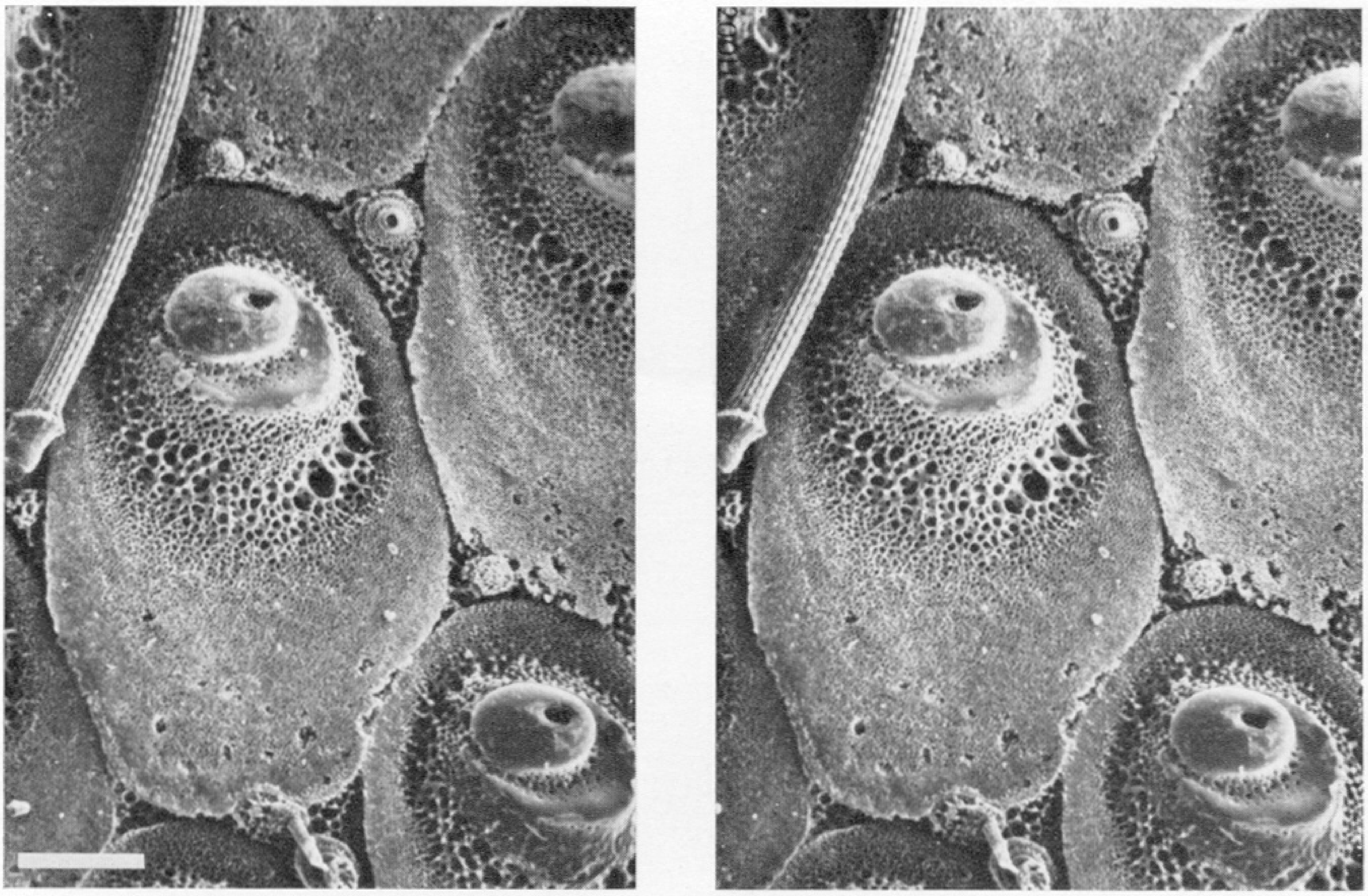

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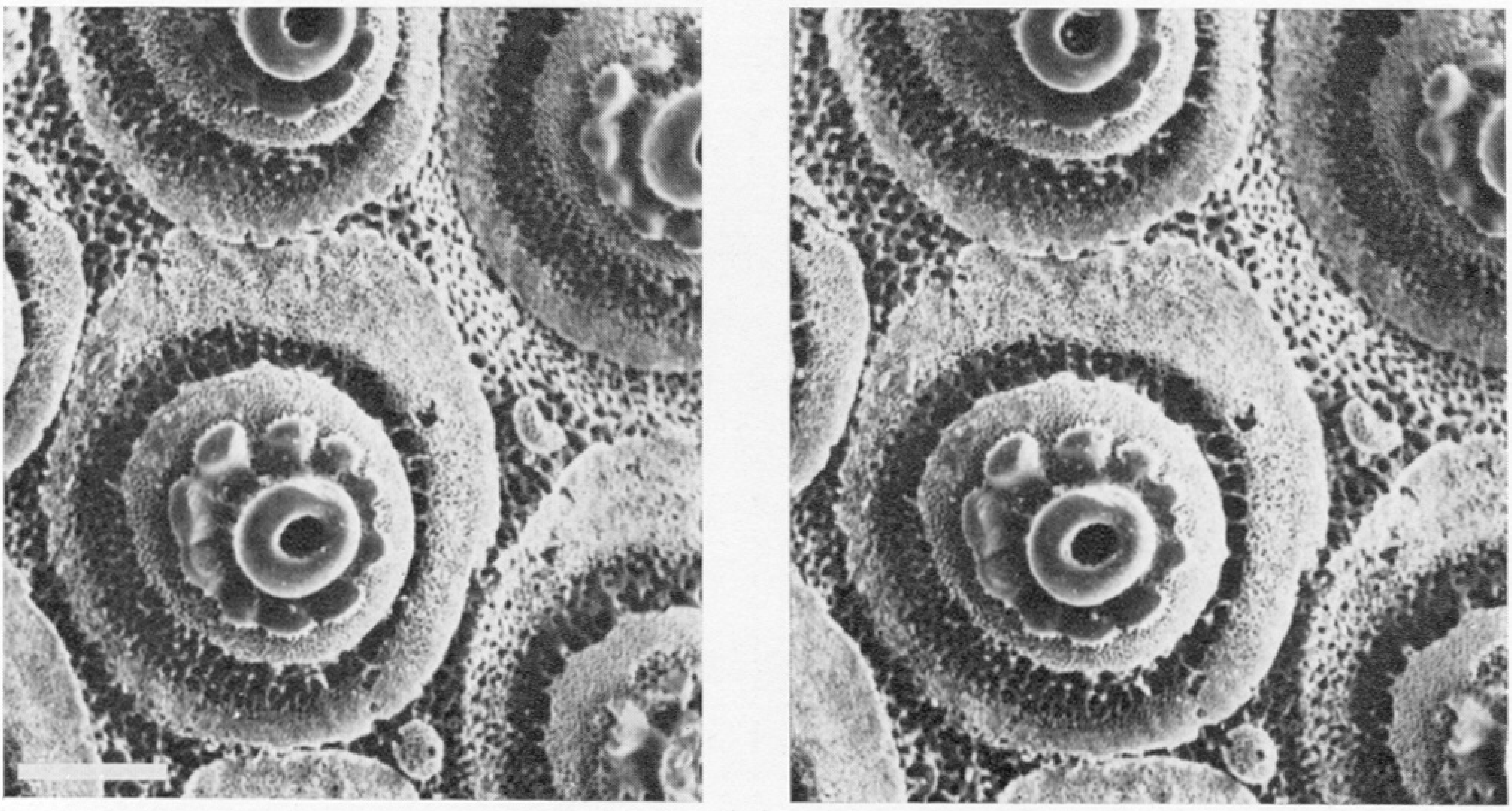

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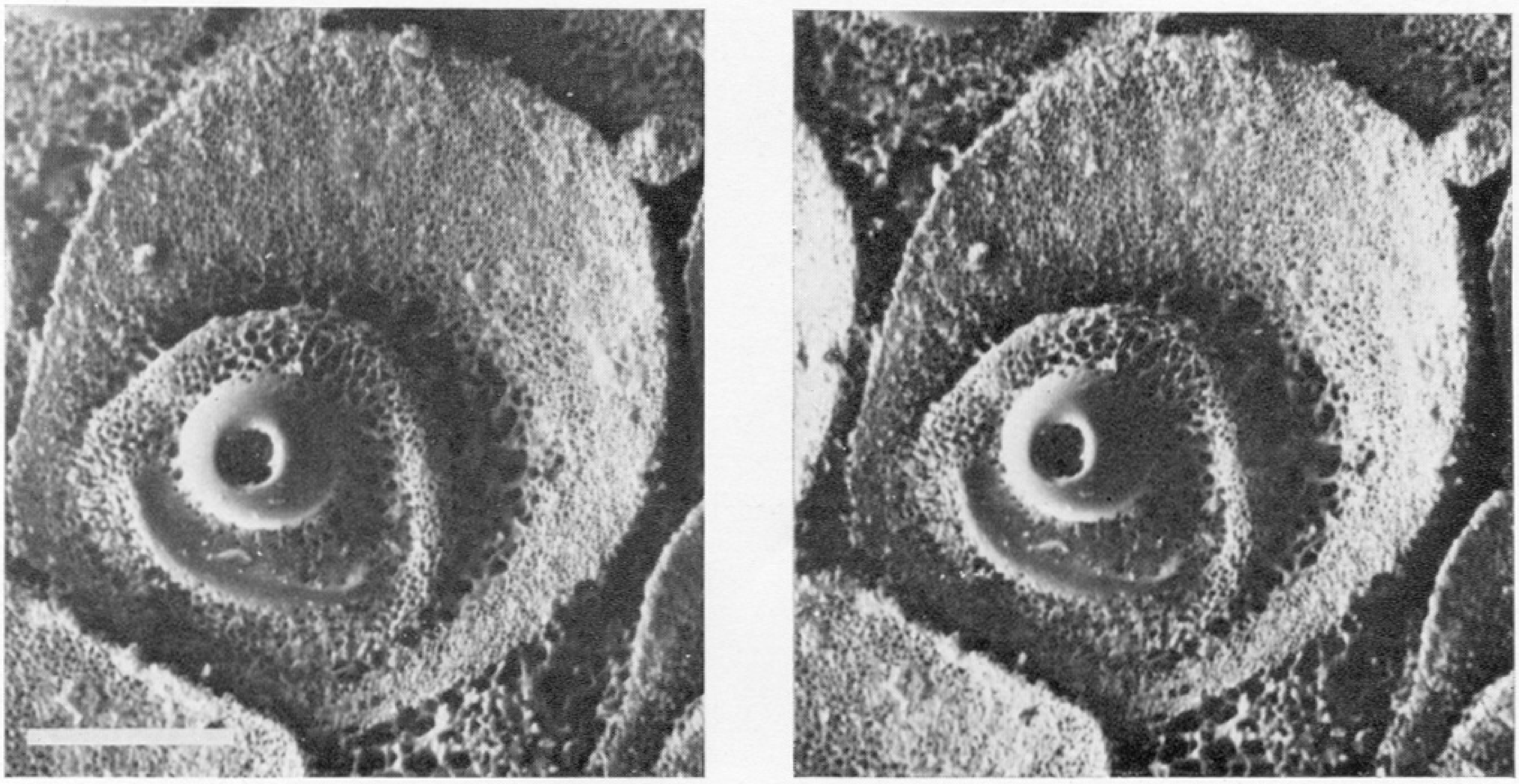

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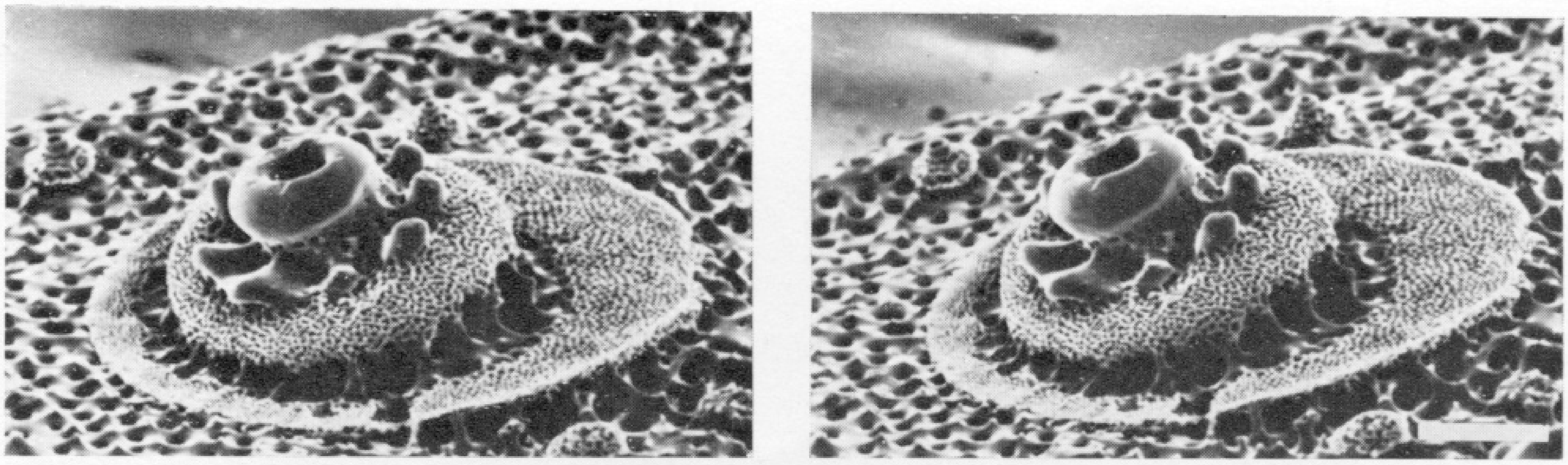

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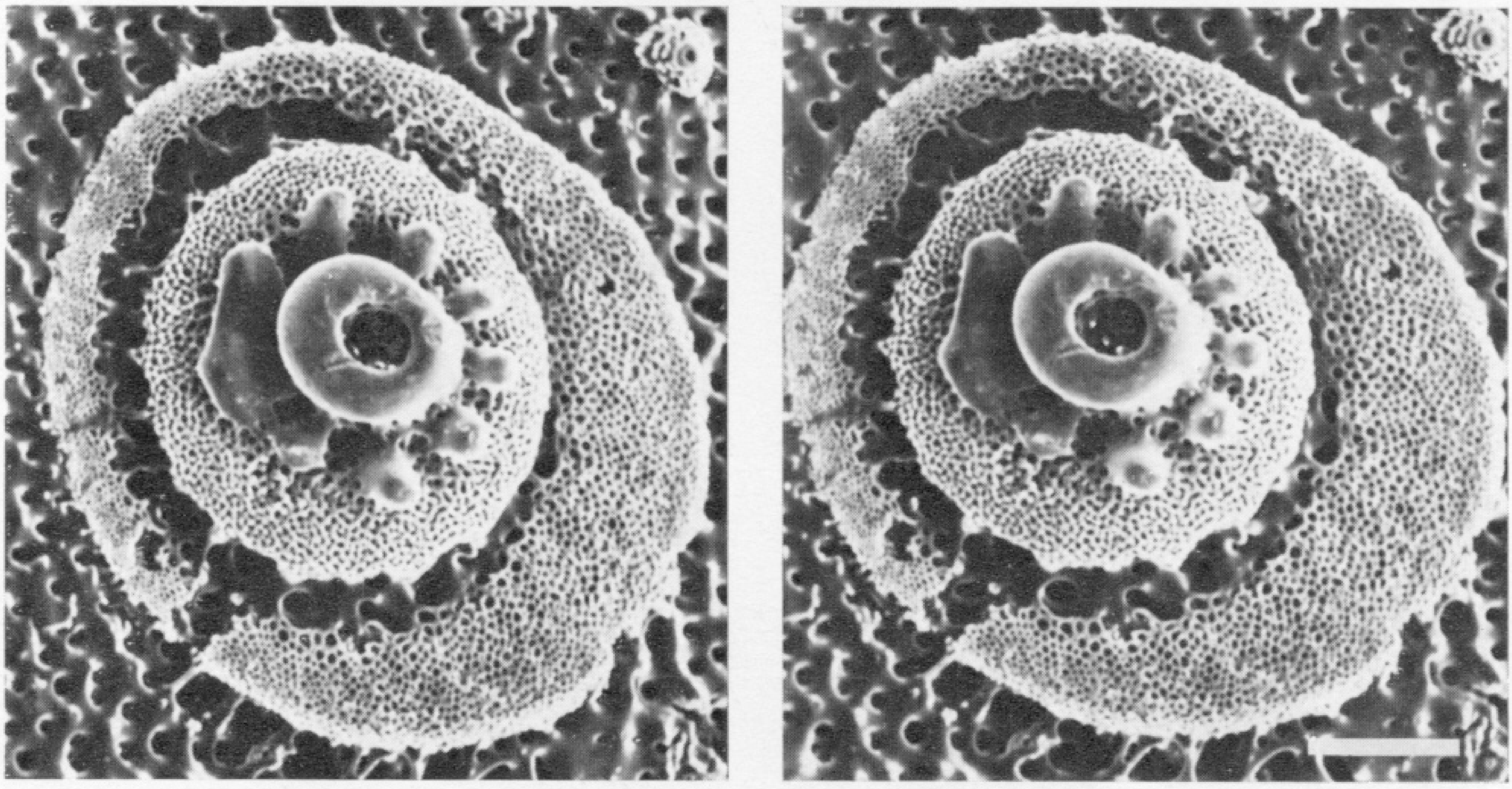

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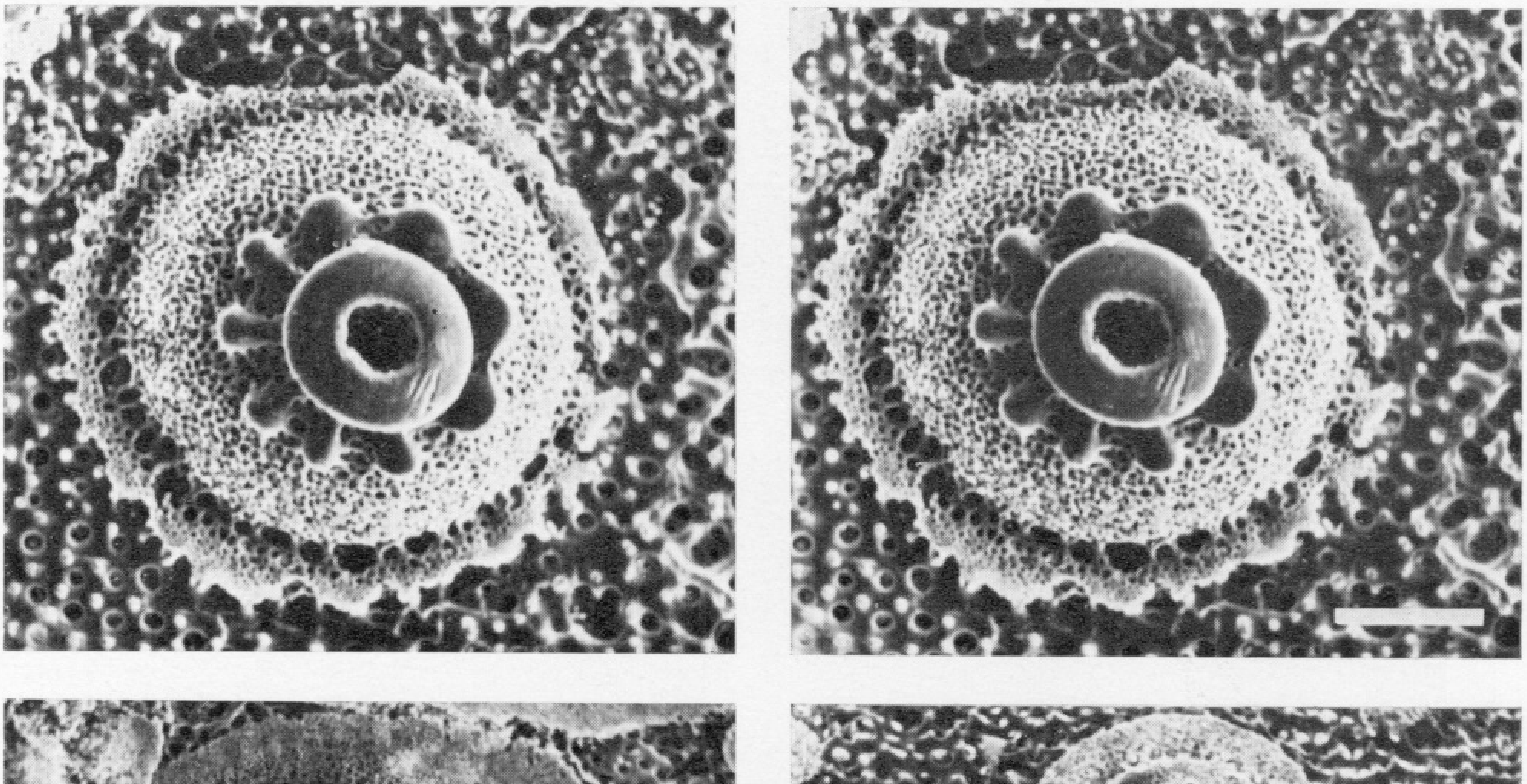

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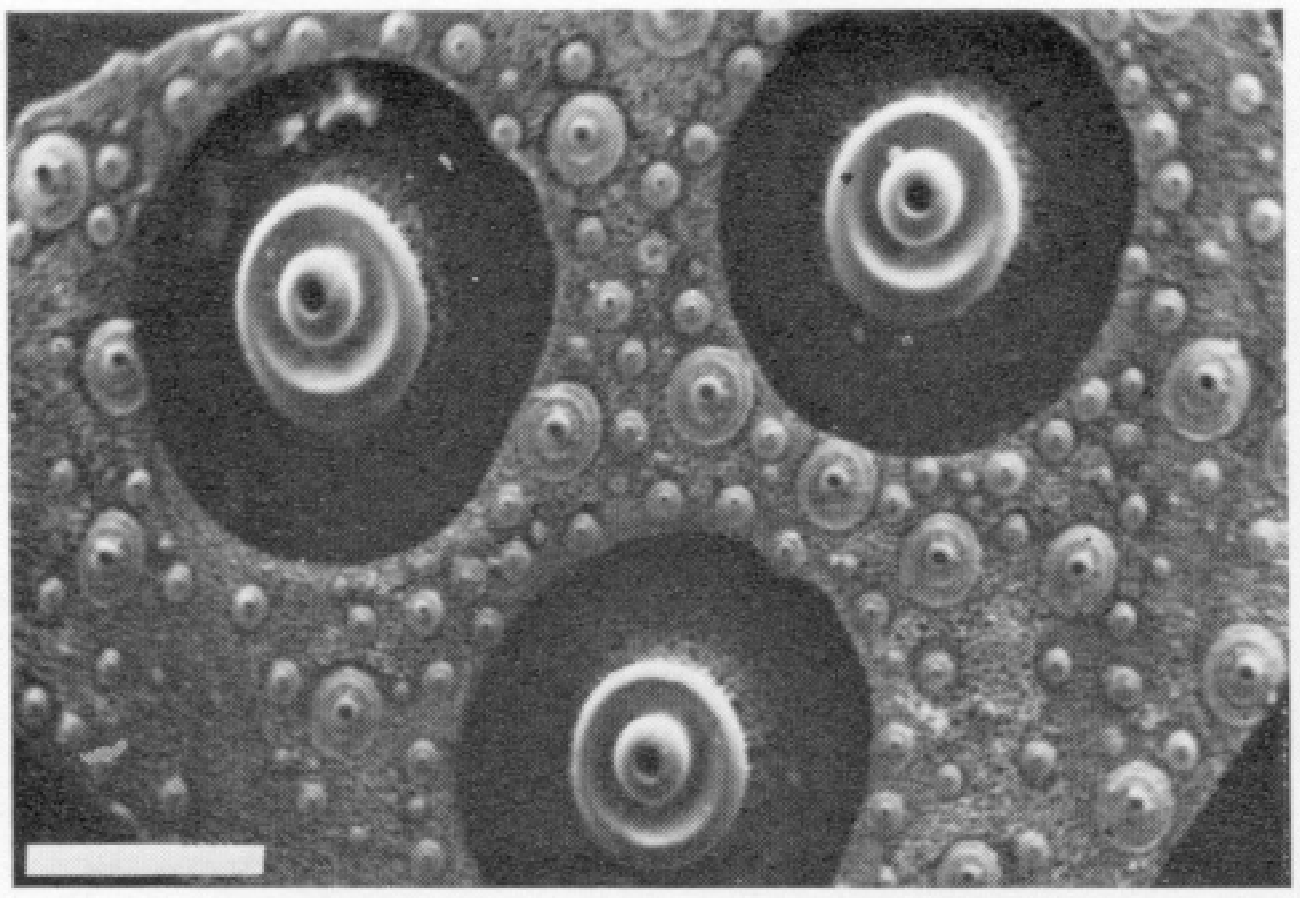

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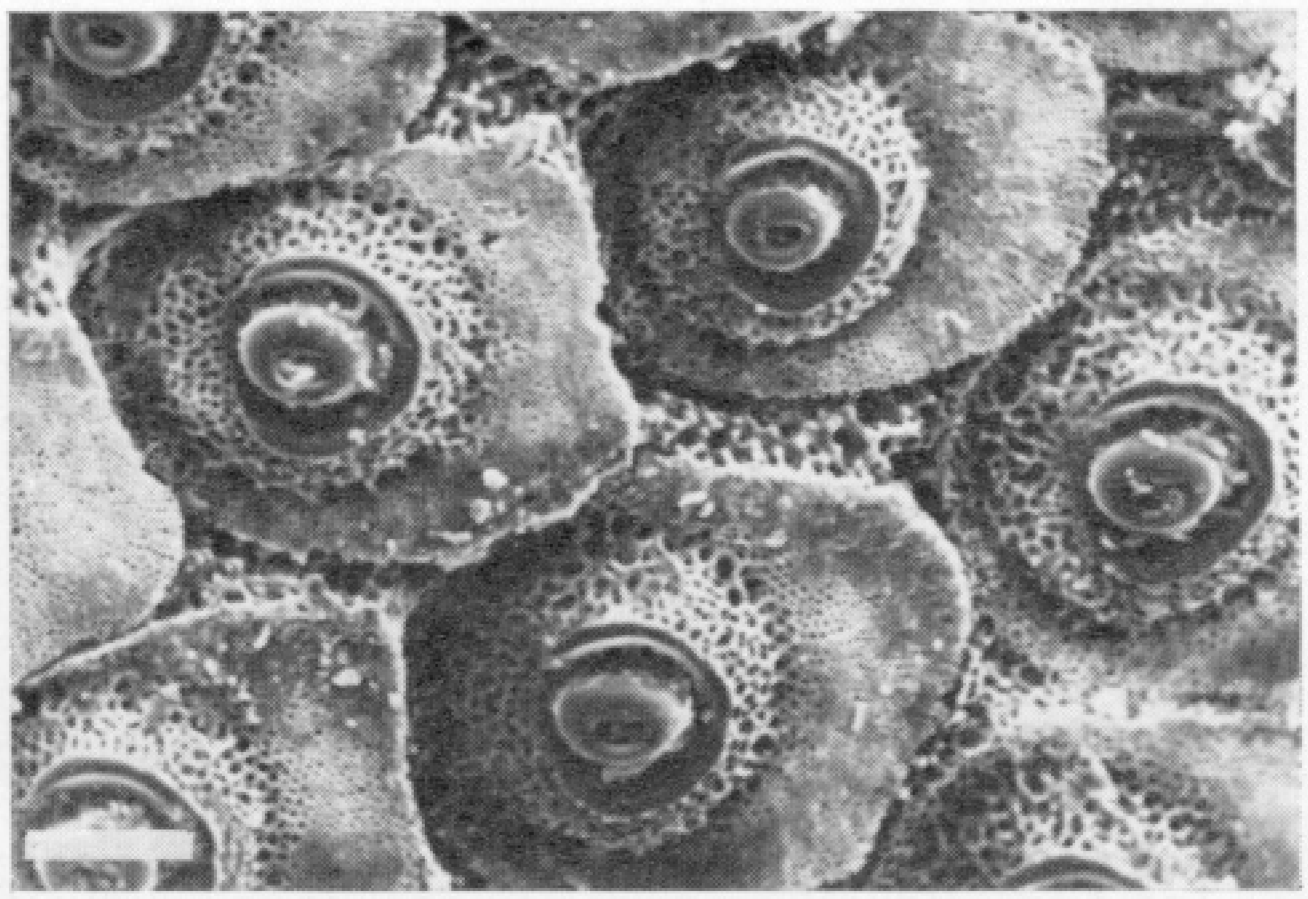

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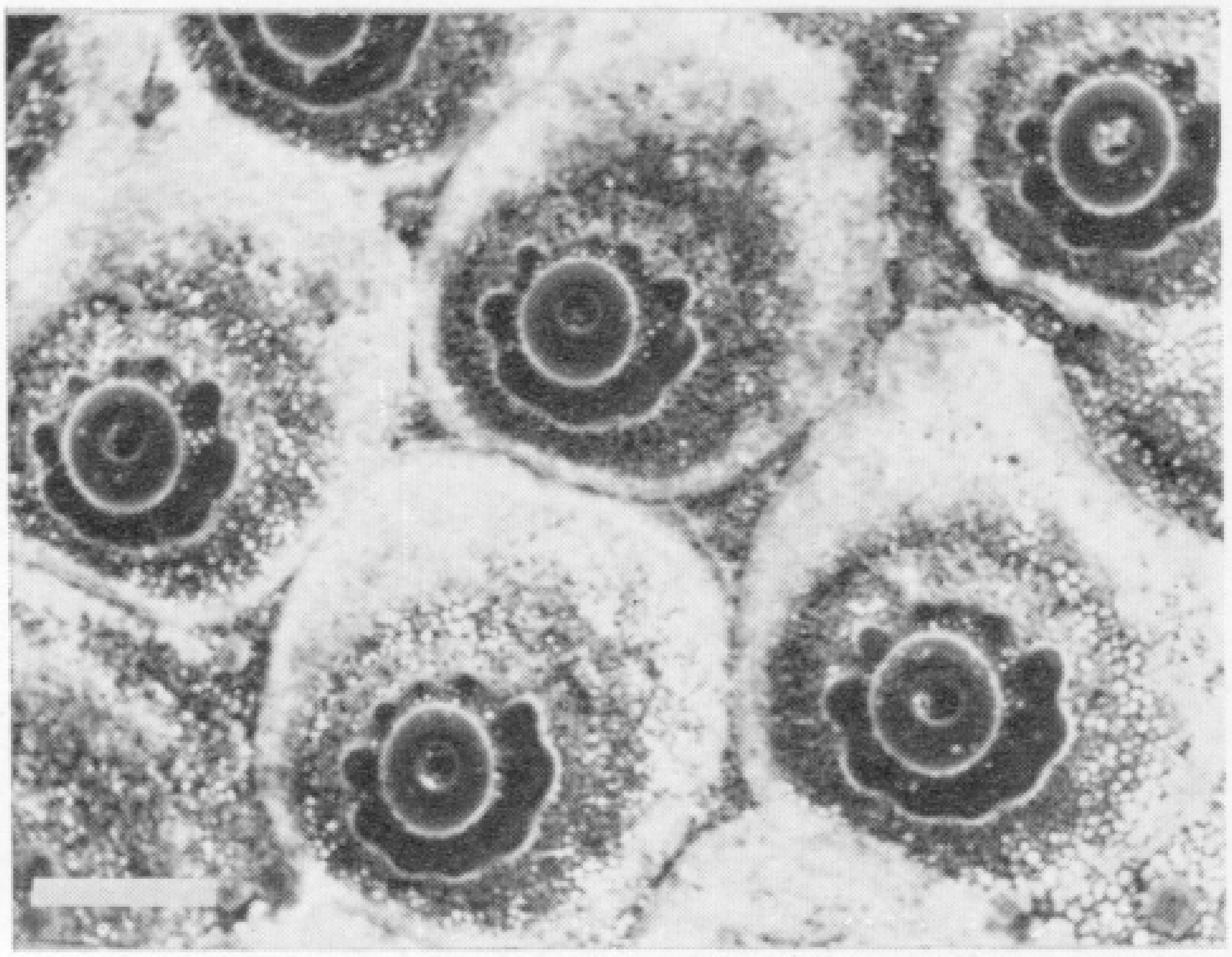

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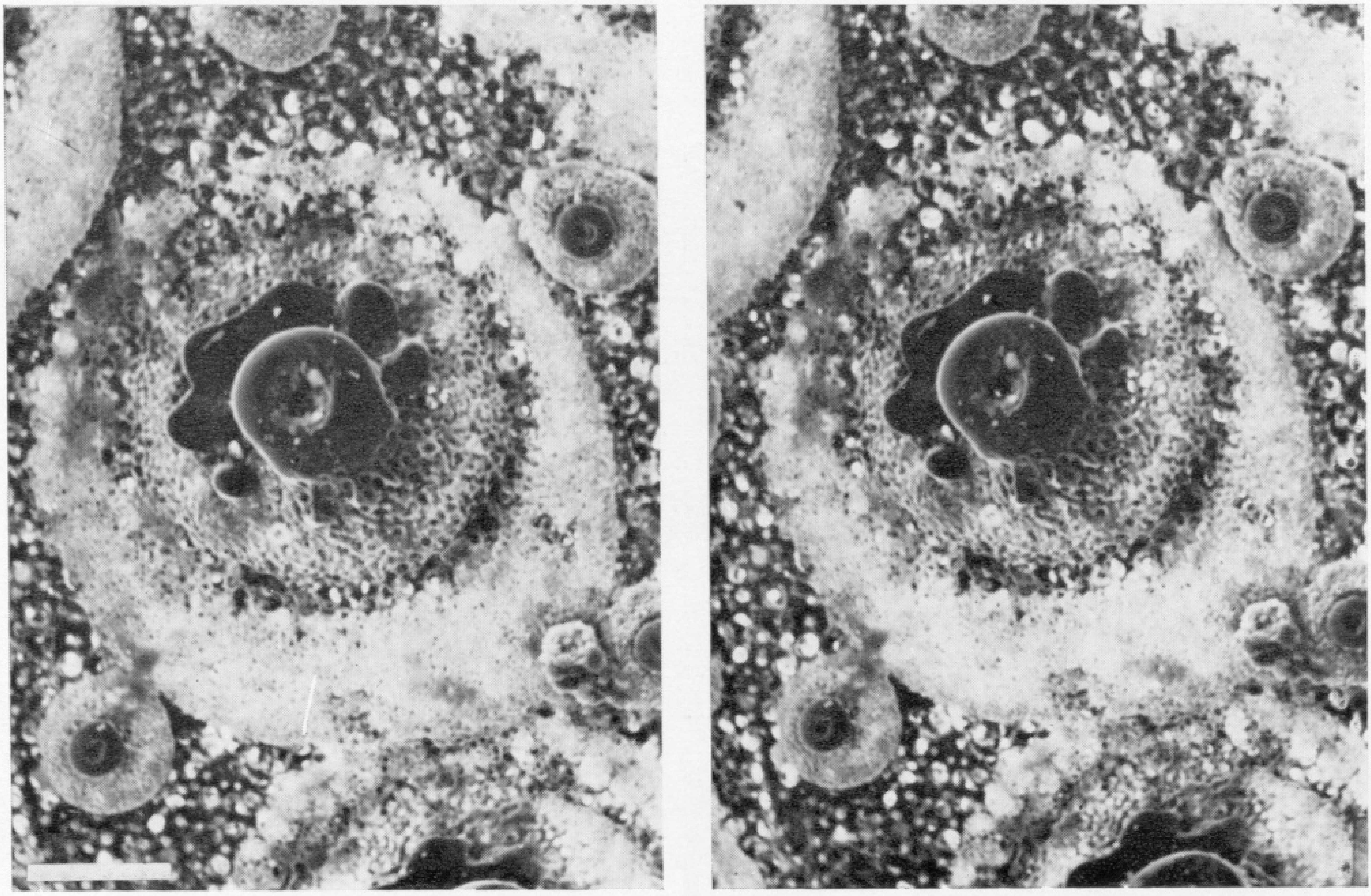

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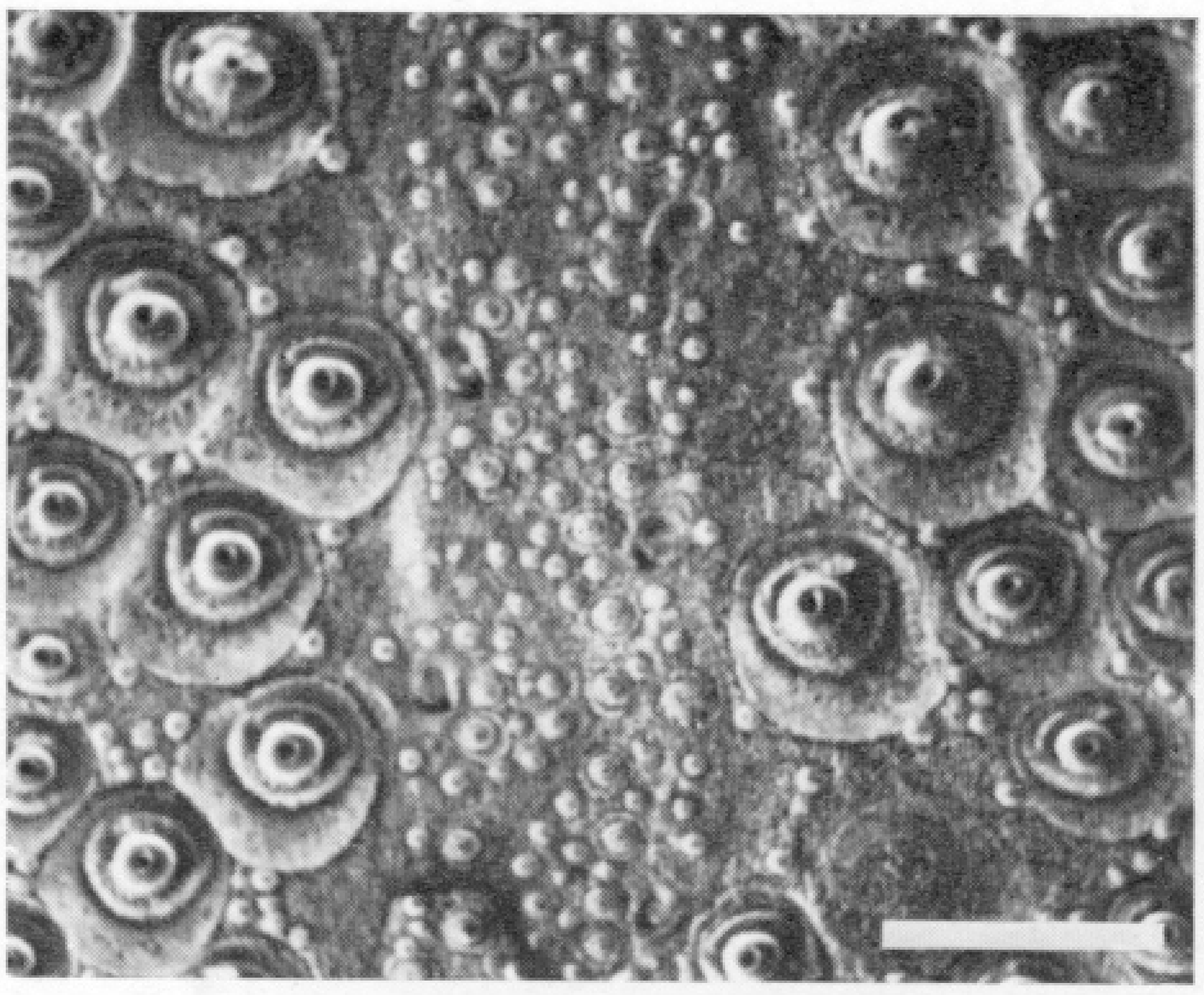

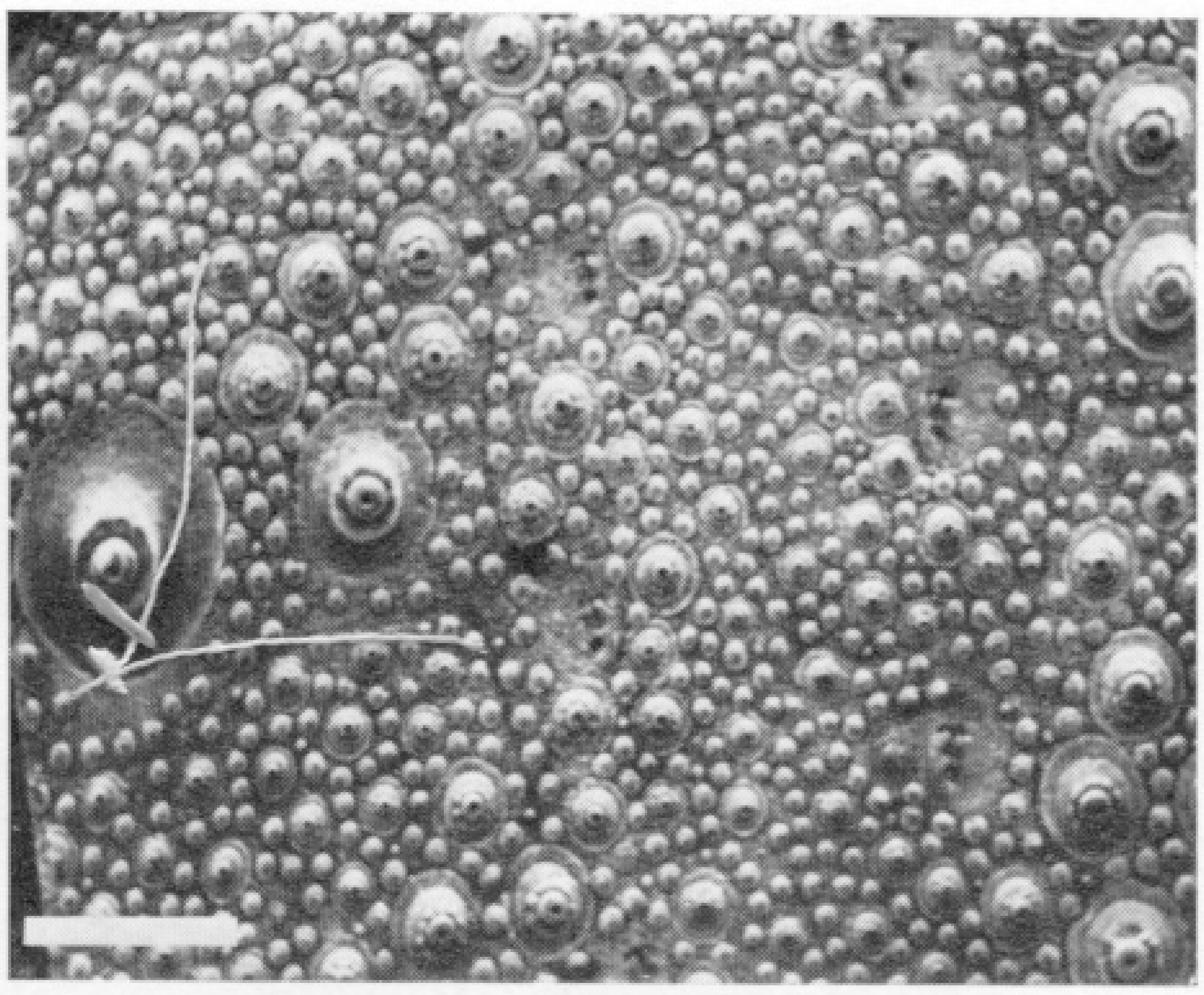

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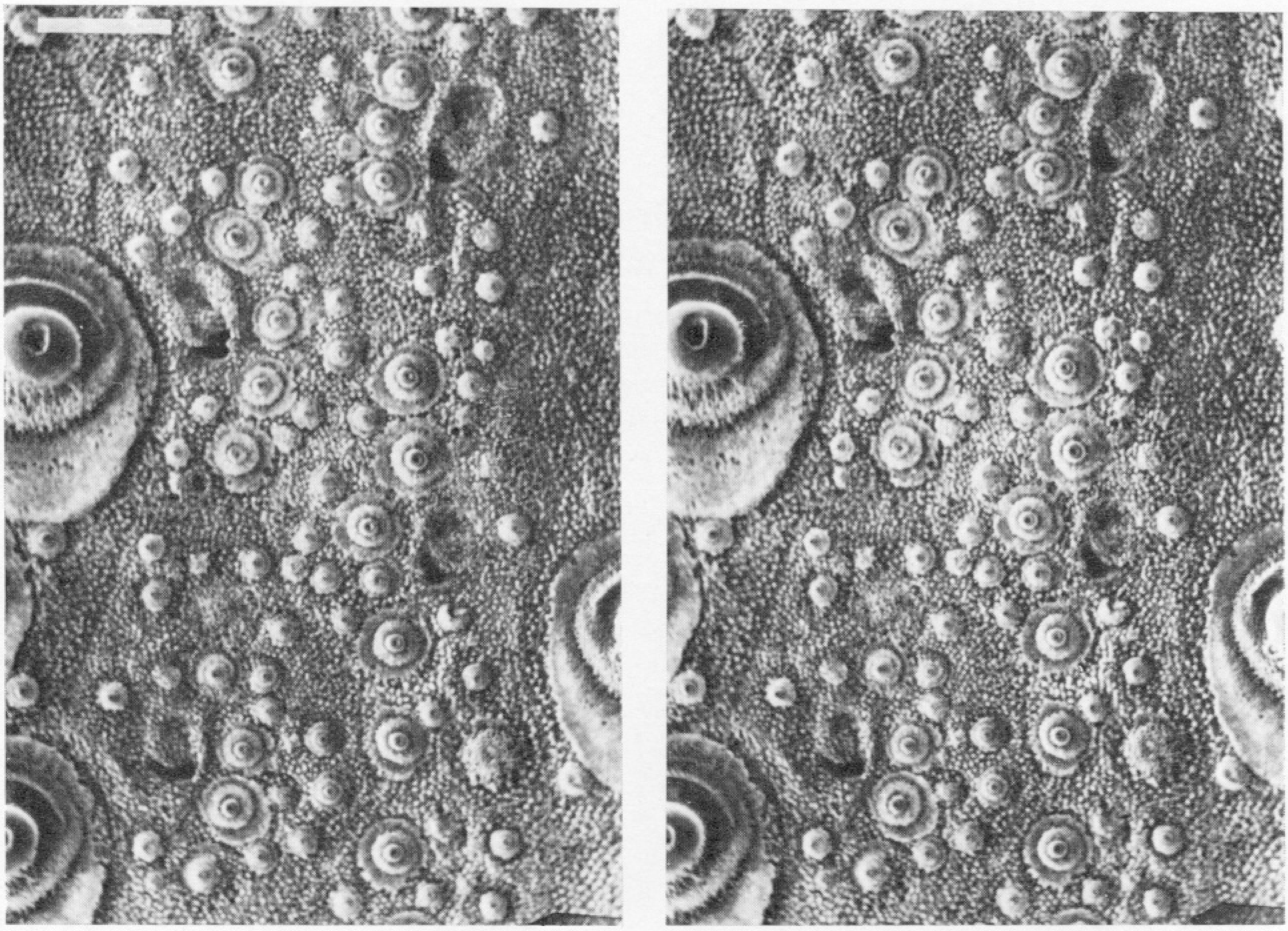

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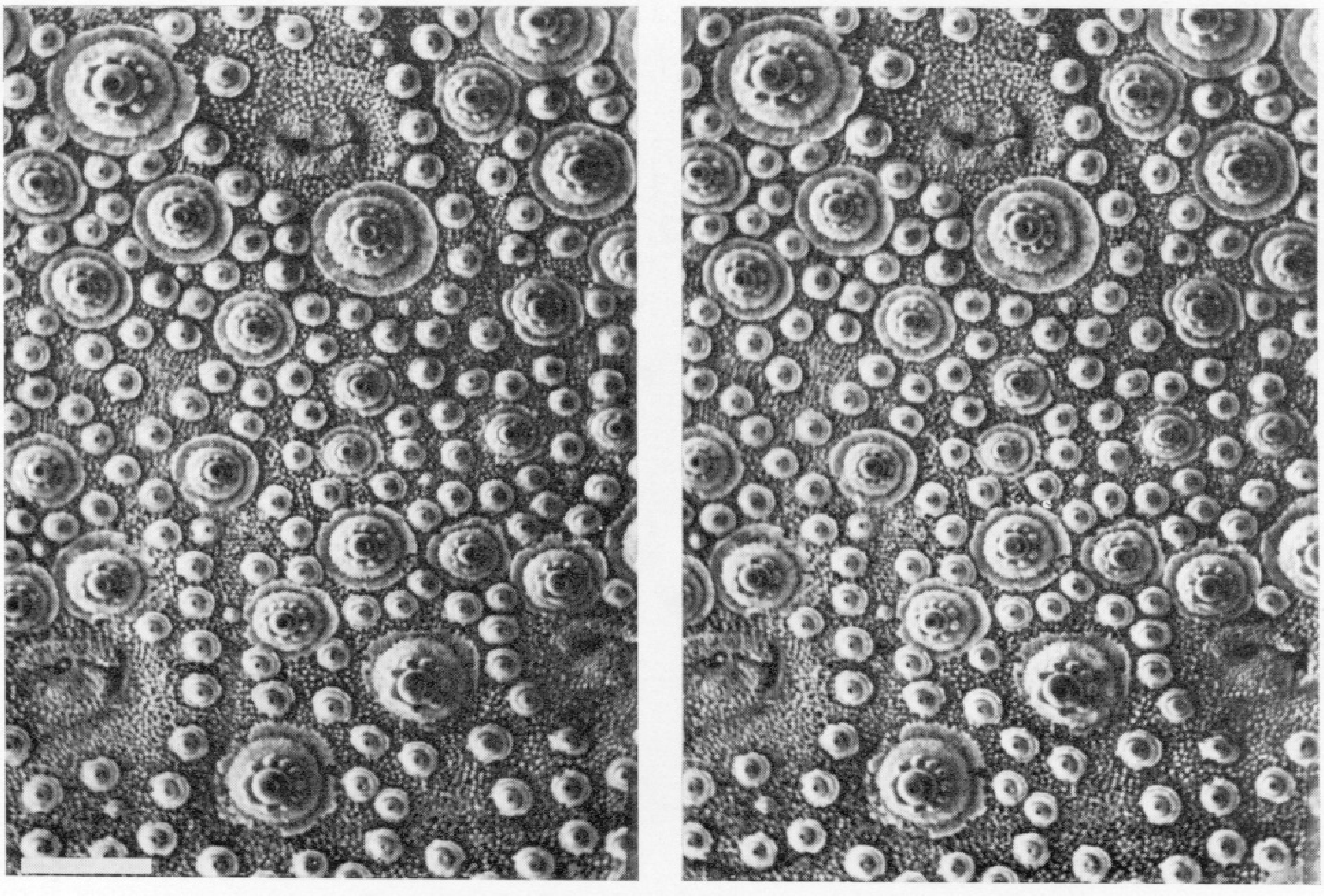

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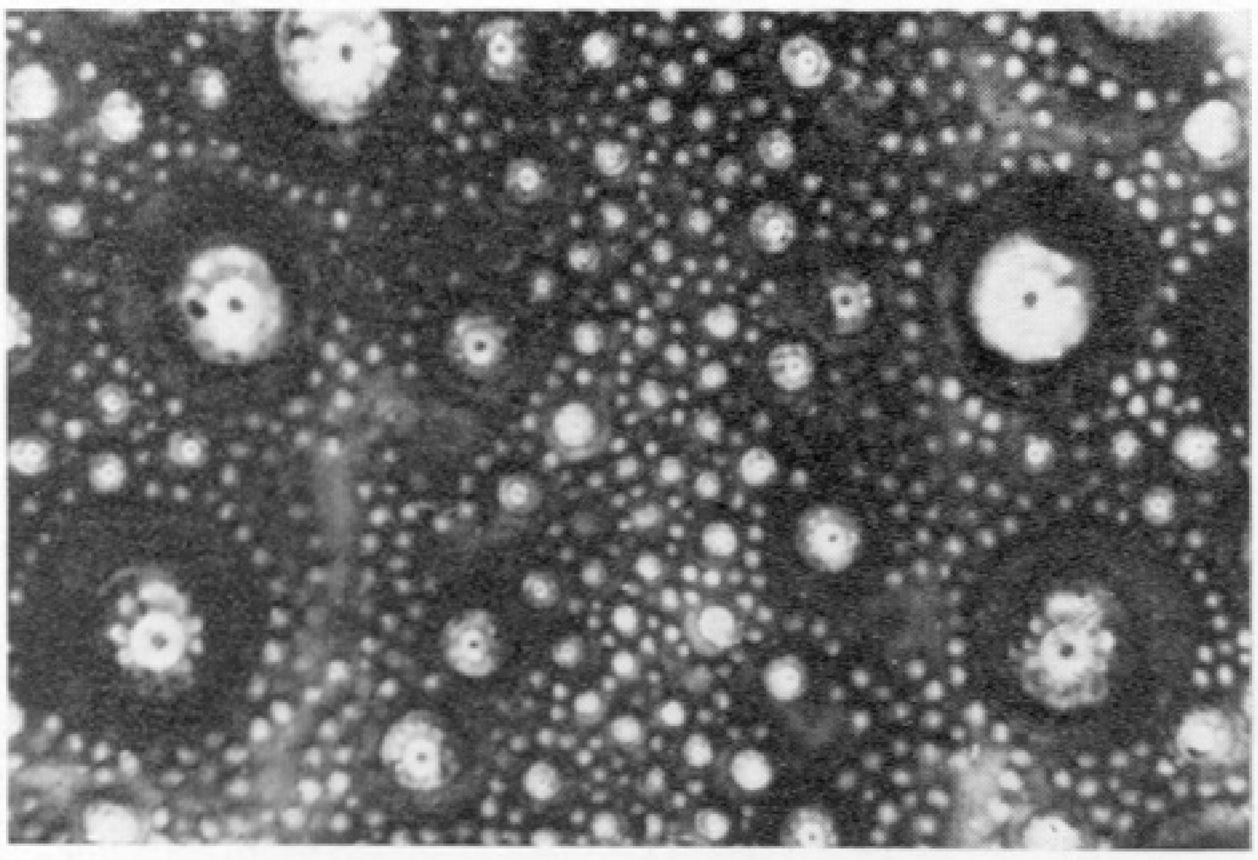

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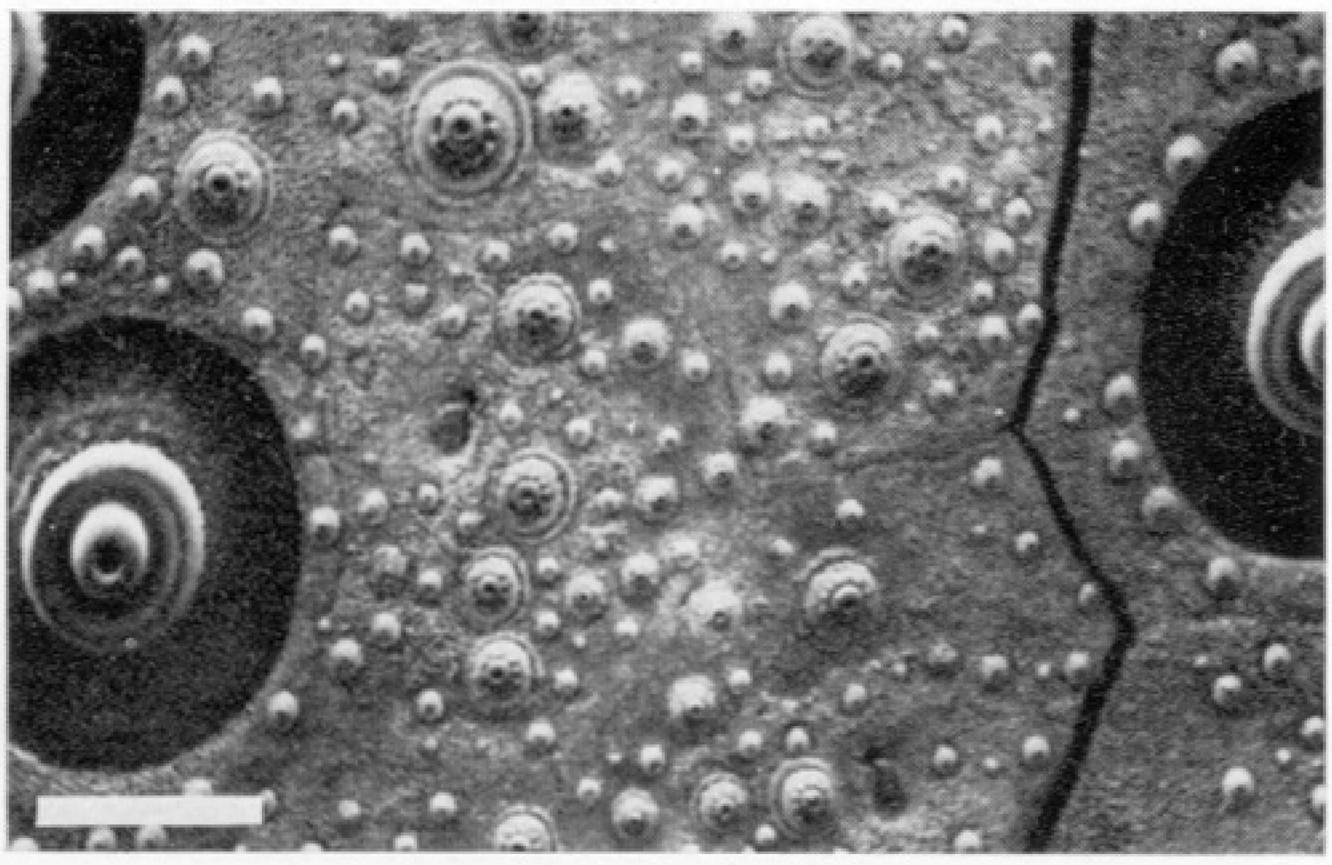

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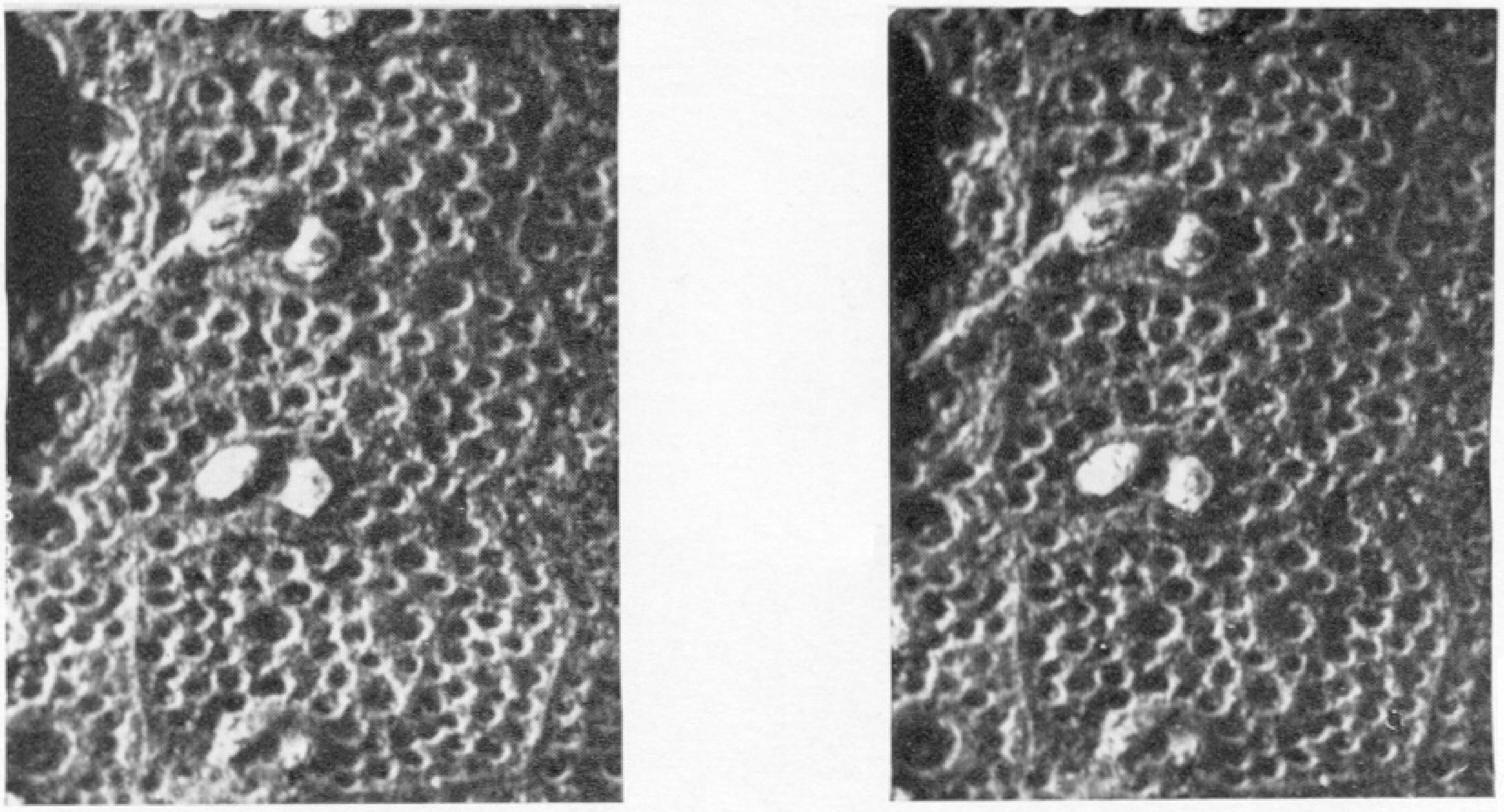

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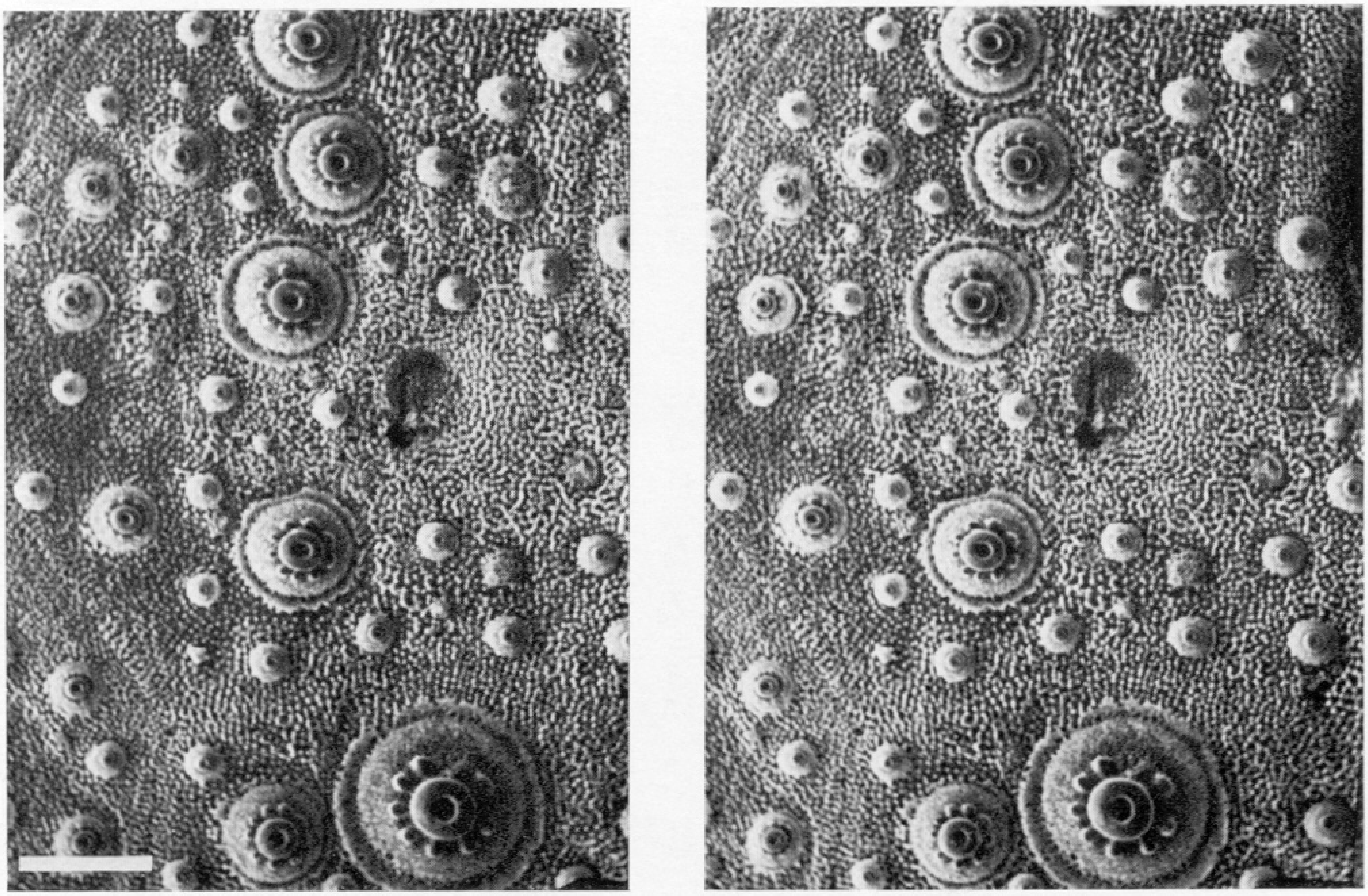

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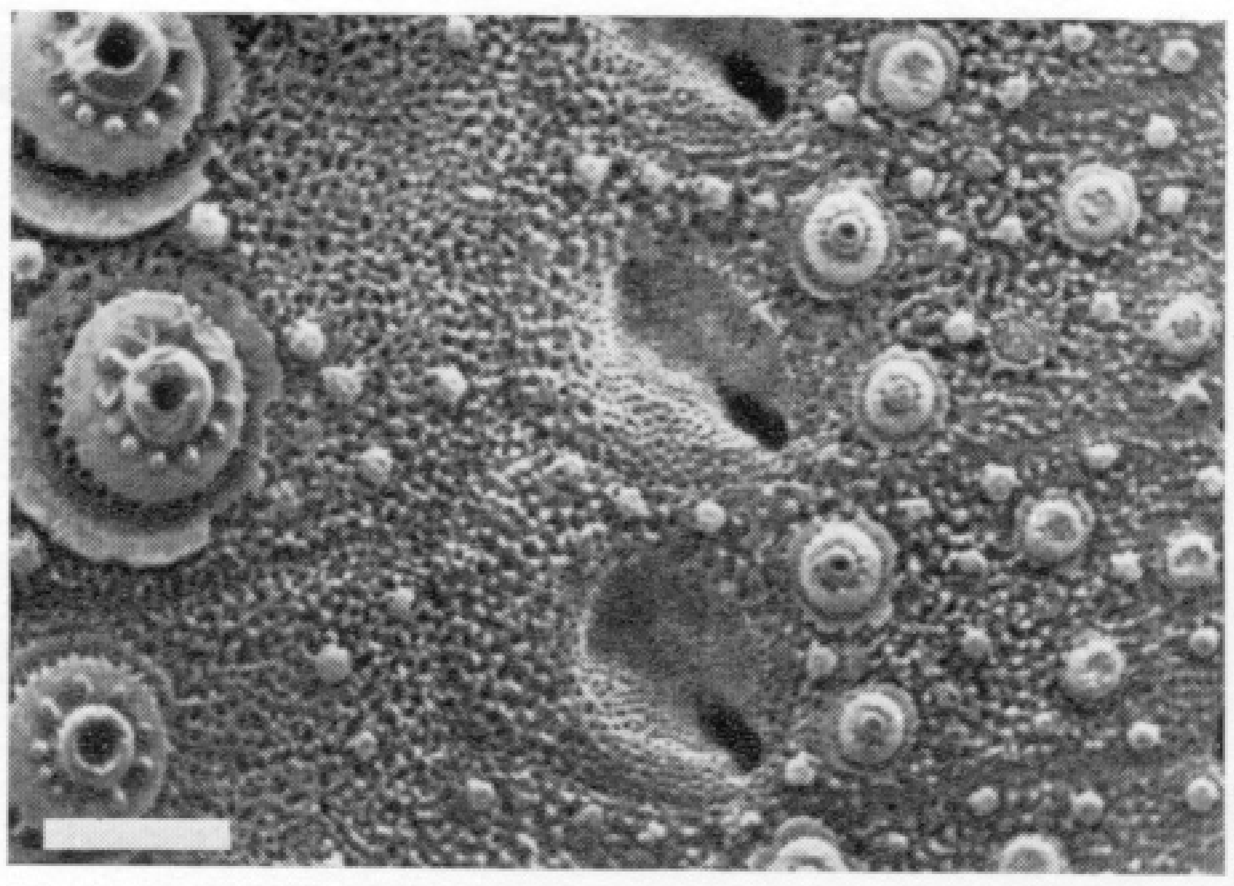
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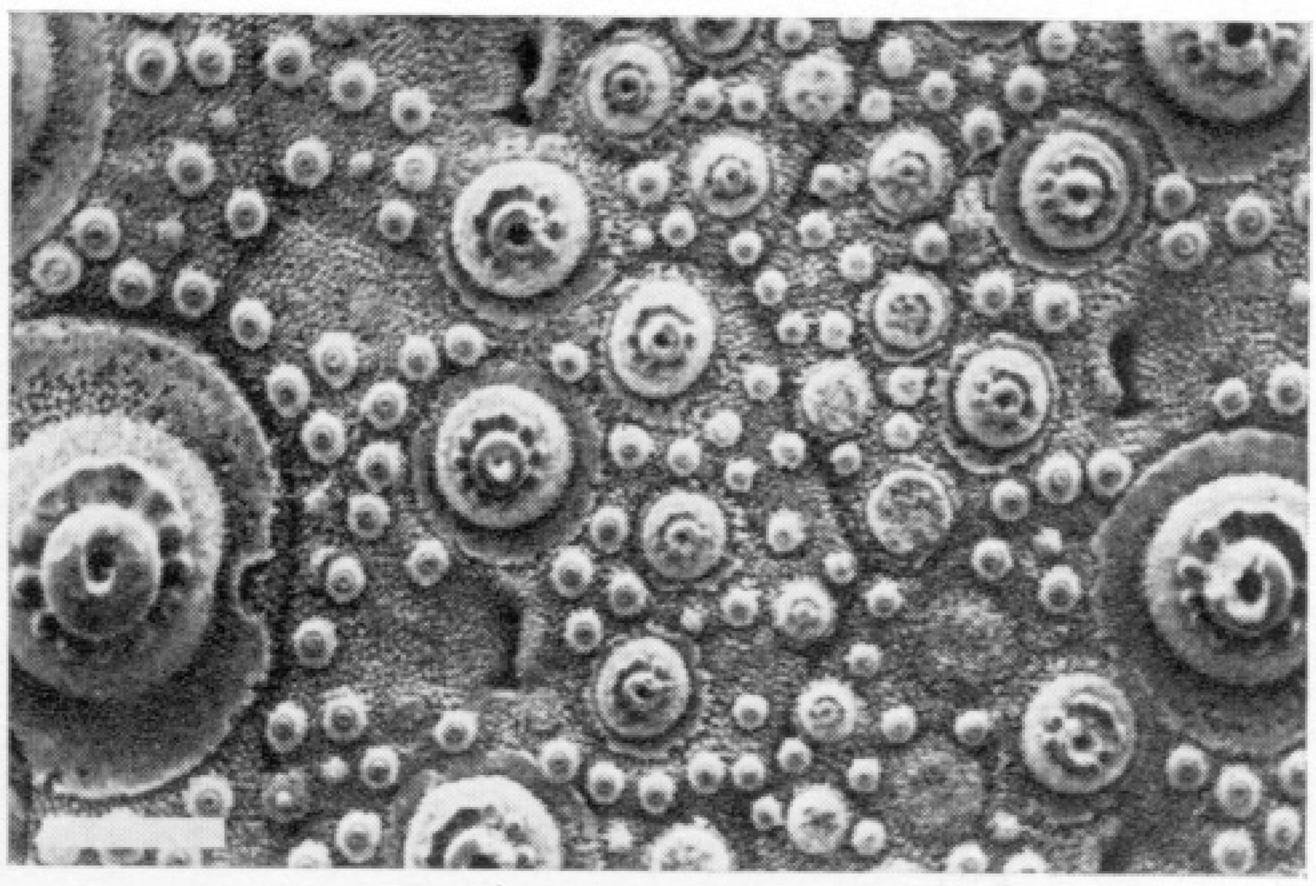
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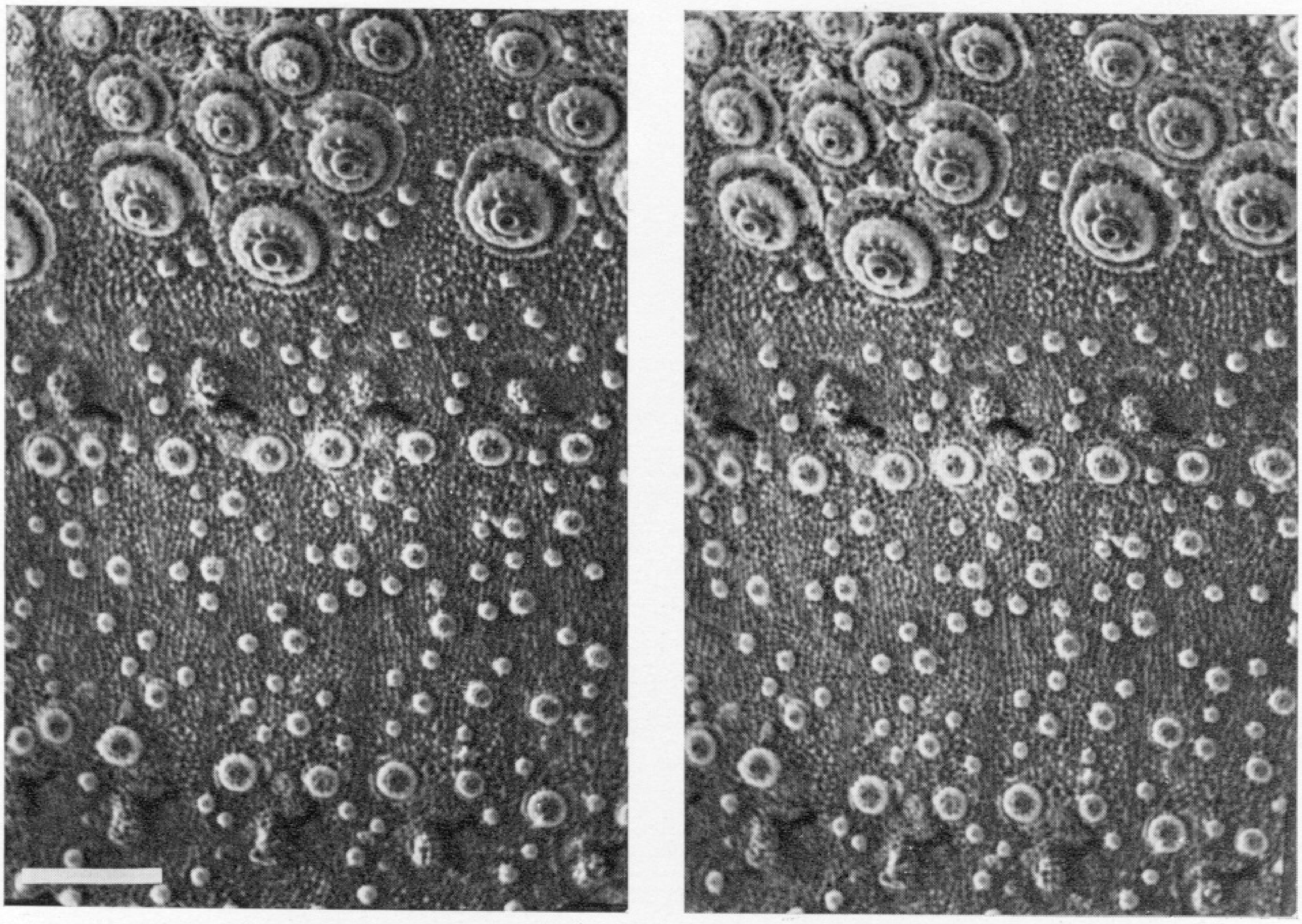
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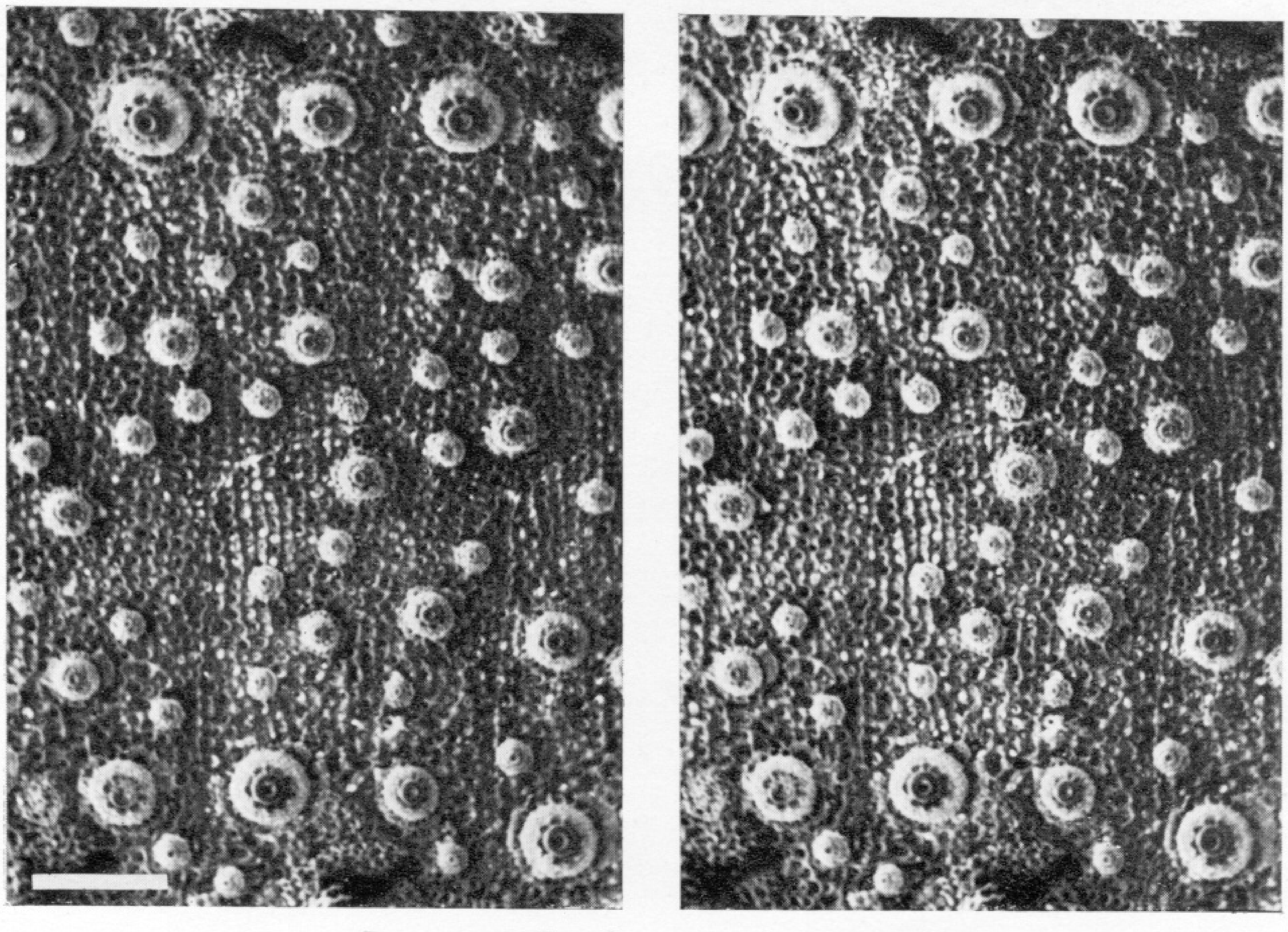
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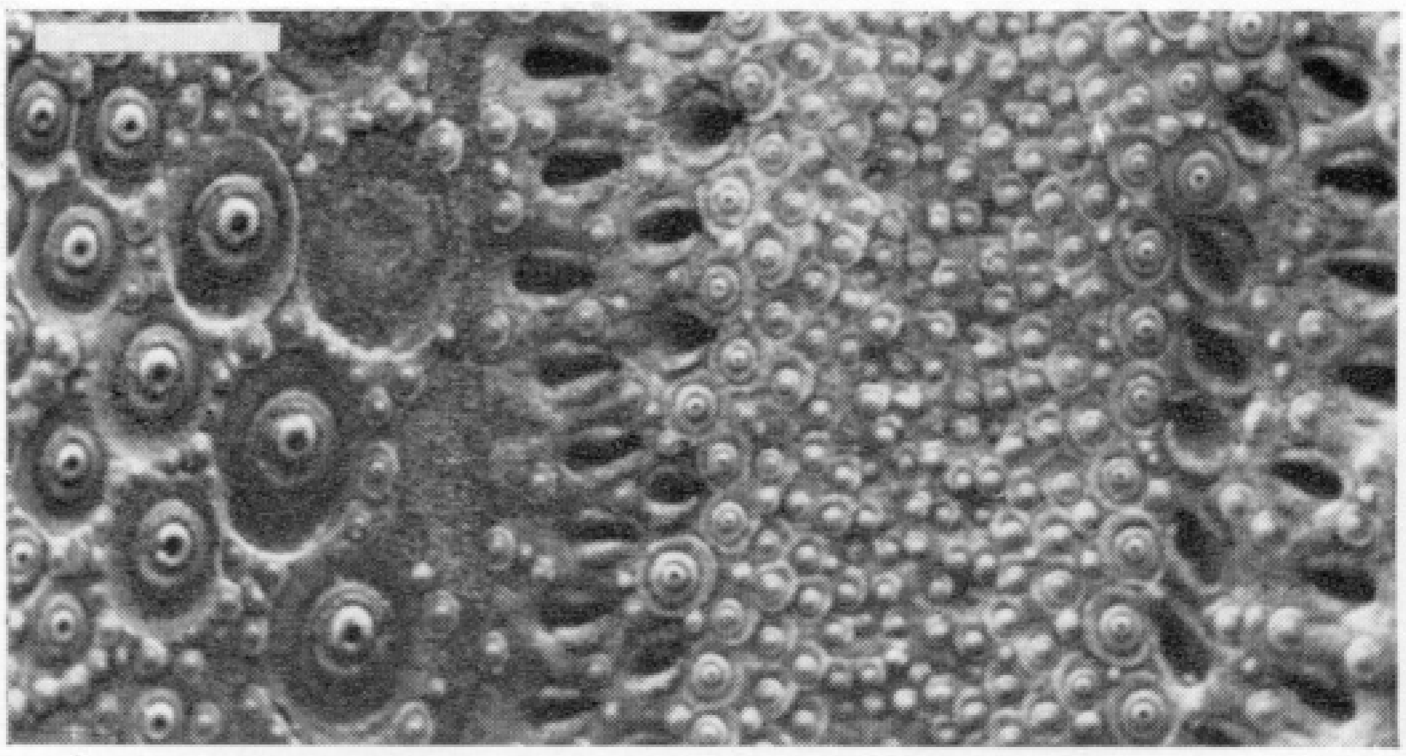
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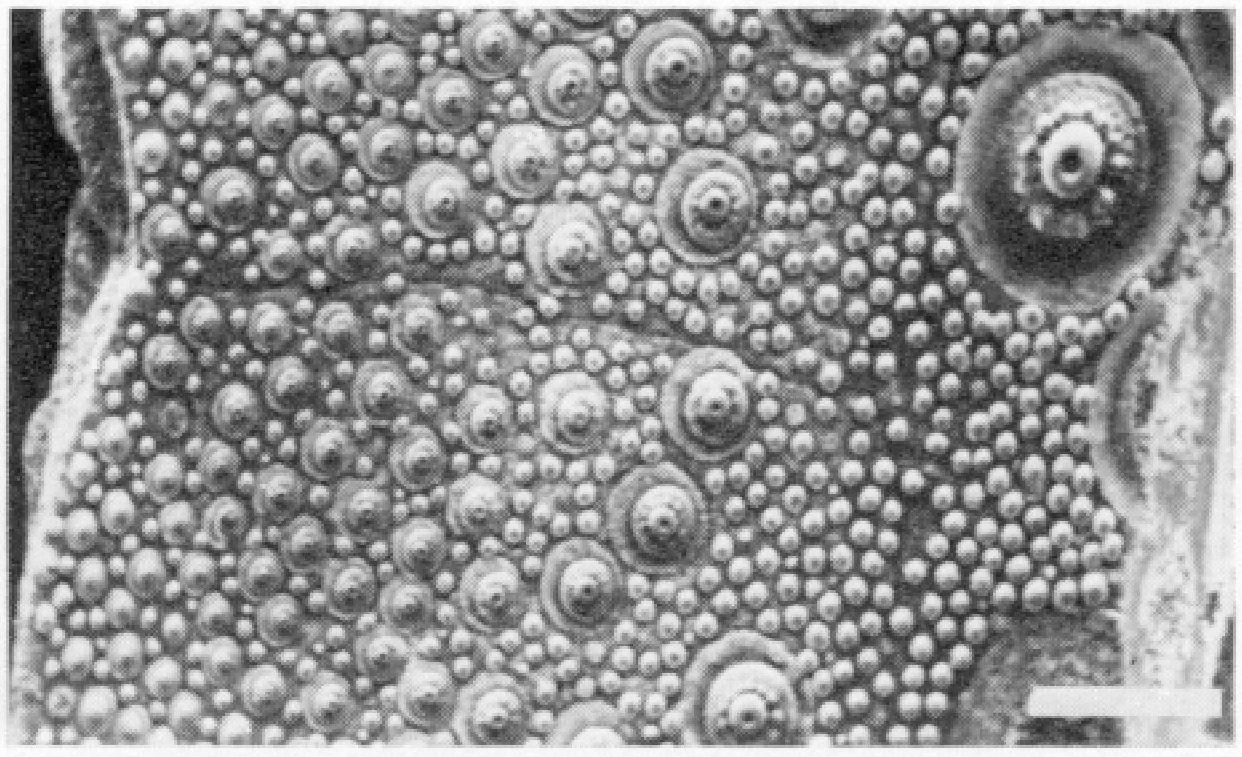
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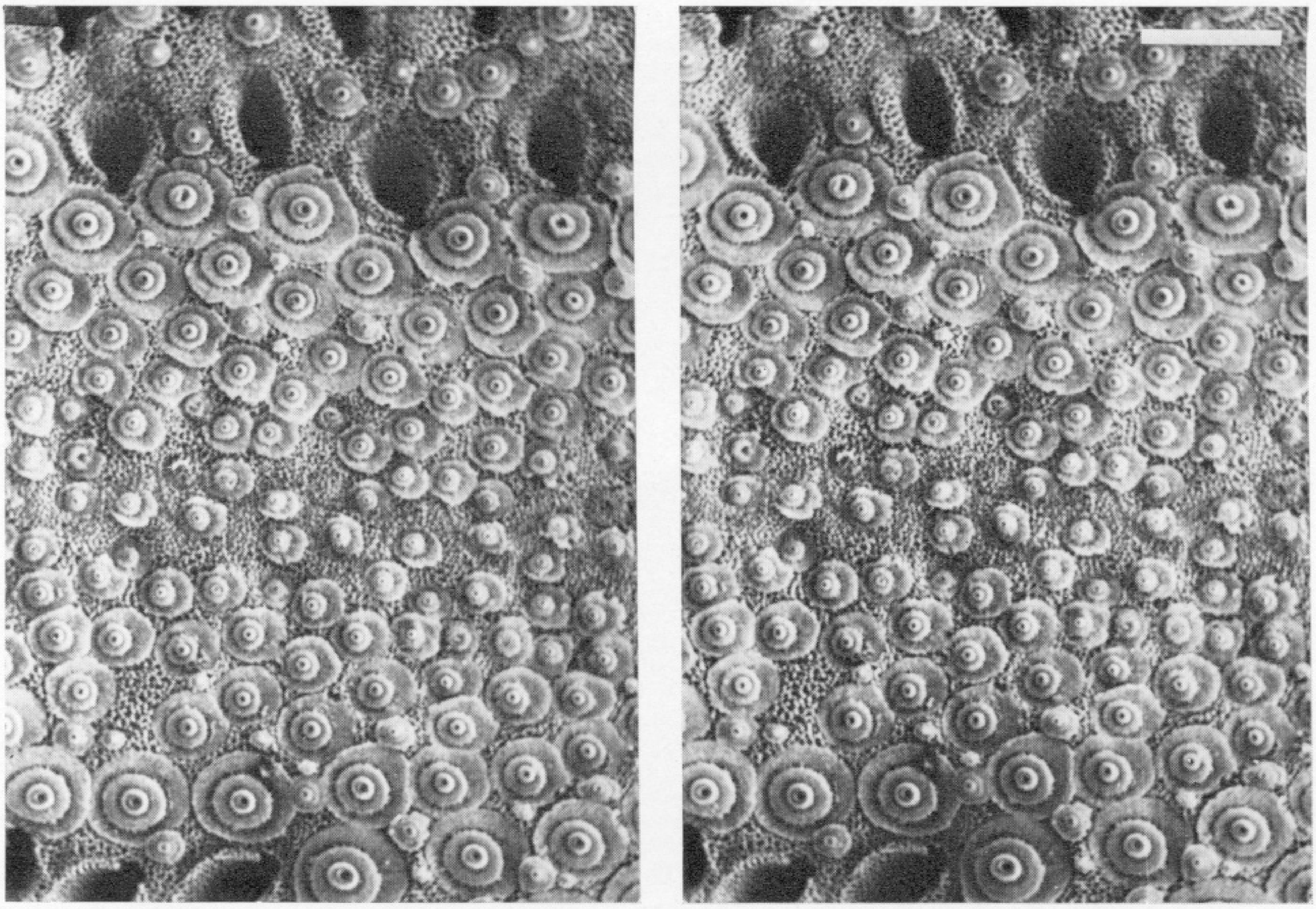
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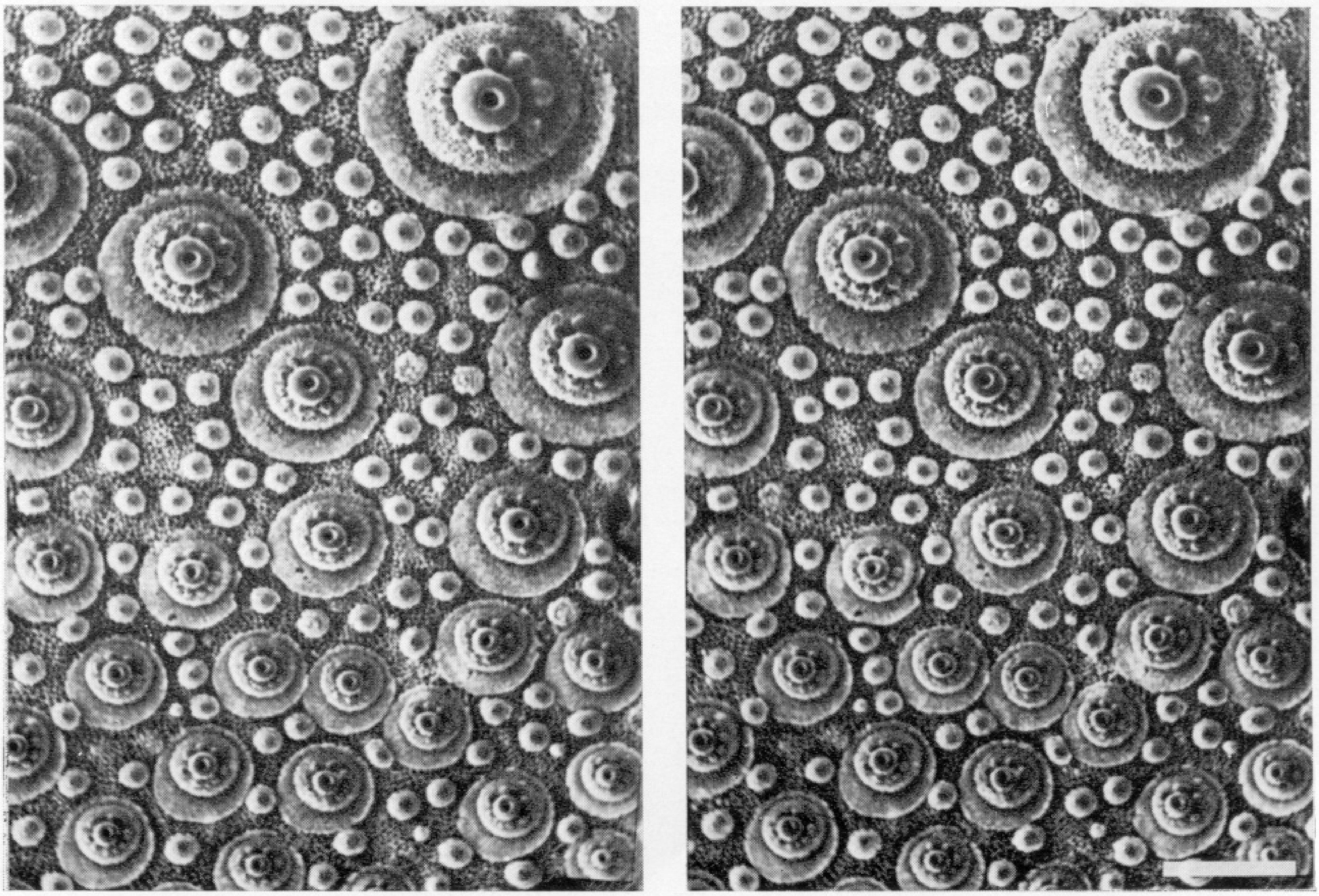
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PLATE 22. For description see page 54.