THE FINE STRUCTURE OF STALKED BACTERIA BELONGING TO THE FAMILY CAULOBACTERACEAE

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ABSTRACT

The fine structure of a series of stalked bacteria belonging to the genera *Caulobacter* and *Asticcacaulis* has been examined in thin sections. The cell wall has the multilayered structure typical of many Gram-negative bacteria, and continues without interruption throughout the length of the stalk. The core of the stalk, continuous with the cytoplasmic region of the cell, is enclosed in an extension of the cell membrane, and contains a system of internal membranes: it is devoid of ribosomes and nucleoplasm. A membranous organelle occupies the juncture of stalk and cell, separating the ribosomal region from the core of the stalk. Typical mesosomes also occur in the cell, being particularly frequent at the plane of division. The secreted holdfast is located at the tip of the stalk in *Caulobacter*, and at the pole of the cell adjacent to the stalk in *Asticcacaulis*.

INTRODUCTION

Among the Gram-negative, polarly flagellated unicellular true bacteria, the caulobacters (family Caulobacteraceae) are distinguished by their unique capacity for structural differentiation. These aerobic, non-photosynthetic organisms are widespread in natural bodies of water, where they probably develop primarily as ectocommensals of larger planktonic microorganisms (1). Their attachment to other microorganisms, as well as to certain inanimate solid substrates, is mediated by a holdfast, which consists of adhesive material secreted at one pole of the cell. They are also able to elaborate a stalk, consisting of a very thin, tubular extension of the cell, which under certain circumstances can attain a length many times that of the cell itself.

Cultures of caulobacters always contain two kinds of cells: actively motile, non-stalked swarmers, and immotile, stalked cells. Only stalked cells can divide; at each division, the apical daughter cell gives rise to a uniflagellate swarmer. The swarmer is free-swimming for a short period following its liberation from the basal stalked cell, but loses its flagellum concomitantly with the formation of the stalk, which grows out from the site of attachment of the flagellum (2). Holdfast material is present on both swarmers and stalked cells. Attachment, if it occurs, generally takes place in the swarmer stage. In pure cultures in which the population density is high, many of the swarmers adhere to one another by means of their holdfasts, giving rise to rosettes (see Figs. 1 to 3).

In the genus *Caulobacter*, the holdfast material is initially secreted around the base of the flagellum of the swarmer, and becomes located around the tip of the stalk following the outgrowth of this structure. The cells of *Caulobacter* are rods, which may be cylindrical, fusiform, or curved, as illustrated in Figs. 1 to 3. A second genus, *Asticcacaulis*, has been recently proposed (1) for caulo-

bacters in which the flagellum and the holdfast occur at different sites on the surface of the swarmer cell. The holdfast material is typically secreted at one pole, whereas the insertion of the flagellum is subpolar. As in *Caulobacter*, the stalk develops at the site of attachment of the flagellum. Consequently, its tip is never embedded in the holdfast, and it plays no role in attachment of the cell to substrates. The cells of *Asticcacaulis* are short rods with blunt ends, and the stalks typically extend laterally from the cells (Fig. 4).

Stalk and holdfast, the distinctive structural features of the caulobacter cell, have dimensions close to the limit of resolution with the light microscope; they can only just be detected by phase contrast illumination or by certain staining methods. Elucidation of their structure and relation to the cell had, therefore, to await study with the electron microscope. The first electron micrographs of shadowed cells, prepared by Houwink and van Iterson (3) and by Houwink (4), showed that the outer region of the stalk is continuous with the cell wall. From electron micrographs of whole cells, shadowed and unshadowed, it could also be inferred (3–5) that the stalk contains a core of material continuous with the cytoplasmic region of the cell. These observations established that the caulobacter stalk is a differentiated region of the cell itself. The holdfast appears in shadowed electron micrographs as an irregular, extracellular structure, physically distinct from the stalk proper (4, 5).

In the hope of further clarifying the organization of the caulobacter cell, we have undertaken a comparative study of the fine structure of representative members of the group, by electron microscopy of ultrathin sections. Some of our results have been briefly described in another publication (1).

MATERIALS AND METHODS

A total of some 20 caulobacter strains has been examined cytologically. Material selected from seven strains is illustrated and discussed in this paper. Two of these strains are vibrioid caulobacters, belonging to the species *Caulobacter crescentus*; one is a straight rod, belonging to the species *C. bacteroides*; one is a fusiform rod, belonging to the species *C. fusiformis*; one is an unnamed vibrioid *Caulobacter*, strain CB 66; and two are strains of *Asticcacaulis excentricus*, the only species in this genus.

Cultures were grown at 30°C with mechanical agitation in a complex liquid medium (0.2 per cent peptone, 0.1 per cent yeast extract, 0.02 per cent $MgSO_4 \cdot 7H_2O$, tapwater base). Cells in the course of exponential growth were harvested by centrifugation and resuspended in the prefixation mixture of Ryter and Kellenberger (6). Fixation and dehydration were carried out by the methods of Ryter and Kellenberger (6), except that the time of fixation was reduced to 2 hours. The dehydrated specimens were embedded in Vestopal and sectioned with a diamond knife on a Porter-Blum microtome. The sections were mounted on uncoated 300-mesh grids, poststained with lead hydroxide as described by Millonig (7), and examined in the Siemens Elmiskop I operating at 80 kv.

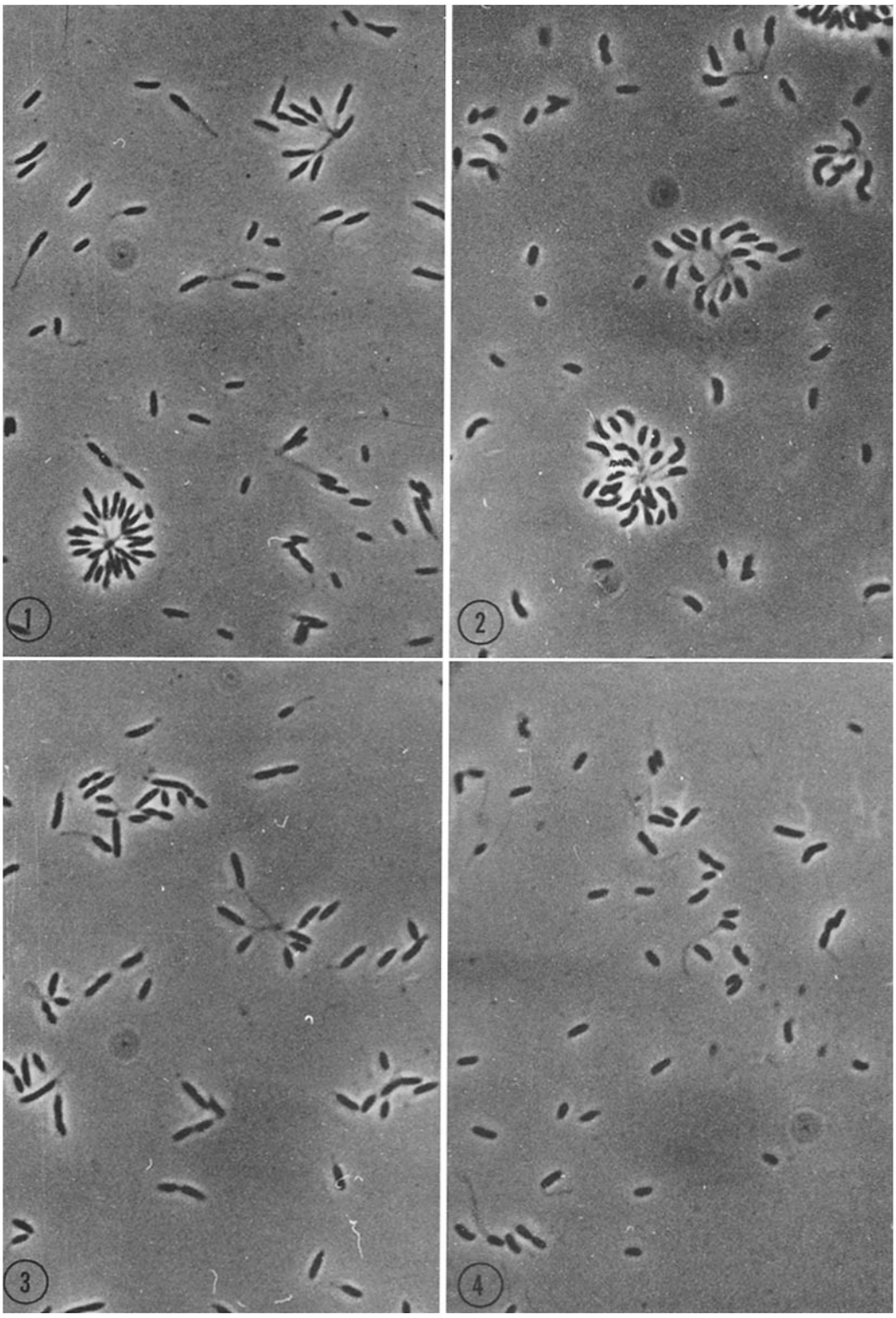
RESULTS

The Genus Caulobacter

The general features of the *Caulobacter* cell are best seen in longitudinal sections of the principal types: *C. bacteroides* (Fig. 5), *C. crescentus* (Fig. 7). and *C. fusiformis* (Fig. 16). The cell wall has the multilayered structure common to many Gram-negative bacteria: there is a wavy, double outer layer, separated by an electron-transparent region from the darkly stained inner layer. Underlying the inner layer of the wall is a typical unit membrane, which invaginates at one or more points in the cell to form mesosomes (8). The origin of a mesosome from the cytoplasmic membrane is particularly clear in Fig. 8. Mesosomes are conspicuous cytoplasmic elements in all the *Caulobacter* strains that we have examined. The granular ribosomal region and fibrillar nucleoplasm constitute the principal internal elements of the cell, as in most bacteria.

Various aspects of the structure of the *Caulobacter* stalk are illustrated in Figs. 5 to 7 and 9 to 15.

FIGURES 1 to 4 Phase contrast photomicrographs of living cells of the four principal morphological types of *Caulobacter*. Fig. 1, *Caulobacter bacteroides*; Fig. 2, *Caulobacter crescentus*; Fig. 3, *Caulobacter fusiformis*; Fig. 4, *Asticcacaulis excentricus*. Note the lateral position of the stalk characteristic of this genus. × 2000.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The outermost layer of the stalk is continuous with the outer, wavy double layer of the cell wall (Figs. 5, 6, 9, 11, and 12), but has a much smoother profile. The densely stained inner layer of the cell wall is clearly visible in the region of the juncture of stalk and extends for a short distance down the stalk (Fig. 5). Its continuation through the length of the stalk is difficult to observe. In this region, it becomes weakly stained, but it can again be seen (heavily stained) in sections through the foot of the stalk (Fig. 15).

The core of the stalk is lightly stained, and never contains either ribosomes or nucleoplasm. In fact, the ribosomal region of the cytoplasm terminates sharply above the juncture of stalk and cell (Figs. 5 to 7, 9, 11, and 12). The narrowing pole of the cell just above the stalk contains an accumulation of internal membranes, which sometimes have the same appearance as a mesosome (compare Figs. 7 and 11). In other sections (*e.g.*, Fig. 5) the membranes of this organelle appear to be arranged more or less parallel to the long axis of the cell and are less distinct than the membranes typical of the mesosome. It seems probable that the core of the stalk consists entirely of material derived from this organelle, enclosed within an extension of the cytoplasmic membrane proper (Figs. 5, 9 to 12).

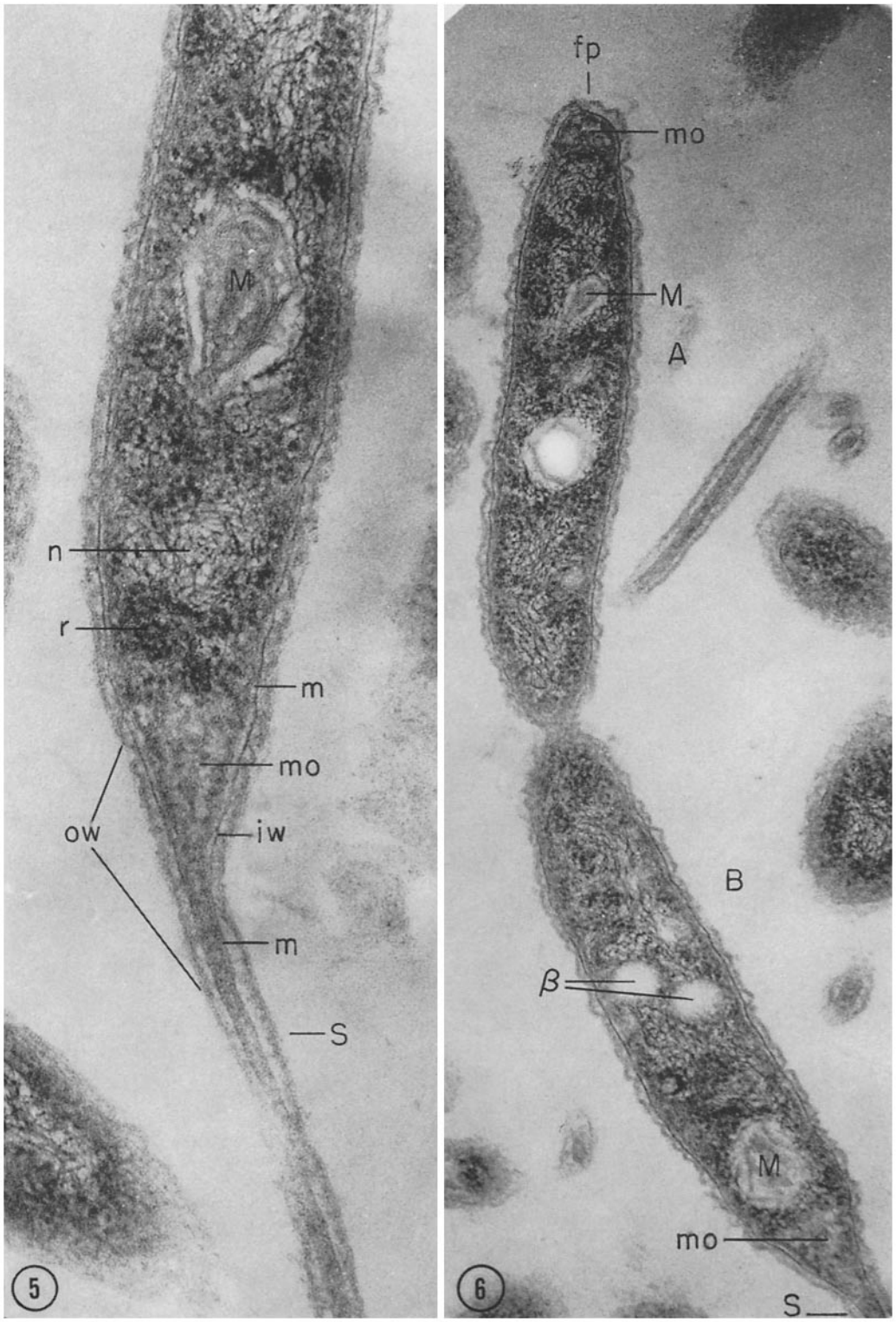
In many sections, the stalk is traversed at irregular intervals by one or more darkly stained cross-bands. These cross-bands (the "Querbalken" of Houwink) had been previously detected in shadowed electron micrographs of stalks (4, 5). As can be seen in Figs. 9, 11, and 12, the cross-bands lie within the external double layer of the wall and can be traced across the width of the stalk. However, they do not interrupt the continuity of the core (Figs. 11 and 12), and can, therefore, be interpreted as electron-opaque annular structures confined to the region of the cell wall, and probably derived from it. Their function is unknown.

The distal region of the stalk terminates in a kind of foot, embedded in the holdfast material. This foot is often slightly wider and more darkly stained than the rest of the stalk (see Figs. 10, 14, and 15). Its greater electron opacity appears to be caused in part by a slight thickening of the wall layers, and in part by the presence of amorphous stained material in the normally transparent region that separates the inner and outer layers of the wall (Fig. 15). This amorphous material may well be the substance of the holdfast in the course of secretion.

The holdfast of *Caulobacter* species is readily recognizable in sections by virtue of its localized accumulation around the distal end of stalks (Figs. 13 to 15). Its extent and form are variable in any given species. The most massive accumulations occur at the center of rosettes (Fig. 15). These rosettes, characteristic of dense *Caulobacter* cultures, are formed by the mutual adhesion of

FIGURE 5 *Caulobacter bacteroides* strain CB11. Longitudinal section of a stalked cell, showing the general features of cell structure and the relation of the stalk to the cell. The wavy outer layer of the cell wall (*ow*) is continuous with the much smoother outer envelope of the stalk. The very densely stained inner layer of the cell wall (*iw*) can be traced to the narrowing juncture between the cell and the stalk, but is not clearly visible in the stalk proper (*S*). Three major structural elements can be seen in the cytoplasm: a large mesosome (*M*), nucleoplasm (*n*), and ribosomes (*r*). A membranous organelle (*mo*) completely occupies the stalked pole of the cell, separating the ribosomal area from the core of the stalk. The core of the stalk appears to be composed of membranous material derived from this organelle enclosed in an extension of the cytoplasmic membrane (*m*). × 105,000.

FIGURE 6 *Caulobacter bacteroides* strain CB11. Thin section which shows a dividing cell cut in the median plane. Note the dissymmetry of the two future daughter cells. The basal cell (*B*) can be identified by its stalk (*S*). The membranous organelle (*mo*) which occupies the stalked pole of the cell is evident. The outer, flagellated pole (*fp*) of the apical cell (*A*) is distinctly narrower than the rest of the cell and contains a membranous organelle (*mo*). Also present are mesosomes (*M*) and clear areas that correspond to deposits of poly-β-hydroxybutyric acid (β). × 70,000.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swarmers, and the resulting coalescence of their individual holdfasts. The physical structure of the holdfast material differs from species to species. In *C. bacteroides* it appears amorphous and darkly stained (Fig. 13); in *C. crescentus*, it is coarsely granular (Fig. 14); in strain CB 66, it appears almost fibrillar (Fig. 15).

Division stages of *Caulobacter* spp. are shown in median section in Figs. 6, 7, and 16. Division appears to proceed by a progressive constriction of the cortical layers of the cell, as is common in many other Gram-negative bacteria; there is never any indication of the formation of a septum. The cytoplasmic region in the area of constriction is very frequently occupied by a large mesosome, which is partitioned between the two daughter cells. Cell division in *Caulobacter* spp. is always asymmetrical, the outer pole of the basal cell bearing a stalk, and the outer pole of the apical cell, a flagellum. As a result, it is often possible to recognize the future swarmer in longitudinal sections of dividing cells, even though the flagellum itself cannot be detected (Figs. 6 and 7). Careful examination of such sections has shown that the differentiation which leads to the development of a stalk has already begun at the flagellated pole of the apical cell, even prior to the completion of cell division. The flagellated pole is distinctly narrowed relative to the rest of the cell (Figs. 6, 13, and 16), and in some cases (Figs. 6 and 13) this narrow polar region contains an internal membranous organelle, no doubt the precursor of the membrane system that will eventually fill the core of the stalk.

The Genus Asticcacaulis

The general features of wall structure and cytoplasmic organization in *Asticcacaulis* are similar to those already described for *Caulobacter* species, and, therefore, need not be discussed. We shall describe only those features which serve to distinguish the two groups of caulobacters: namely, the location and structure of the stalk, the holdfast, and the mode of cell division.

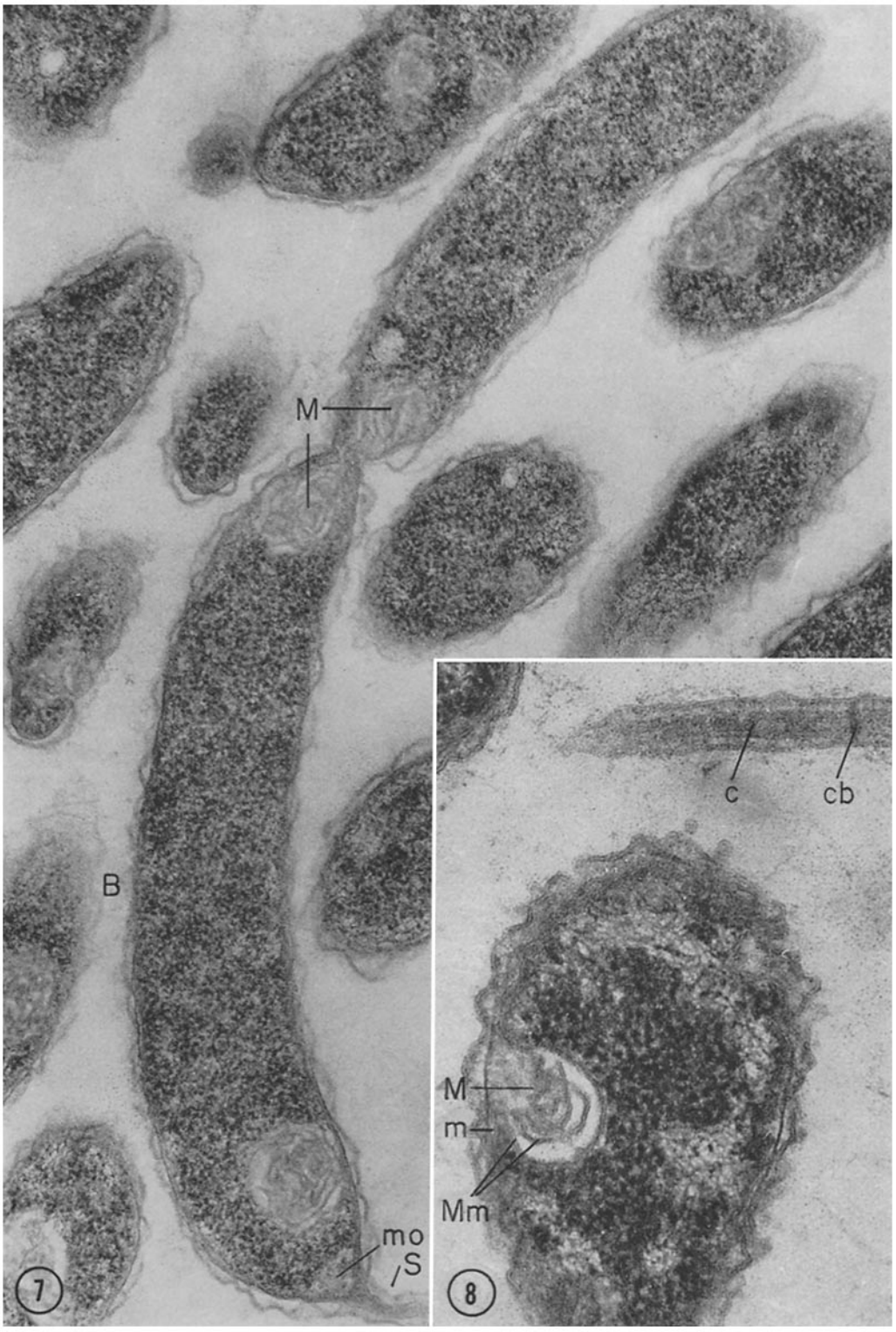
The stalk of *Asticcacaulis excentricus* arises at a subpolar position on the cell, and typically extends laterally from it (Figs. 18 and 20). As in *Caulobacter*, the cytoplasm at the junction of stalk and cell is occupied by a membranous organelle, which is, however, much smaller than that of *Caulobacter*, and hence not easy to detect in sections. It can be seen most clearly in Fig. 20. The stalk itself is structurally homologous with that of *Caulobacter*, containing a membranous core enclosed by an extension of the cell wall (Figs. 18–20, and 28). However, the distal end is unmodified, closely resembling the rest of the stalk in width and structure (Figs. 19, 20, and 28). The lack of distal differentiation in the stalk of *Asticcacaulis* is probably related to the fact that holdfast material is not secreted from the tip, as it is in *Caulobacter*.

The holdfast material, secreted from the pole of the cell at a point adjacent to the site of stalk formation, is shown in Figs. 18 and 21 to 26. The outer layer of the cell wall appears smooth in profile at the site of holdfast formation, and there is typically an accumulation of stainable material between the inner and outer layers of the wall in this region (see Figs. 21, 23, and 24). The underlying cytoplasm does not appear to be differentiated; specifically, there is no accumulation of internal membranes.

Cell division in *Asticcacaulis* is markedly different from that in *Caulobacter*. Firstly, the apical swarmer cell is always much smaller than the basal stalked

FIGURE 7 *Caulobacter crescentus* strain CB15. Thin section which shows a dividing cell cut in the median plane. The basal cell (*B*) is identifiable by its stalk (*S*). A membranous organelle (*mo*) occupies the stalked pole of the cell and separates the ribosomal region from the core of the stalk. Note the large mesosome (*M*) which occupies the site of division. × 66,000.

FIGURE 8 *Caulobacter crescentus* strain CB2. Transverse section, showing the cortical location of a mesosome (*M*) and the connection between the mesosomal membranes (*Mm*) and the cytoplasmic membrane (*m*). In the upper part of the figure a longitudinal section of a stalk shows the membranous structure of the core (*c*) and a darkly stained cross-band (*cb*). × 120,000.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cell at the time of their separation (2). This can be seen in Figs. 17 and 18, which show a median section of a dividing *Asticcacaulis* cell, and should be compared with Figs. 6 and 16, which show a comparable division figure for *Caulobacter bacteroides* and *Caulobacter fusiformis*. As in *Caulobacter*, the area of division is commonly occupied by a large mesosome, which seems to be partitioned between the daughter cells (Figs. 17 and 18). The division of *Asticcacaulis* involves the formation of a septum which seems to arise from the centripetal ingrowth of the inner layer of the cell wall (Figs. 25–27, and 29). As is evident from Figs. 25 and 29, the septum is complete at a time when the double outer layer of the wall still extends uninterrupted across the plane of division; the two daughter cells, physically separated from one another by the septum, are accordingly still bound together by their common outer wall. A very similar type of cell division has been described in another group of Gram-negative bacteria, the photosynthetic organisms of the genus *Chlorobium* (9).

DISCUSSION

The present observations fully confirm the contention of Houwink (4) and Bowers *et al.* (5) that the so-called "stalk" of the caulobacters is a specialized region of the cell. More specifically, we have established that it represents an outgrowth of the cortical layers of the cell: the wall and the cytoplasmic membrane. Ribosomes and nucleoplasm do not extend into the stalk, since these internal components of the cell are separated from the core of the stalk by a membranous organelle similar to a mesosome, which occupies the narrowing juncture between the main body of the cell and the stalk. In members of the genus *Caulobacter*, it is evident that the future stalked pole of the cell is already partly differentiated in the swarmer stage: the flagellated pole of the swarmer is characteristically narrowed relative to the rest of the cell, and often contains a membranous organelle which appears identical to the organelle at the base of the stalk in the mature stalked cell.

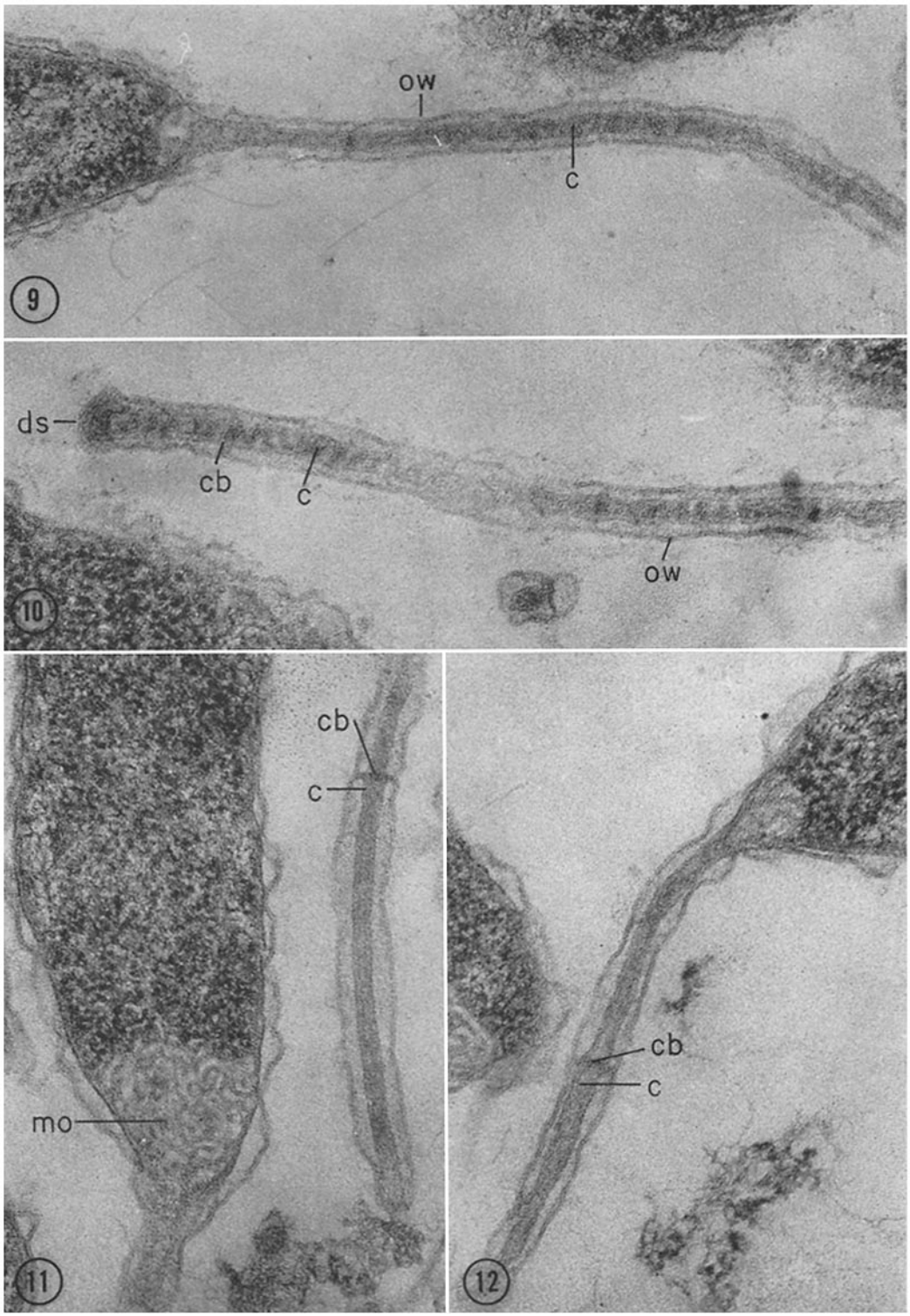
At the site of holdfast formation, the structure of the cell wall is slightly modified. In the genus *Caulobacter*, where the holdfast surrounds the tip of the stalk, the end of the stalk is somewhat enlarged and its surface is thickened. These modifications of the tip of the stalk do not occur in *Asticcacaulis*, where holdfast material is secreted only from the pole of the cell. At the point of secretion in *Asticcacaulis*, the outer layers of the cell wall lose their normal wavy profile, and become smooth.

Although it has been interpreted as an organelle of attachment, the caulobacter stalk clearly does not have this function. Both in *Caulobacter* and in *Asticcacaulis*, attachment is mediated exclusively by the holdfast, and frequently takes place prior to the outgrowth of the stalk. In *Asticcacaulis*, furthermore, the stalk is never associated with the site of attachment, and extends laterally from attached cells. The presence of a stalk markedly reduces the rate of sedimentation of the cell; it is possible to effect an almost complete physical separation of stalked and swarmer cells by centrifugation of a culture at an appropriate speed (2). This observation has led one of us to interpret the stalk as an organelle of flotation (1), functionally equivalent to the filiform cellular appendages that occur on some pelagic diatoms and dinoflagellates.

We wish to acknowledge the skilled technical assistance of Miss Riyo Kunisawa and Miss Paula Finch. We have also received generous help and advice from Dr. J. H. McAlear and his associates on the staff of

FIGURES 9 AND 10 *Caulobacter crescentus* strain CB2. Longitudinal sections of stalks, showing the outer wall (*ow*) and the membranous core (*c*). In Fig. 10, the distal end (*ds*) of the stalk is present in the section. Note its enlargement and greater relative electron opacity. Several rather indistinct cross-bands (*cb*) are present. Fig. 9, × 105,000; Fig. 10, × 120,000.

FIGURES 11 AND 12 *Caulobacter crescentus* strain CB15. Longitudinal sections of stalks showing a particularly large membranous organelle (*mo*) at the base of a stalk (Fig. 11), and two cross-bands (*cb*). Note the continuity of the stalk core (*c*) through the region of the cross-bands. × 105,000.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the Electron Microscope Laboratory, notably Mr. Philip Spencer, who was responsible for the photographic work.

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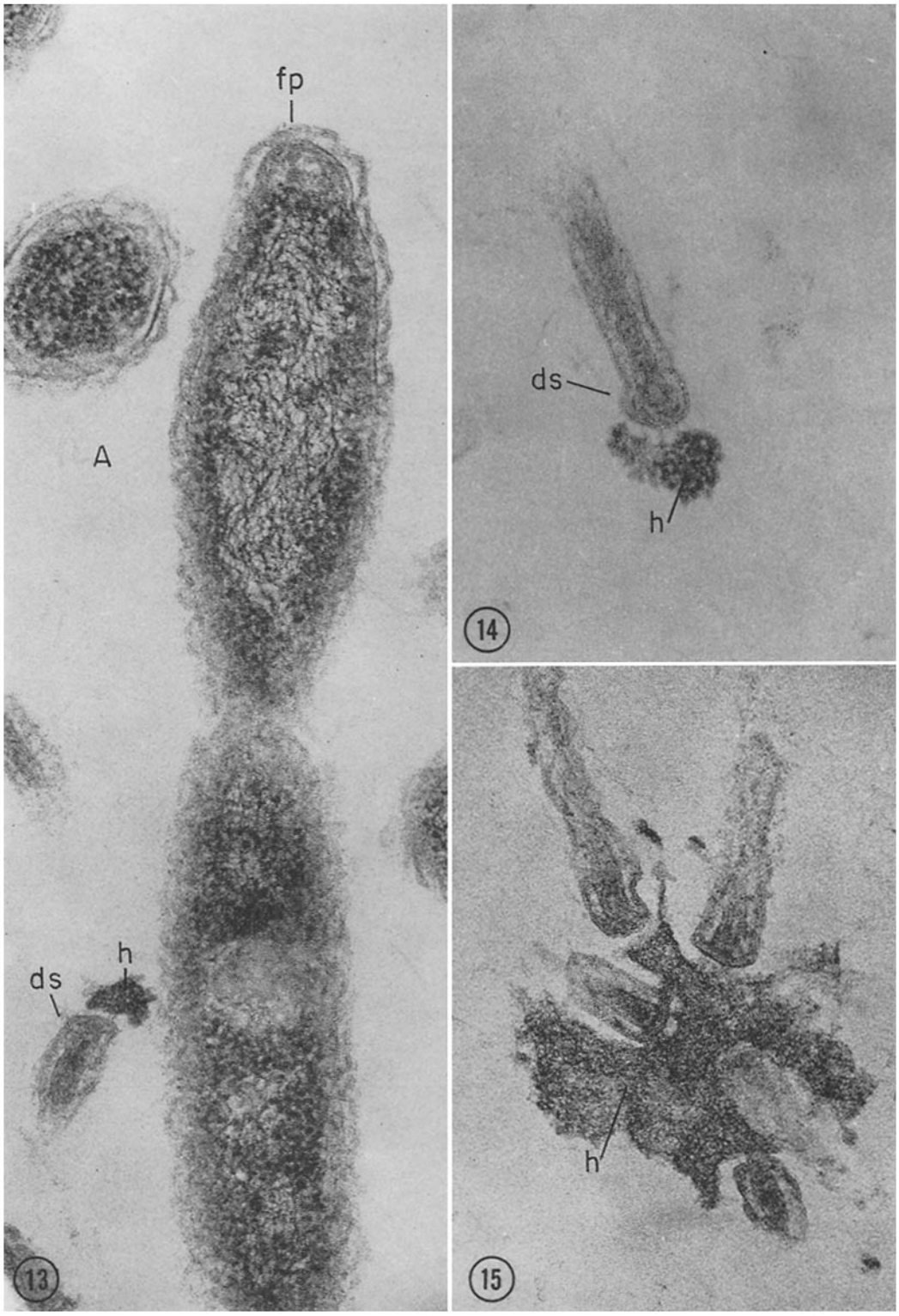
FIGURE 13 *Caulobacter bacteroides* strain CB11. A dividing cell is shown in longitudinal section; the flagellated pole (*fp*) of the apical cell (*A*) shows the differentiation already described in Fig. 6. Also present is the distal end of a stalk (*ds*), with an adjacent, darkly stained holdfast (*h*). × 98,000.

FIGURE 14 *Caulobacter crescentus* strain CB2. Section showing the distal end of a stalk (*ds*) and the holdfast (*h*). Note the enlargement of the stalk at its distal end and the coarse granular structure of the holdfast. × 112,000.

FIGURE 15 *Caulobacter* sp. strain CB66, section through the center of a rosette, showing the distal ends of four stalks attached to a common mass of holdfast material (*h*). Note the relatively heavy staining of both the core and the wall of the stalk at the distal ends, and the close contact between core and wall at the tip. × 112,000.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15

FIGURE 16 *Caulobacter fusiformis* strain CB27. Longitudinal section of a dividing cell. Note the narrowing of the flagellated pole (*fp*) of the apical cell (*A*), and the large mesosome (*M*) in the region of constriction between the apical (*A*) and basal cells (*B*). × 84,000.

FIGURE 17 *Asticcacaulis excentricus* strain AC12. Longitudinal section of a dividing cell, showing the marked disparity in size between the apical cell (*A*) and the basal cell (*B*). The region of cell division is occupied by a large mesosome (*M*). The outer pole (*op*) of the apical cell, which is the future site of holdfast secretion, shows a slight thickening of the inner cortical layers. × 84,000.

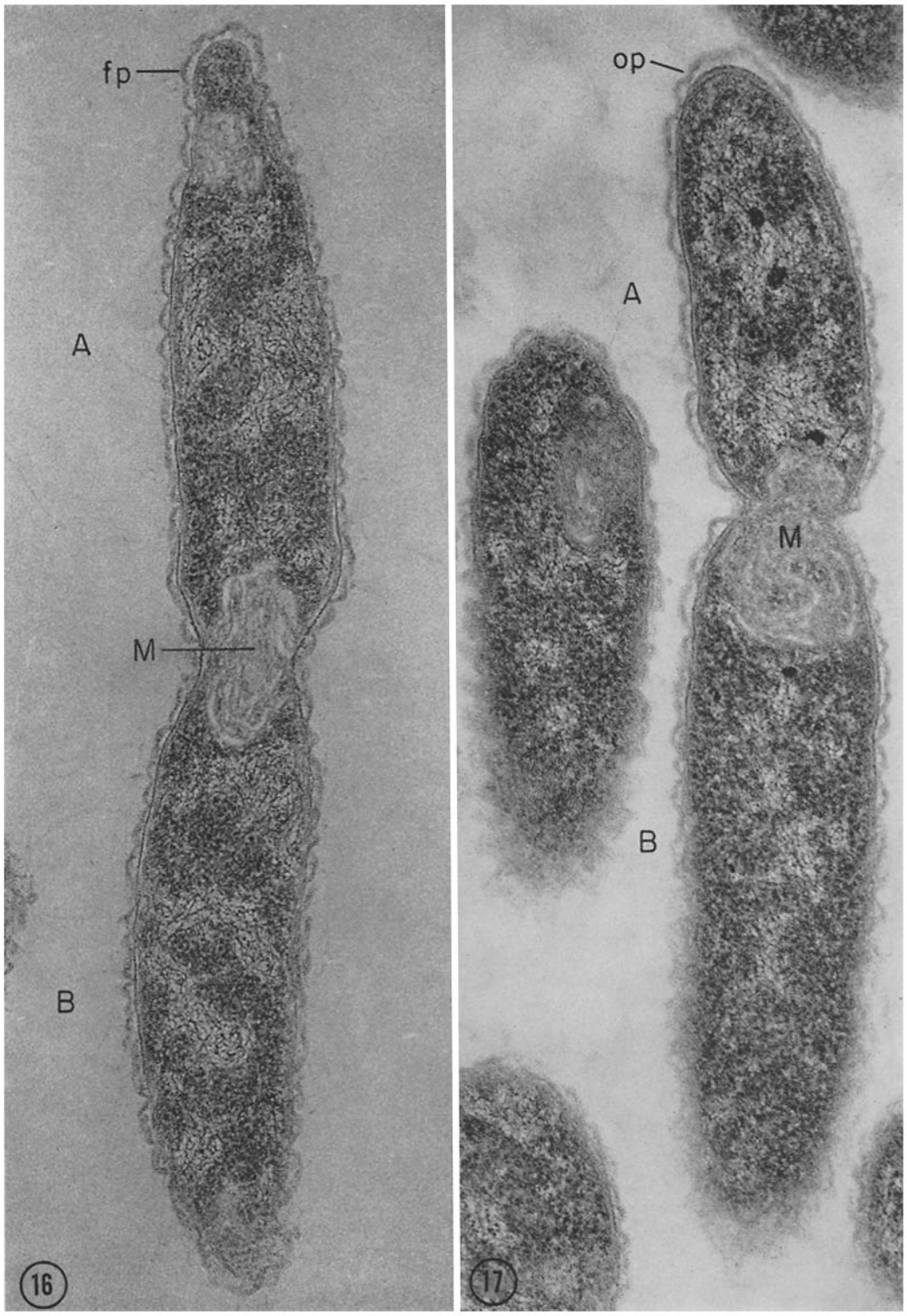
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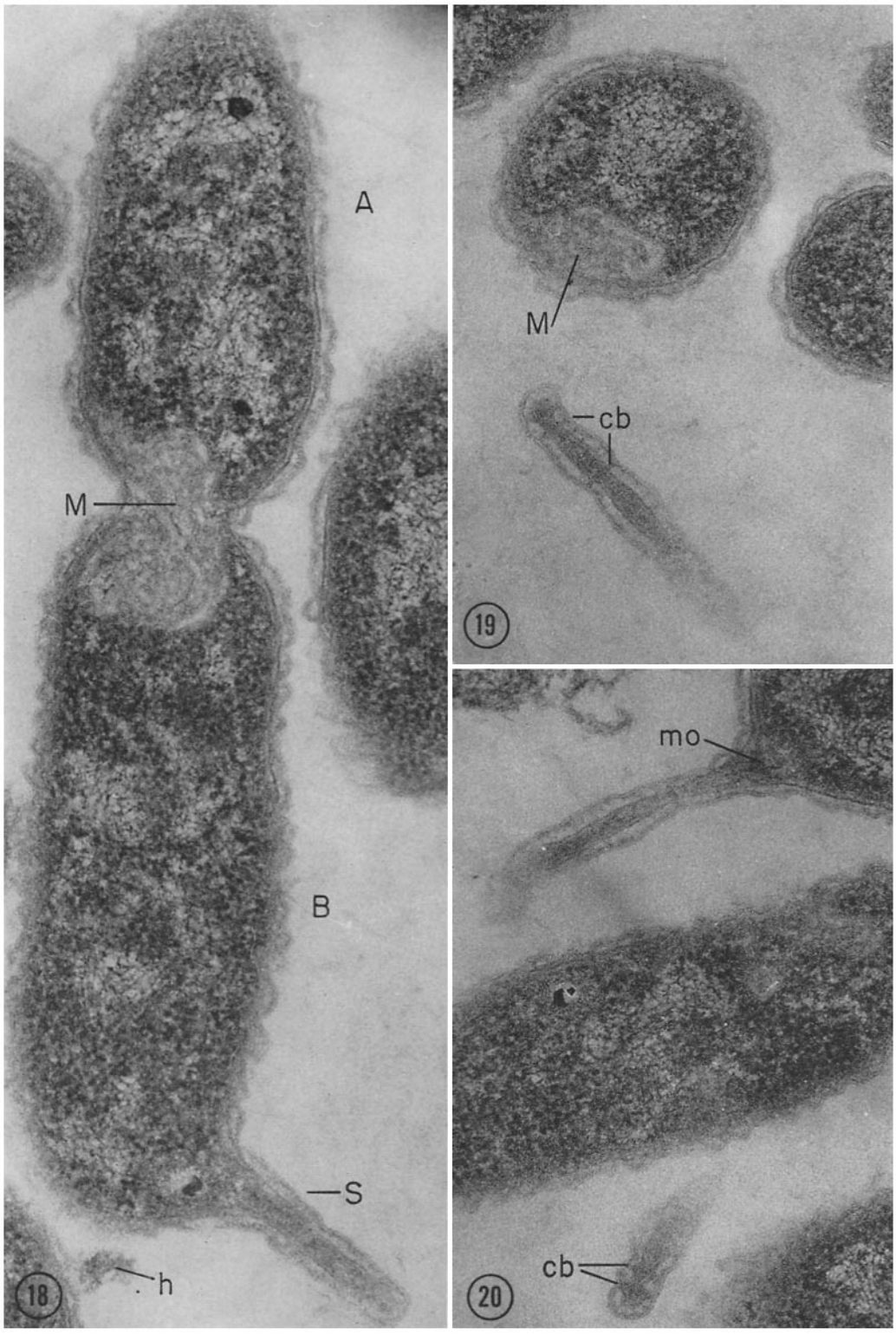
FIGURE 18 *Asticcacaulis excentricus* strain AC12. Longitudinal section of a dividing cell. Note again the marked disparity in size between the apical cell (*A*) and the basal cell (*B*), here clearly recognizable by the presence of a lateral stalk (*S*) and a polar holdfast (*h*). The region of division is occupied by a mesosome (*M*). × 100,000.

FIGURE 19 *Asticcacaulis excentricus* strain AC12. Section showing the distal end of a stalk, which is not differentiated in the fashion characteristic of *Caulobacter* spp. Several cross-bands (*cb*) are evident. Note also the laterally located mesosome (*M*) in a cross-section of a cell. × 100,000.

FIGURE 20 *Asticcacaulis excentricus* strain AC12. Section showing the proximal end of a stalk and its juncture with the cell. As in *Caulobacter* spp, a membranous organelle (*mo*) occupies the cytoplasm at the point of origin of the stalk. In the lower part of the figure, the typical undifferentiated distal end of a stalk containing two cross-bands (*cb*) can be seen. The slight constriction of the stalk at or near the site of cross-band occurrence is also visible in Fig. 19. × 100,000.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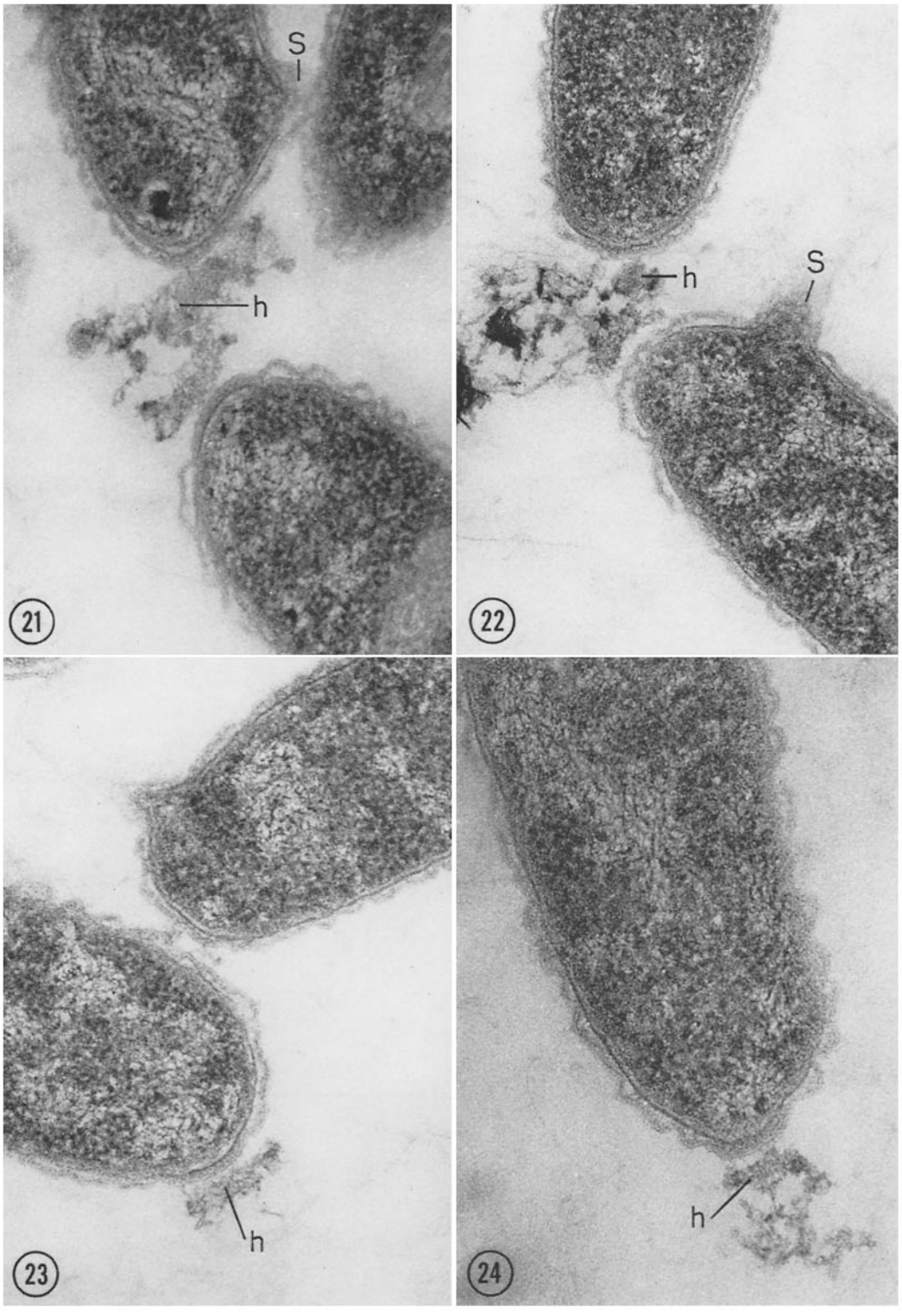
FIGURES 21 AND 22 *Asticcacaulis excentricus* strain AC12. Two sections through the base of rosettes, showing the common holdfast material (*h*) lying between two component cells of the rosette. In each figure, the origin of the stalk (*S*) as a lateral appendage is visible in one of the cells. The characteristic modification of the cortical layers of the cell at the site of holdfast secretion is evident in both cells of Fig. 21 and in the upper cell of Fig. 22. In this region, the outer layer of the cell wall is smooth in profile and electron-opaque material (possibly holdfast material) fills the space between the outer and inner layers of the cell wall. × 100,000.

FIGURES 23 AND 24 *Asticcacaulis excentricus* strain AC12. Sections through the poles of cells showing the relationship between the cell and the holdfast (*h*). Note the characteristic modification of the cell wall in the region of holdfast secretion. Fig. 23, × 100,000, Fig. 24, × 125,000.


S
h
21
h
S
22
h
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24

FIGURES 25 AND 26 *Asticcacaulis excentricus* strain AC12. Two longitudinal sections through dividing cells: in each case, the basal cell (*B*) can be identified by its larger size and by the conspicuous holdfast (*h*) secreted at its outer pole. In Fig. 25, the two daughter cells are separated by a septum (*s*) which appears to be continuous with and derived from the inner layer of the cell wall (*iw*). The outer layer of the cell wall (*ow*) extends uninterrupted across the plane of division, although it is somewhat constricted in this region. In Fig. 26, a septum (*s*) can also be seen, although its structure and origin are less distinct than in Fig. 25. A large mesosome (*M*) occupies the region of division and appears to have been bisected by the septum. Fig. 25, × 100,000; Fig. 26, × 112,000.

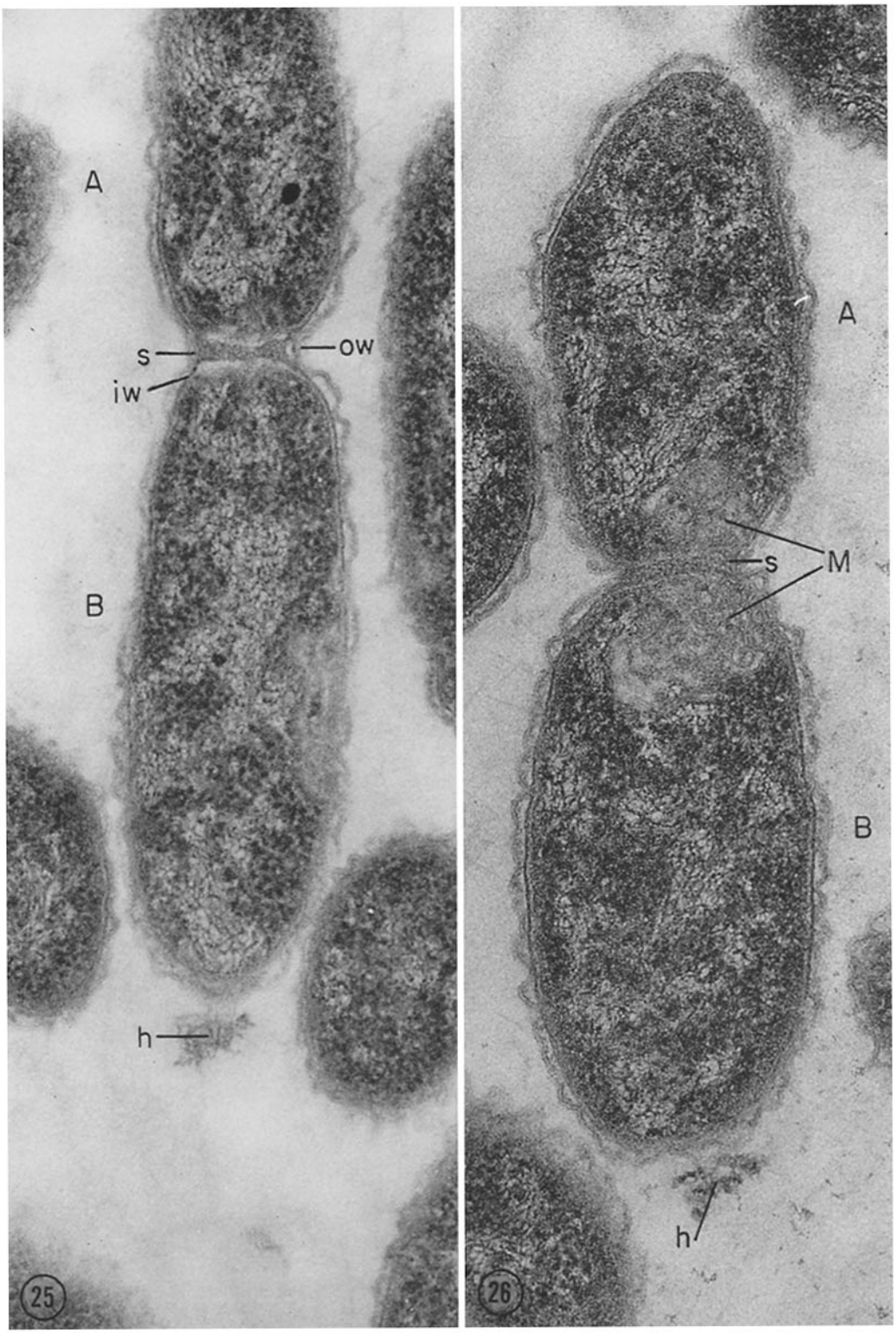
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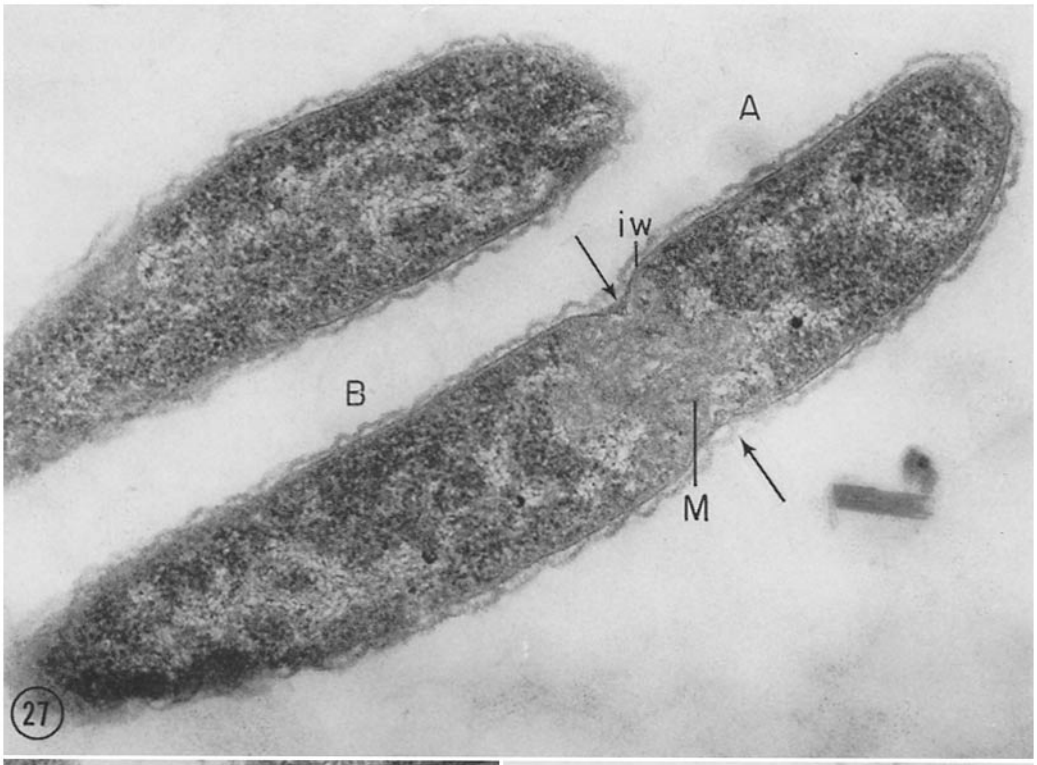
FIGURE 27 *Asticcacaulis excentricus* strain AC48. Longitudinal section of a cell at an early stage in division, showing the thickening and intrusion of the inner layer of the wall (*iw*) at the plane of future division (arrows). A large mesosome (*M*) occupies this area. Note difference in size between apical (*A*) and basal (*B*) cells. × 70,000.

FIGURE 28 *Asticcacaulis excentricus* strain AC48. Longitudinal section of a typical stalk (*S*) showing its lateral origin and its undifferentiated tip. × 70,000.

FIGURE 29 *Asticcacaulis excentricus* strain AC48. Section through a dividing cell showing a septum (*s*) closely similar to that shown for strain AC12 in Fig. 25. × 70,000.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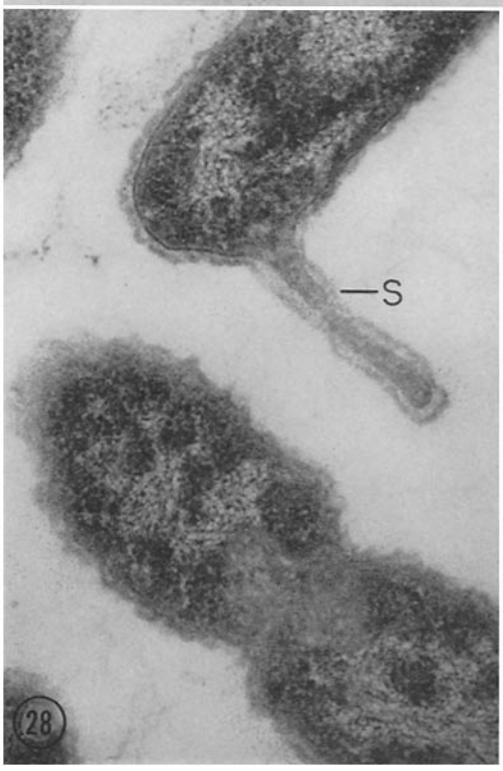
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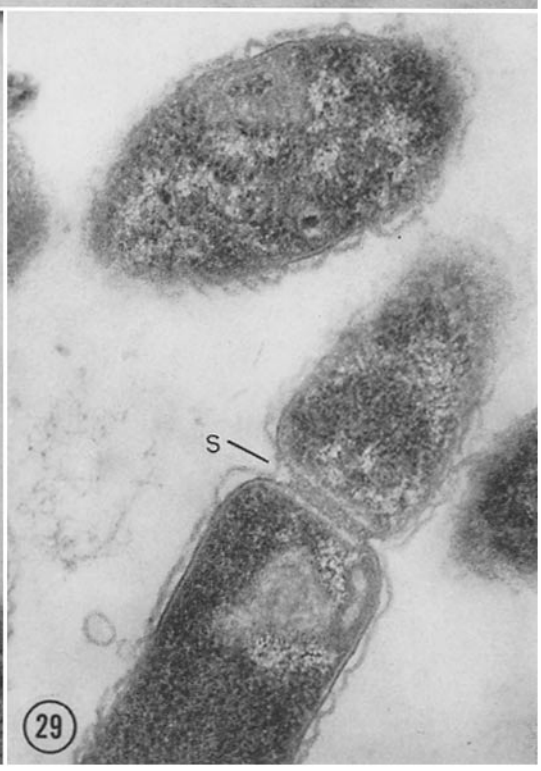
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