MICROTUBULES AND CONTROL OF INSECT EGG SHAPE

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ABSTRACT

This study provides evidence for tension transmission by microtubules and desmosomes in the follicular epithelium during anisometric growth of certain insect eggs. Most insect oocytes, and the follicles which surround them, grow anisometrically as they assume shapes which approximate to those of long prolate spheroids. Surface growth is most rapid in directions which parallel the polar axis of an oocyte and slowest in circumferential directions at right angles to this axis. The longitudinal axes of microtubule bundles in follicle cells of the gall midge *Heteropeza* and the cockroach *Periplaneta* are oriented circumferentially with respect to the surfaces of developing eggs and at right angles to the polar axes of eggs. At cell boundaries, the tubules appear to be attached to spot desmosomes. It is suggested that microtubules and desmosomes form a mechanical continuum throughout a follicular epithelium which transmits tensile forces around the circumference of a growing egg. Follicular resistance to circumferential expansion may be largely responsible for defining the elongate form of insect eggs.

Most insect oocytes are initially more or less spherical in shape. As they grow, they usually become more elongate and spheroidal. Examination of elongating cells from a variety of organisms has usually revealed that they include large numbers of microtubules, the longitudinal axes of which are oriented parallel to the longitudinal axes of the cells (for example, references 4, 6, 25, 30). Elongation usually ceases if the cells are treated with colchicine; their microtubules break down and the cells often revert to a spherical shape (13, 18, 21, 29). In some cases, they elongate again after treatment as the microtubules reassemble (2). There is little doubt that the tubules have a skeletal role and are largely responsible for defining cell shape in these instances. However, there are no reports of microtubules running along the lengths of elongating insect oocytes. Such oocytes are surrounded by a follicular epithelium. The account which follows investigates the possibility that the shape of an insect egg is largely determined by forces imposed on it from outside by a skeleton of microtubules and desmosomes located in its follicle. This study raises the possibility that oriented microtubule arrays may transmit forces *between*, as well as within, the cells of an epithelium.

Egg growth has been examined for two markedly different modes of insect oogenesis. Development of the eggs of the cecidomyiid dipteran *Heteropeza* and the dictyopteran *Periplaneta* has been studied. A syncytial nurse chamber which supplies nutrients is included in each follicle alongside an oocyte at the start of the growth of the polytrophic eggs of *Heteropeza*. In addition, *Heteropeza* larvae have been maintained under conditions in which they reproduce paedogenetically and parthenogenetically. Their oocytes and follicles undertake most of their growth in the larval hemocele after release from the ovaries (19). The panoistic eggs

of *Periplaneta* do not possess a nurse chamber or nurse cells and remain in the ovarioles throughout growth.

MATERIALS AND METHODS

Female *Heteropeza pygmaea* larvae were obtained from Mr. I. J. Wyatt (Glasshouse Crops Research Institute, Littlehampton, Sussex, England). Paedogenetic female larvae were cultured at 25°C in Petri dishes containing a sterile medium of 3% (aqueous) agar and 3% malt extract. The mould *Stereum purpureum* was supplied as food source. Dishes were inoculated with *S. purpureum* 1 week before the introduction of larvae.

Heteropeza oocytes, eggs, and embryos, together with the follicles which surround them, were teased out of the hemoceles of living larvae with tungsten needles. They were mounted in a physiological saline (31) on microscope slides and beneath cover slips supported at their corners by drops of silicone grease to prevent compression and flattening of follicles and their contents. The lengths and diameters of follicles isolated in this way were measured with a Carl Zeiss Universal microscope fitted with a micrometer eyepiece. Oocytes were fixed in a 3:1 mixture of absolute ethanol and glacial acetic acid before Feulgen staining. Follicle cell boundaries were stained with silver, using the same method as that employed for demonstrating the cortical "silver-line-system" of ciliates (8). Larvae were immersed in a glutaraldehyde fixative; follicles and their contents were teased out and prepared for electron microscopy as described elsewhere (26).

Cockroaches (*Periplaneta americana*) were supplied by Mr. J. Stevenson (Gatty Marine Laboratory, St. Andrews, Scotland). Oocytes and their follicles were studied using the procedures outlined above. Ovaries for electron microscopy were dissected from the insects immediately after decapitation and were placed in a glutaraldehyde fixative.

RESULTS

Heteropeza Eggs and their Follicles

GROWTH OF EGGS AND FOLLICLES: Oocytes and their follicles are released from ovaries into the hemocele at an early stage of growth and vitellogenesis. The germinal vesicle in each oocyte undertakes a maturation division shortly afterwards. This event marks the transition from the oocyte stage to the egg stage. When release occurs, the follicle is slightly ovoidal in shape and surrounds two relatively large cells. One of the cells, the *egg chamber* (*e*), contains the germinal vesicle (*g*). The other cell is the *nurse chamber* (*n*) which includes 3–7 polyploid nuclei (Fig. 1). As the egg grows, the contents of the nurse chamber are apparently resorbed by the egg chamber which finally occupies the whole of the space surrounded by the follicle.

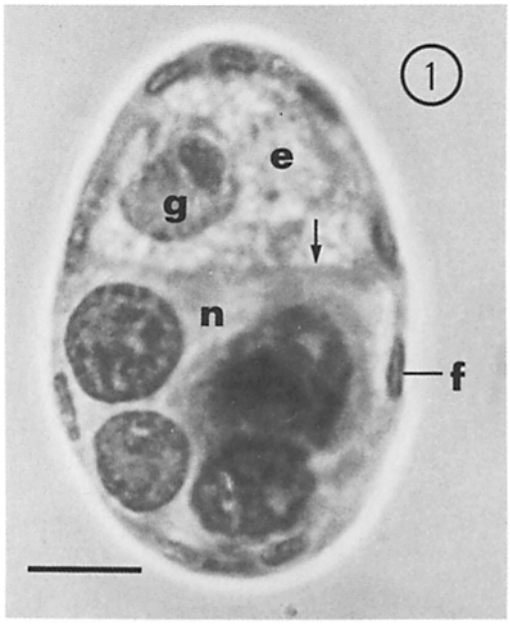


FIGURE 1 Lateral view of a Feulgen-stained *Heteropeza* oocyte and its follicle. The oocyte was fixed shortly after release from the ovary. The germinal vesicle (*g*) is situated in the egg chamber (*e*). The nurse chamber (*n*) contains several polyploid nuclei. The partition which separates the two chambers is indicated by the arrow. Several follicle cell nuclei (*f*) are also apparent. Phase contrast. × 1,500. Bar = 10 μm.

Most insect eggs reach their final sizes before fertilization and the subsequent events which lead to blastoderm formation. The parthenogenetic eggs of female *Heteropeza* larvae grow continuously (19). The first pole cell forms when eggs and their follicles are about 95 μm long; blastoderm formation proceeds as eggs lengthen from 100 to about 180 μm. The morphogenetic movements associated with anterior migration of pole cells start when embryos are about 200 μm long. The follicular epithelium remains intact, surrounding the oocyte, subsequently the egg, and finally the embryo, throughout these events. It does not secrete a chorion or vitelline membrane.

The diameters (measured at their widest points and at right angles to the polar axis) and lengths of follicles have been measured from the time at which they are released from ovaries until they reach lengths of 350 μm. During this period, three growth phases can be distinguished. During the first phase, follicle length and circumference in-

crease at about the same rate. In the second phase, elongation continues, but circumference decreases. Throughout the third phase, circumference increases again but less rapidly than length (Fig. 2).

The single layer of flattened follicle cells forms a pavement epithelium which is fairly closely applied to the surface of the egg and nurse chambers, and later to the blastoderm of the embryo. The cell boundaries where adjacent follicle cells abut are not apparent when freshly isolated follicles are examined by phase-contrast or differential interference-contrast microscopy. A polygonal lattice on the outer surface of the follicle can be stained with silver (see Materials and Methods) (Figs. 3, 4). Such lattices are present before blastoderm formation begins (blastoderm cells do not stain with silver). The "silver lines" of the lattice mark the follicle cell boundaries and reveal the shapes and sizes of the cells. A follicle shortly after release from the ovary is composed of about 14 cells. When an embryo and its follicle reach a length of about 250 μm, there are about 100 follicle cells. The cells have surface areas which are three or four times greater than those of cells which surround freshly released oocytes (cf. Figs. 3, 4).

FOLLICULAR MICROTUBULES AND DESMOSOMES: The follicular epithelium grows more rapidly in directions which parallel the follicle's polar axis than it does in directions which parallel follicle circumference throughout the second and third phases of follicle growth. During these two growth phases, follicle cells contain considerable numbers of microtubules. Most of the tubules are situated close to the *outer surfaces* of the cells (the surfaces most distant from the egg or embryo). They are oriented so that their longitudinal axes run more or less circumferentially around the follicle at right angles to its polar axis (Fig. 5). A few tubules are situated at other levels in the cells. Some of these are randomly oriented; others are associated with belt desmosomes (see below), and the remainder run parallel to the follicle's polar axis. For example, when follicles reach

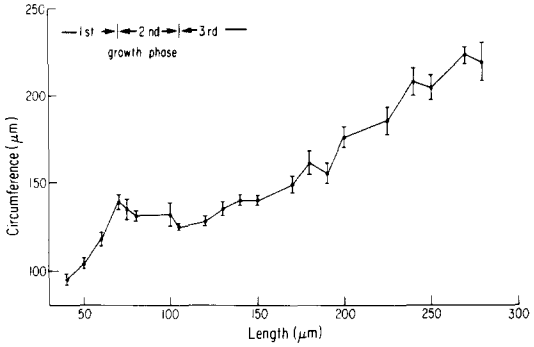


FIGURE 2 Graph showing changes in length and circumference for *Heteropeza* egg follicles during the three growth phases. The black dots show the mean values of samples (of at least five follicles each), and the vertical lines show the standard errors of the means. It was not possible to follow the growth of individual follicles because growth ceases when follicles are removed from larvae for measurement.

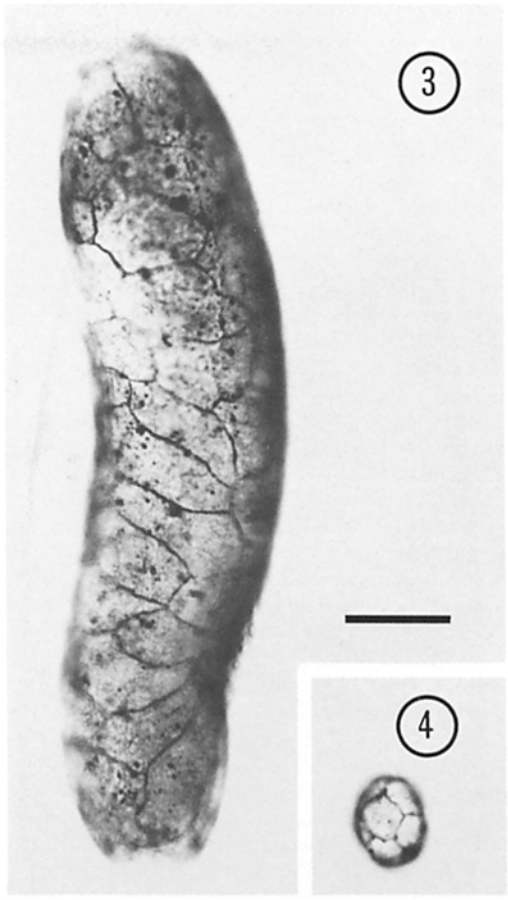


FIGURE 3 Lateral view of a silver-stained *Heteropeza* follicle which was fixed during the third growth phase. The network of silver lines shows where the edges of adjacent cells meet each other. × 470. Bar = 30 μm.

FIGURE 4 Lateral view of a silver-stained *Heteropeza* follicle which was fixed during the first growth phase. Magnification is the same as for Fig. 3.

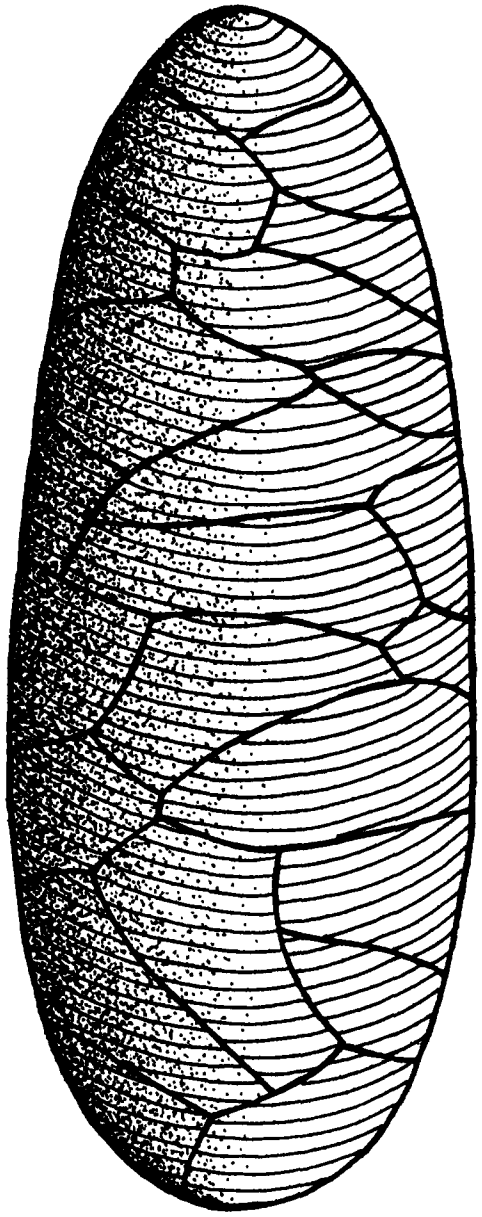


FIGURE 5 Diagrammatic lateral view of a *Heteropeza* egg follicle showing the arrangement of follicle cell boundaries (thick black lines) and the layout of the meshwork formed by belt desmosomes which follow these boundaries. The thin lines indicate the courses followed by circumferentially oriented microtubules situated just beneath the outer surfaces of follicle cells.

lengths of about 200 μm, each cell has about 300 circumferentially oriented tubules and about 40 running parallel to the polar axis.

During the first growth phase, while a follicle's length increases at the same rate as its circumference, its cells contain few microtubules. The tubules' longitudinal axes are more or less parallel to the inner and outer surfaces of the cells but otherwise appear to be randomly oriented. Throughout the second and third growth phases, circumferentially oriented tubules (*m*) mostly occur in small groups of 2–5 tubules just beneath the cell membrane (*c*) at the outer surfaces of follicle cells (Fig. 6). Often a strip (*d*) of densely staining material is associated with the cell membrane in regions where tubules are present (Fig. 6). Like the tubules, these strips are oriented circumferentially (Fig. 12). Whether strips run right across the cells has not been ascertained. Fine dense links or bridges (arrow) appear to connect tubules (*m*) to the strips (*d*) (Fig. 6).

Throughout the three growth phases, a single layer (about 9 nm thick) of secreted material covers the follicle. This basement lamina, the tunica propria (*t*), lies close to the outer surfaces of follicle cells (Figs. 6, 10, 11).

Throughout the first growth phase, follicle cells are not connected by specialized cell junctions. During the second and third growth phases, they are joined by septate junctions (*j*) at many points (Fig. 8). In addition, two types of attachment desmosomes (maculae adherentes) are situated at certain levels. *Belt desmosomes* (22) are positioned where the inner surfaces (those closest to the egg or embryo) of adjacent cells meet each other (Fig. 8, *b*). A belt desmosome runs around the inner boundary of every follicle cell. Microtubules (*m*) run alongside the belt desmosomes (*b*) and are apparently joined to them by bridges (arrow) (Figs. 7, 8). *Spot desmosomes* (22) are situated near the outer surfaces of cells. Each one is a short strip (*s*) rather than a long continuous belt and is often positioned close to circumferentially oriented microtubules (*m*) (Figs. 9, 11). Fine strands of dense material appear to connect these tubules to spot demosomes. As is the case for belt desmosomes, microtubules (*m*) run alongside spot desmosomes with their longitudinal axes parallel to the longitudinal axes of the desmosomes (*s*) (Fig. 11). The way in which tubules terminate has not been ascertained. No definite indications that tubule tips abut against desmosomes or the cell membrane were obtained.

Short processes extend from follicle cells near their outer surfaces. The processes of adjacent cells overlap each other and interdigitate (Fig.

11). Sequences of sections oriented either parallel to, or at right angles to, the polar axes of follicles reveal that most of these processes are oriented circumferentially and at right angles to the polar axes. Circumferentially oriented microtubules (*m*) extend into the processes and are sometimes situated against spot desmosomes (*s*) which run along the sides of the processes (Figs. 11, 13). A process (*p*) is often joined to an adjacent cell by patches (arrow) of densely staining material which connect the surface membranes of adjacent cells; circumferentially oriented microtubules (*m*) sometimes appear to be linked to the patches (Fig. 10). The fine structural appearance of patches (arrow) differs from that of spot desmosomes (*s*) (cf. Figs. 9, 10). Whether patches represent poorly preserved spot desmosomes has not been determined.

Although large numbers of well preserved microtubules have been found in dividing egg nuclei (12) and in follicle cells, very few have been detected in the egg chamber cytoplasm during the early stages of egg elongation. Those that are present are not packed together in bundles and appear to be randomly oriented. After an egg has reached a length of about 100 μm, and blastoderm formation has started, considerable numbers of microtubules are present near the periphery of the egg. As in *Drosophila* eggs (11), many of these lie alongside blastoderm nuclei; they are oriented radially with respect to the egg's polar axis and parallel to furrows in the egg surface membrane. Peripheral to the level at which these nuclei are situated, tubules are not oriented with respect to the polar axis; some of them radiate from the environs of centrioles.

The longitudinal axes of many follicle cells are oriented more or less circumferentially and roughly parallel to the orientation of most of the microtubules in the cells (Figs. 3, 5), although the follicular epithelium is expanding most rapidly in a direction at right angles to this orientation. This may be an indication that most cleavage furrows are oriented circumferentially when the cells divide.

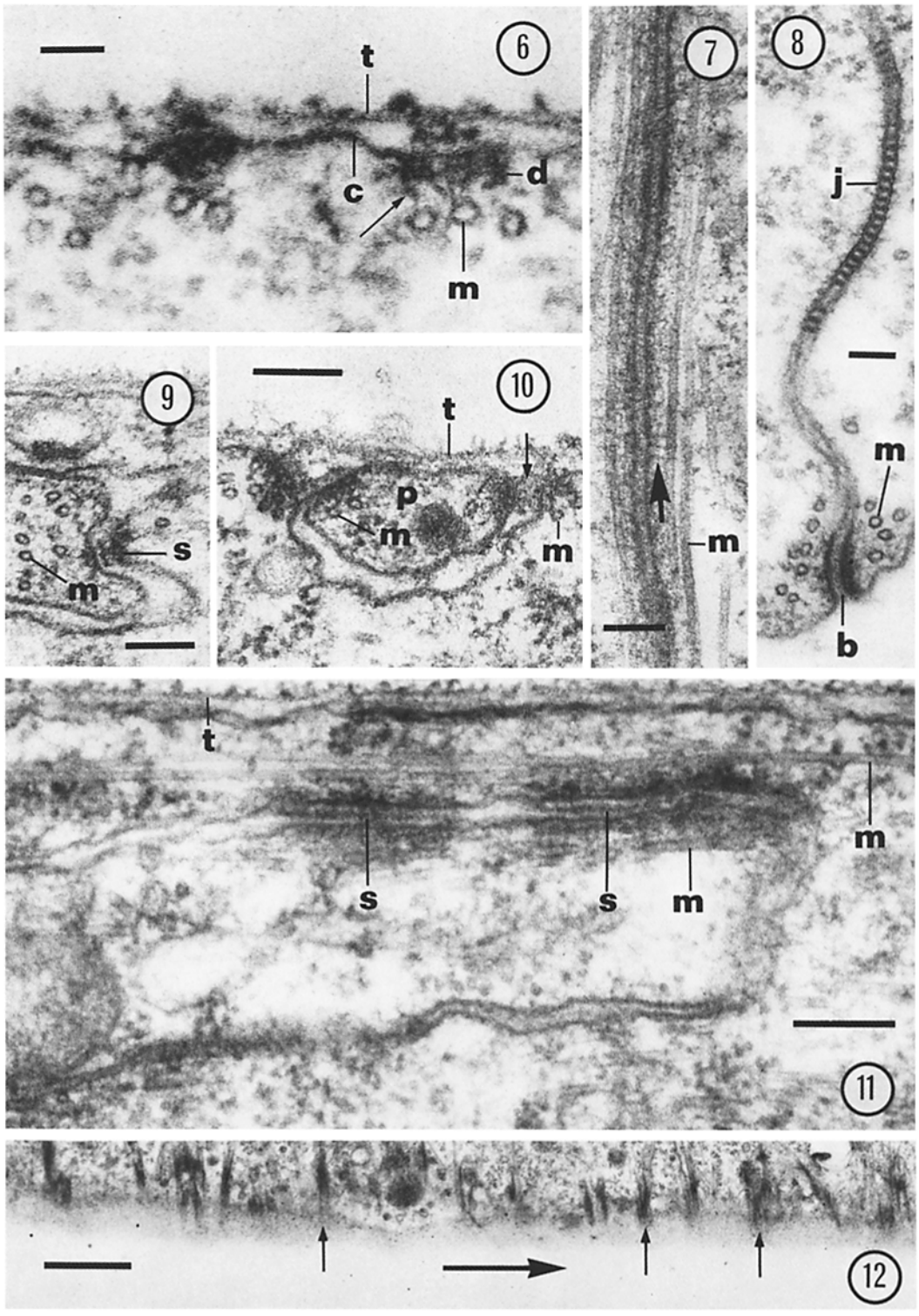
The inner surfaces of follicle cells are closely applied to the egg surface throughout the first growth phase and during the initial stages of the second growth phase. After this, they are separated from the surface of the egg, and later the embryo, by a liquid-filled space. Microvilli project into this space from the inner surfaces of follicle cells. Since liquids are relatively incompressible, any anisometric mechanical resistance to expansion on the part of the follicle could be transmitted and influence the shaping of the egg or embryo inside it.

Cockroach Egg-Follicle Microtubules and Desmosomes

Growth of cockroach oocytes is completed while they are contained in ovarioles. Near the anterior end of an ovariole, just posterior to the germarium, oocytes are closely juxtaposed in a single linear array. The length of each roughly cylindrical or disc-shaped oocyte is less than its diameter (Fig. 14). Oocytes grow anisometrically and elongate as they pass (posteriorly) down the ovariole (Fig. 15). Their lengths increase more rapidly than their circumferences (measured at their widest points along their polar axes). No region of an ovariole includes oocytes with diameters smaller than those of oocytes at an earlier stage of growth. Hence, a circumferential contraction like that described above for *Heteropeza* apparently does not occur during elongation of cockroach oocytes.

The fine structure of anisometrically growing oocytes and their follicles with lengths of 200–300 μm have been examined. The follicles of adjacent oocytes contact one another. A follicle consists of a single layer of cells where it surrounds the sides of an oocyte. Near the poles of oocytes, the layer is several cells deep where it forms *plugs* (9) separating the poles of adjacent oocytes. A tunica propria is situated against the outer surfaces of follicle cells. It is secreted by cells positioned at the sides of oocytes and forms a long hollow tube (tapering anteriorly) which surrounds the ovariole along most of its length. The tunica propria (*t*) has a laminated appearance (Fig. 16). Longitudinal and cross sections of cockroach follicles show that at the ultrastructural level the tunica propria definitely has a layered composition rather than a fibrous one.

Oocytes contain very few microtubules. These are not grouped in bundles and appear to be randomly oriented. By contrast, follicle cells contain large numbers of tubules (*m*); these are situated near the outer surfaces of cells which cover the sides of oocytes (Fig. 16). Some of the tubules occur singly; others are grouped together in bundles of varying sizes (Fig. 17). The longitudinal axes of nearly all the microtubules run circumferentially around a follicle at right angles to the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polar axis of the elongating oocyte. A certain amount of material which appears to have a finely particulate or fibrous composition is associated with the microtubule bundles (Fig. 17).

The outer surfaces of adjacent follicle cells overlap and interdigitate to some extent. Whether such interdigitations are circumferentially oriented has not been established. Adjacent follicle cells are joined together by spot desmosomes near their outer surfaces. Circumferentially oriented microtubules (*m*) are often situated on either side of spot desmosomes (*s*) and appear to be connected to them by strands of dense material (Fig. 18). Belt desmosomes have not been detected near the inner surfaces of the cells where their surface membranes form complex arrays associated with the layer of bacterial symbionts which surrounds each oocyte (1).

DISCUSSION

Influence of Follicle Cell Microtubules on Egg Growth and Shaping

The results presented above indicate that insect oocytes grow anisometrically and become spheroidal in shape because their follicles resist expansion anisometrically. The arrangement of microtubules and spot desmosomes in the follicles of *Heteropeza* and *Periplaneta* is such that they probably form a mechanical continuum capable of transmitting tensile forces throughout the follicular epithelium. This may provide greater resistance to circumferential expansion than to elongation of the follicle parallel to its polar axis. If this is the case, and if a growing oocyte tends to put the follicular epithelium under a certain amount of tension, an

FIGURE 6 Part of the outer surface of a *Heteropeza* follicle cell. The section was cut at right angles to the outer surface and parallel to the polar axis of the follicle. Circumferentially oriented microtubules (*m*) are connected by strands of dense material (arrow) to dense strips (*d*) which are attached to the cell membrane (*c*). The tunica propria (*t*) lies against the cell membrane. × 208,000. Bar = 50 nm.

FIGURE 7 Longitudinal section through part of a belt desmosome joining the inner surfaces of *Heteropeza* follicle cells. Microtubules (*m*) run alongside the desmosome and are joined to it by fine strands of dense material (arrow). × 70,000. Bar = 200 nm.

FIGURE 8 Section through part of a *Heteropeza* follicle where adjacent cells are joined at, and near, its inner surface by a septate junction (*j*) and a belt desmosome (*b*). Microtubules (*m*) are joined to the desmosome by fine strands of dense material. × 83,000. Bar = 100 nm.

FIGURE 9 Part of the outer surface of a *Heteropeza* follicle where adjacent cells overlap and interdigitate. The plane of the section is oriented perpendicular to the surface of the follicle and parallel to its polar axis. Some of the circumferentially oriented microtubules (*m*) are joined to a spot desmosome (*s*) by strands of dense material. × 75,000. Bar = 200 nm.

FIGURE 10 Part of the outer surface of a *Heteropeza* follicle. Section orientation as in Fig. 9. A circumferentially oriented process (*p*) from one cell extends into a surface depression in an adjacent cell. Some of the circumferentially oriented microtubules (*m*) run closely alongside patches of dense material (arrow) which appear to connect the two cells together. The tunica propria (*t*) is also shown. × 80,000. Bar = 200 nm.

FIGURE 11 Part of the outer surface of a *Heteropeza* follicle where two adjacent cells overlap and interdigitate. The plane of the section is oriented perpendicular to the surface of the follicle and the follicle's polar axis. The cells are joined by two spot desmosomes (*s*). Circumferentially oriented microtubules (*m*) run alongside the desmosomes and appear to be connected to them by strands of dense material. The tunica propria (*t*) lies against the follicle's outer surface. × 90,000. Bar = 200 nm.

FIGURE 12 Section grazing through part of the outer surface of a *Heteropeza* follicle cell. The dense strips which are positioned just beneath the cell membrane are oriented at right angles (as indicated by short arrows) to the polar axis of the follicle (the long arrow is parallel to this axis). × 15,300. Bar = 1 μm.

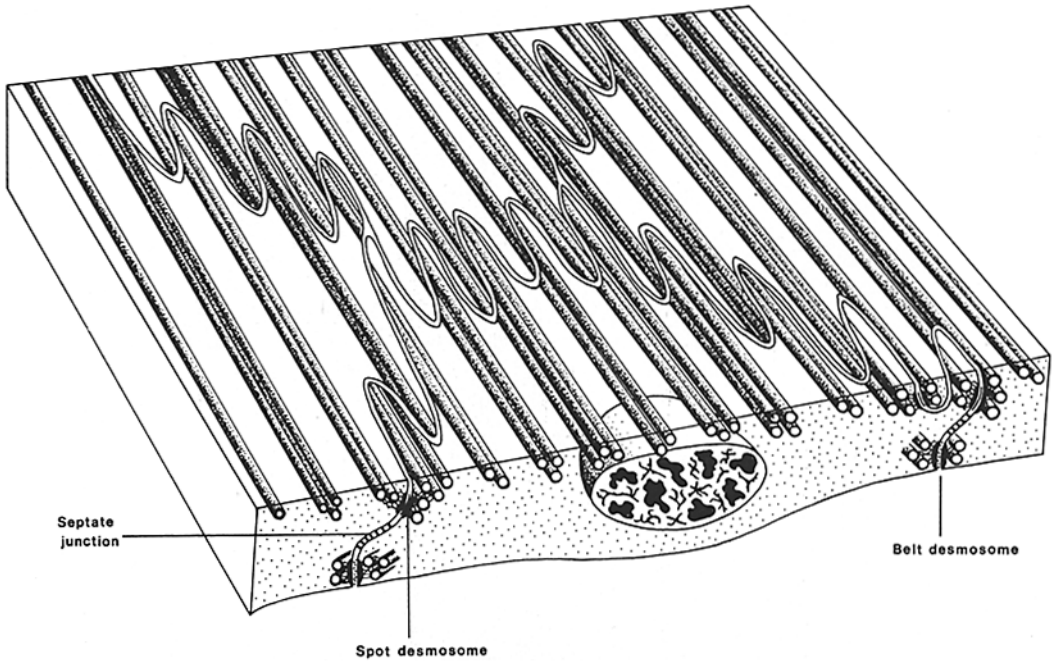

FIGURE 13 Schematic diagram showing the general organization of a portion of *Heteropeza* follicular epithelium and the ways in which its cells interdigitate during the second and third growth phases. The arrangement of desmosomes and most of the cells' microtubules are portrayed as they would be revealed at an edge (stippled) formed by a cut perpendicular to the plane of the epithelium and parallel to the follicle's polar axis. The circumferentially oriented paths followed by microtubules beneath the outer surfaces of follicle cells (towards the top of the figure) are also shown. For clarity, the microvilli which project from the inner surfaces of the cells have been omitted; interdigitating cell processes and all the organelles shown are represented as disproportionately large structures with respect to cell size.

oocyte's shape may be defined and moulded by the mechanical properties of its follicle.

Examination of a wide range of cell types leaves little doubt that microtubules are fairly stiff skeletal elements (17, 27), capable of transmitting tensile and compressive forces along their lengths (16, 28), and that these properties are employed in numerous instances in which oriented microtubule arrays are involved in defining and maintaining the shapes of individual cells and cell processes (see references 3, 24). In theory, oriented microtubules could also influence the growth and expansion of an epithelium, provided the tubules pass right across cells, are similarly oriented in adjacent cells, and some means of transmitting forces across cell junctions from the tubules of one cell to those of a neighbor is present. These conditions appear to be satisfied in the follicular epithelia of *Heteropeza* and *Periplaneta*. Whether individual tubules pass from one side of a cell to the other has not been established. There is also the possibility that even if tubules do not span cells completely, transcellular mechanical continuity could be effected because tubules overlap each other and are bound together by links and bridges. Microtubules may not be entirely responsible for providing resistance to the circumferential expansion of a follicle. Materials bound alongside the tubules, such as the dense material associated with cockroach follicle tubules, or microfilaments which have not been detected, may help to transmit forces across cells. Circumferentially oriented follicle cell microtubules appear to be joined to spot desmosomes which could transmit tension from one cell to another. In several epithelia, particularly those subjected to severe mechanical stress, spot desmosomes seem to act as intercellular rivets. They are structurally associated with skeletal frameworks of 10-nm tonofilament bundles so that shearing forces can be distributed throughout the epithelium (see reference 22). Desmosomes of the fascia adherens variety can almost certainly transmit ten-

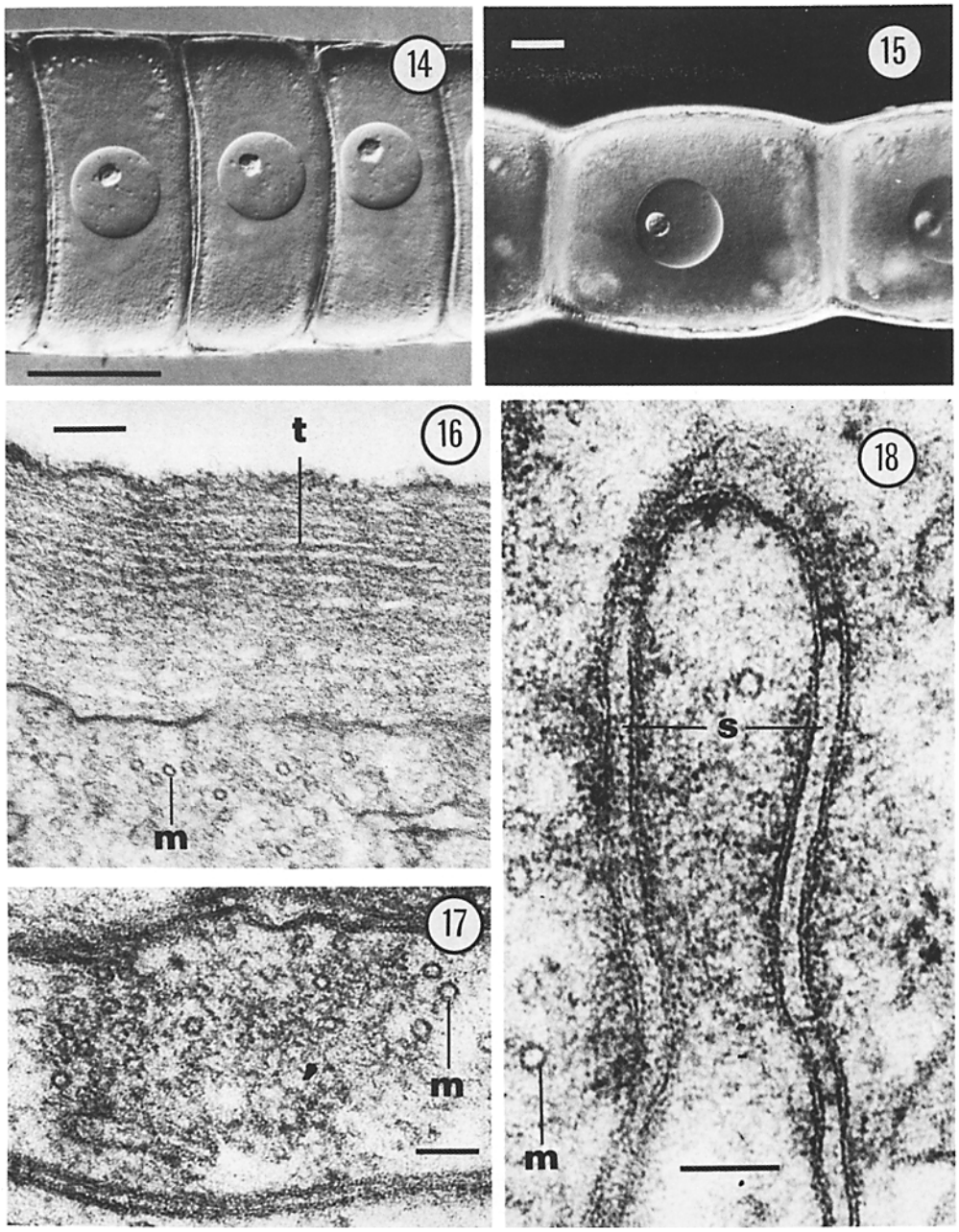

FIGURE 14 Lateral view of an unfixed cockroach ovariole freshly isolated in saline. This portion of the ovariole includes disc-shaped oocytes and was situated close to the germarium. Nomarski interference contrast. × 360. Bar = 50 μm.

FIGURE 15 Lateral view of a part of a cockroach ovariole freshly isolated in saline. This portion of the ovariole contains oocytes which are more elongate and at a later stage of development than those shown in Fig. 14. Nomarski interference contrast. × 140. Bar = 50 μm.

FIGURE 16 Part of the outer surface of a cockroach follicle cell and its laminated tunica propria (*t*). The section is perpendicular to the outer surface and parallel to the polar axis of the follicle. Circumferentially oriented microtubules (*m*) are clustered near the cell surface. × 50,000. Bar = 200 nm.

FIGURE 17 Part of the outer surface of a cockroach follicle. Section orientation as in Fig. 16. Circumferentially oriented microtubules (*m*) are grouped in a bundle; dense material with a finely fibrous or granular appearance lies between the tubules. × 115,000. Bar = 100 nm.

FIGURE 18 Section through part of a cockroach follicle near its outer surface where two cells interdigitate. Section orientation as in Fig. 16. Some of the circumferentially oriented microtubules (*m*) appear to be joined to spot desmosomes (*s*) by a meshwork of fine dense strands. × 167,000. Bar = 100 nm.

sile forces of considerable magnitude from one cell to another; this is indicated by the nature of their association with the actin filaments of adjacent cells in cardiac muscle (10). Microtubules and desmosomes seem to have a particularly important role as tension transmitters in arthropods where they join muscles to the cuticular exoskeleton (see references 5, 7).

Belt desmosomes and the microtubules alongside them which pass around the inner surfaces of *Heteropeza* follicle cells presumably assist in transmitting tensile forces through the epithelium. They form a meshwork over the surface of the egg or embryo (Fig. 5) which probably resists tension more or less equally in all directions and hence is likely to be of little direct importance in providing anisometric resistance to circumferential expansion of elongating eggs and embryos. Belt desmosomes seem to be similarly positioned and associated with microtubules in *Drosophila* follicles (14).

Other Means of Defining Egg Shape

The follicular microtubule/desmosome scheme suggested above is proposed as the most probable one for control of egg shape. The unlikelihood of other components having direct influence on shape is considered below.

The molecular organisation of the tunica propria may be such that it offers anisometric resistance to surface expansion similar to that suggested for the follicle. In certain plant cells, microtubules are situated close to the cell membrane where they apparently help to determine that cellulose microfibrils secreted at the cell surface are oriented parallel to their longitudinal axes (see reference 20). Circumferentially oriented microtubules at the outer surfaces of *Heteropeza* follicle cells might be directing secretion and orientation of fibrous elements for the tunica propria. However, most of the circumferentially oriented microtubules in *Periplaneta* are not closely applied to the outer surfaces of follicle cells and hence are unlikely to influence the orientation of secreted material. In any case, a tunica propria presumably could not generate the active contraction which is necessary to account for the circumferential contraction of *Heteropeza* eggs during the second growth phase. On the other hand, contractile activity is associated with several types of microtubule bundles (for example, references 15, 23). It is also unlikely that a program of oriented follicle cell division, growth, and positioning could impose forces at the egg surface sufficient to account for egg elongation and circumferential contraction without direct involvement of follicle cell microtubules along the lines suggested above.

The possibility remains that insect oocytes and their follicles elongate purely as a result of forces which are generated and directed inside oocytes by cytoskeletal elements which are as yet undetected. But, if this is the case, what is the role of the circumferentially oriented follicle cell microtubules? Most elongating animal cells contain well oriented microtubule arrays (see introductory paragraph). *Periplaneta* oocytes do not include such tubules, and no specialized layers of cortical material or bundles of microfilaments were found. These elements also seem to be lacking in *Heteropeza* eggs when elongation begins; considerable numbers of tubules are oriented radially with respect to the polar axis during blastoderm formation, but it is difficult to see how these tubules could promote egg elongation. Hence, it is probably correct to conclude that the shapes of some insect eggs are mainly defined by the mechanical properties of microtubule/desmosome lattices in their follicles. Examination of egg growth and shaping after the application of procedures which induce microtubule depolymerization has yet to be undertaken.

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