Three-Dimensional Structure Identified from Single Sections

Misinterpretation of flat images can lead to perpetuated errors.

Hans Elias

Scientists have a reputation of infallibility. It is assumed that they examine nature objectively, and that they pay no attention to verbal statements and to merely subjective appraisals. It is admitted that they can devote their talent to evil ends, as, for example, to warfare. But they are, in the opinion of the public and their own, incapable of committing gross errors about the phenomena of nature.

This was also my opinion when, more than 20 years ago, I was given the assignment of producing visual teaching materials concerning the structure of a specific human organ. Faithfully I studied the literature from the beginning [Gerlach (1)] to the most modern textbooks. All the authors, with one exception [Hering (2)] and among them the greatest authorities, agreed that the organ was a threedimensional network of crooked cylinders. It was easy enough to draw stereograms according to these unanimous verbal descriptions. But when it came to documentation by means of photomicrographs it was impossible to obtain pictures that could verify the classical descriptions. For me, this was one of the most devastating, shocking experiences in my life. How could it be possible that the greatest anatomists of the 19th century and contemporary authorities whom I venerated could have made such a blunder? They had "documented" their erroneous statements with correct pictures which. when examined objectively, showed a structure quite different and exactly the reverse of what the text affirmed. In this article the mechanism of establishing and perpetuating erroneous concepts is dealt with briefly as far as histology and other sciences based on examining sections are concerned. The narrow sector of scientific methodology, however, is an example of opinion forming and perpetuation of the errors in general.

Sectioning

In the biological sciences and in the materials sciences many objects must be cut, in order to make them accessible to microscopic study of their internal structure. In biology and geology one uses slices as thin as possible, but of finite thickness. In laboratory jargon these are called sections. In stereology we avoid the use of this word for a translucent slice of finite thickness. But for simplicity's sake I will use, in this article, the word section even if I mean a slice, since it is a section for all practical purposes if its thickness is negligible compared to the size of the parts to be examined. In the study of metals the plane of polish is a true section of thickness zero, because of the opacity of metals. These considerations apply to light microscopy and to low power electron microscopy. In high power electron microscopy the thickness of the slices, although they are called ultrathin, introduces difficulties which I shall not discuss here.

Identifying Sections with Reality

Persons who look routinely at "sections" (slides or slices) soon begin to identify the section with the real object, even if it is projected on a screen. Instead of saying, "this is a projected image of a stained slice showing an oblique section through the duct of the gland," we are accustomed to saying, "this *is* the duct of the gland."

From our early student days we have become conditioned to identify the magnified image of an artificially stained slice with reality. During a scientific meeting of whose time and place I have not kept a record, I introduced a talk on spatial interpretation of sections with a lantern slide, a copy of which is shown on the cover of this issue, saying, "Ladies and Gentlemen, I give you 30 seconds to identify the structure seen on the screen. As a clue, be informed that it is a section." Those who responded said unanimously, "It is a fiber." In reality this picture is a photograph of a section through a large, folded sheet of lasagna, embedded in blackened gelatine. In short, a section through a large flat sheet is a long stripe. All those in the audience had been trained to identify a section with reality. They saw a long, narrow thing. For them it did not only look like a fiber. It was a fiber. In an extremely lucky cut one might find a fiber which, by chance, could be located entirely in the cutting plane. But if it were a fiber, that fiber, twisted as it is, would in all probability cross itself at various points. However, in the case of a highly folded sheet crossing is impossible in three-dimensional space. In the cover picture there is not a single point of crossing.

Dimensional Reduction

Sectioning reduces solid bodies to flat, two-dimensional images. All parts contained within that solid body are reduced in sections to formations one dimension less than their own. Sections through solids are areas, sections through surfaces (interfaces or membranes) are lines, sections through lines (edges between three cells, or fibers) are points or dots; true sections through points do not exist, but granules may be enclosed in a translucent slice of finite thickness. To state it concisely: A section through an n-dimensional object is, in general, an (n - 1)-dimensional figure. Conversely, an n-dimensional figure in a section results, in general, from cutting an (n + 1)-dimensional object. This statement is called in stereology the principle of dimen-

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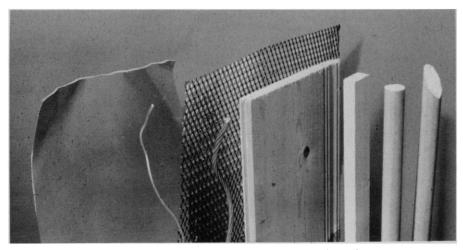


Fig. 1. A few pieces of building material and their sections.

sional reduction. If an investigator has this principle in mind he will, in most cases, make the correct spatial identification of a structure of which he sees a section or a micrograph. I have used above the word stereology. Now I owe the reader a definition, but I promise that I will keep rigorous stereology down to a minimum. Stereology is extrapolation from two- to three-dimensional space, or three-dimensional interpretation of two-dimensional images, by methods of geometrical probability. Stereology, in the strictest sense, involves measuring and counting "profiles" of cut tissue elements, as well as counting intersection points of traces with testlines and "point hits" of areas. Data thus obtained can lead to rather accurate quantitative information on the internal structure of an organ or a rock or an alloy. Such data can also lead to the identification of three-dimensional shapes.

Is Form Essential?

When I first announced at a meeting of anatomists that the liver consists of plates rather than of cords one member said, "Why do you stress this? After all, we all know what we are talking about. Whether you call these structures plates or cords is merely a matter of semantics." This, I admit, is a viewpoint rarely expressed. It is a minority opinion. Yet there are persons among us who think shape is entirely unimportant. A look at Fig. 1 will convince anybody that there are vast differences in structural usefulness between a rod, a lath, a board, a cable, a single wire, a sheet of metal foil, or a sheet of "metal lath" (wire netting). Sections through these structures seen in oblique view at the upper end of each are a circle or an ellipse, a rectangle or a trapezoid, a stripe, a collection of dots, a single dot, a line, and a row of dots. If one sees any of these shapes in section one can form a tentative opinion about the shapes of the objects that were cut. Shapes are functionally important, as I will show with a few examples. Membranes, represented by the sheet or foil, delimit compartments and represent barriers. Fibers represented by the single wire strengthen organs. If bundled into tendons they can exert traction. A fiber is not an obstacle to the passage of substances or microbes. They can pass around it. The cable corresponds to a trabecula that supports without separating compartments. Let us examine the last-named structures as they may occur in a liver. Laennec's cirrhosis (3) is characterized by the presence of membranous walls that divide the liver into isolated nodules. They contribute to blockage of diffusion and blood flow. It is the presence of membranous connective tissue that makes the condition incurable and in-

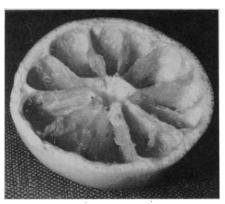


Fig. 2. A spooned-out half grapefruit showing membranous septa (flat walls, practically two-dimensional structures).

evitably leads to death. The liver of the raccoon is also divided into compartments by septa. These, however, have the structure of a lattice, like the sheet of metal lath. Blood vessels and even strands of liver cells pass through its meshes. Thus, to the raccoon, these septa do not constitute a health problem. In human biliary cirrhosis the liver is pervaded by trabeculae, that is, bundles of fibers. They arise around the smallest bile ducts as a consequence of an inflammation. They do not present an immediate obstacle to blood flow, although in biliary cirrhosis there is frequently a secondary development of membranes. When this stage is reached the condition becomes dangerous.

Epithelia, represented by the board, are more or less thick sheets made of cells in contact with each other. They line cavities, are used in the construction of glands, and cover the entire body. They separate the "internal medium" from the "outer world." The rods in Fig. 1 represent cylindrical structures, solid or hollow. Cylindrical organ components such as nerve fibers and ducts conduct impulses and liquids. Closed spheres, not represented in the model, may serve for storage (fat cells, thyroid follicles).

With this I hope to have made the point that shape, often contemptuously called a merely quantitative attribute of structure, is not so unimportant, even in these modern, number-happy days.

Before I discuss specific examples, however, I must present a common example of dimensional reduction: The cut surface of a grapefruit cut in half as we eat it for breakfast shows a few thin lines (one-dimensional figures) radiating from the center. These lines are profiles of membranes (two-dimensional interfaces) which separate the carpels (compartments of angiosperm ovaries, containing the seeds in mature fruits) as one can verify after spooning out the flesh (Fig. 2).

A Few Historical Errors and Their Correction

In this article, a few concrete examples will be given on how to identify shape and structure by simply combining a "feel" for three-dimensional space with common sense. Malicious as I am, I will first point out some errors that were made in the past and then correct them. I shall not be malicious enough to name the authors who made the mistakes.

Slitlike Glands in Bird Stomachs

The glandular stomach (proventriculus) of birds has two types of glands. Toward the outer wall there are large, saclike parietal glands. In the superficial (inner, mucosal) layer there are glands that have been described consistently as "simple *tubular* glands" (Fig. 3A). As the name implies, they were alleged to be hollow cylinders. Writing and illustrating an outline of veterinary histology (4), I endeavored to illustrate the "fact" of their cylindrical shape by showing a few of their cross sections.

Sections through tubular glands (cylinders) would be round, having predominantly short, elliptical shapes. In random cuts, longitudinal sections as seen in Fig. 3A would be very rare if the glands in question were really tubular. Yet no round or oval transverse or oblique sections through these tubules were found. My conclusion was: Something must be wrong with the story of the simple, tubular glands. All objects that yield predominantly long, narrow sections must be flat and cannot be cylindrical. Tangential sections through the inner layer of the proventriculus (Fig. 3B) also show long and narrow stripes. But one can see now that many of them surround, concentrically, the exits of the large parietal glands. The conclusion was that these glands were not tubular but had the shape of long, narrow slits. They were called slitlike or sulciform glands. Surface views (Fig. 4) verify that conclusion.

Liver Plates

For 100 years (1) the livers of vertebrates (and only vertebrates have a liver) were described as three-dimensional networks of crooked, interconnected cylinders. In mammals these presumed cylinders were called cords, and they were said to be two cells thick. They had to be two cells thick because this was necessary to account for the presence of bile canaliculi-thin capillaries bounded by two liver cells. In lower vertebrates the supposed cylinders were described as tubules having a lumen with a layer of five cells around them. All the authors who described these interconnected "cylinders" seemed to be favored by unbelievable luck. For they found in their slides, always, neat longitudinal sections. They never found a cross section or an oblique section through these cylinders, as if a fairy had guided their microtome knives and a genie had prearranged the cylinders exactly in the cutting plane. All their illustrations show this miracle.

Those who do not believe in fairies and genies must find a different explanation for the hepatic miracle. The simplest explanation is that a section like that shown in Fig. 5 cannot derive from cutting interconnected cylinders. The figure shows long, narrow stripes, that is, in essence one-dimensional figures. According to the inverted principle of dimensional reduction, they

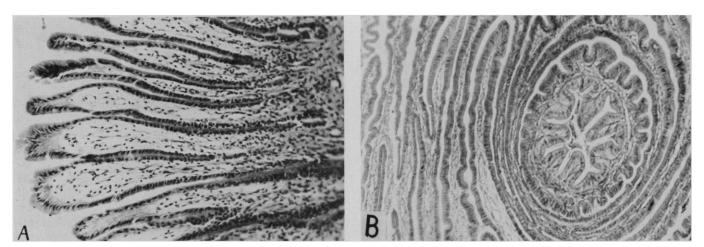
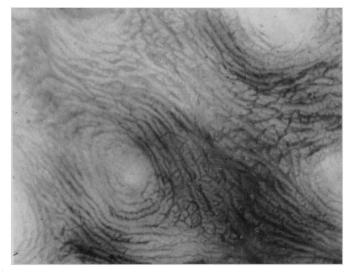


Fig. 3. Sections of mucosal glands of a chicken's proventriculus; (A) cut perpendicularly to the wall of the organ, and (B) cut tangentially to the wall of the organ.



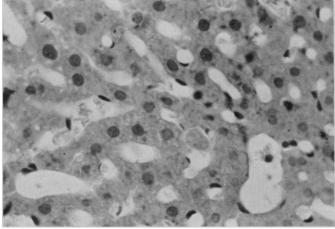
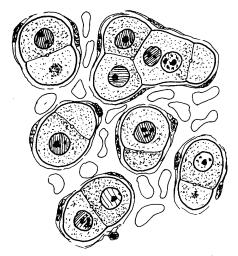


Fig. 4 (left). Surface view of the inner aspect of a chicken's proventriculus. Fig. 5 (right). Section through a rat's liver.

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in a building (5). In short, the liver is a muralium. If the liver had the structure previously postulated, round profiles should predominate in sections, and oblong profiles should be very rare. Such a section should look like Fig. 6. But no sections of this kind are ever found in slides of normal livers. I have reviewed the literature of this perpetuated error in an attempt to better understand its origins and continued propagation (6).

The Endoplasmic Reticulum

Fig. 6. Imaginary section through the imaginary cord liver.

must result from cutting two-dimensional objects. In other words, sheets, plates, or walls. Since the stripes are interconnected, we conclude that the plates are interconnected like the walls The early sectional electron microscopists (7) described the endoplasmic reticulum in 1952 (Fig. 7) as double filaments. It is most fortunate that the paper in which this misinterpretation was made had not yet appeared when another author (8) sent his 1953 paper to *Nature*. He identified the double lines studded with dark dots immediately and correctly as double membranes. Their membranous shape was verified in 1955 (9) by quantitative stereological analysis.

"Spongy" Bone

Textbooks of histology distinguish between compact bone and spongy or cancellous bone. The last two terms mean the same thing. Cancelli means lattice work, that is, a structure put together of thin rods such as a wrought iron fence or a grille. This is also the structure of the skeletons of Porifera (sponges). They are made of interlacing and often branching needles called spicules (from spiculum, meaning a lance, spear, or javelin). Figure 8 shows a section through "spongy" bone. To all those familiar with the principle of dimensional reduction it is immediately evident that the long, narrow, interconnected stripes are sections of thin

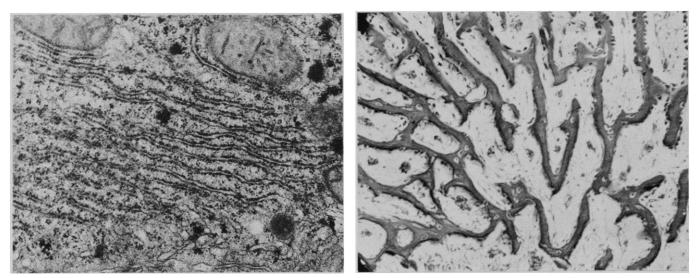
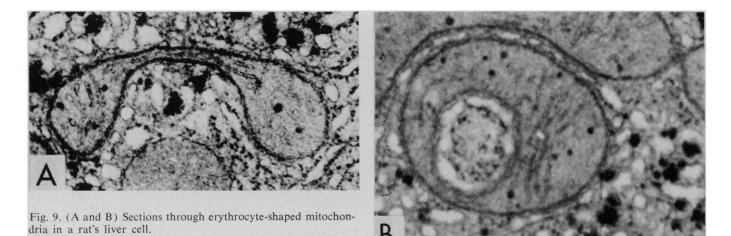


Fig. 7 (left). Section of rough-surfaced endoplasmic reticulum in a rat liver cell, originally interpretated as double filaments. Fig. 8 (right). Section through the mandible of a human fetus featuring "spongy" or "cancellous" bone, in reality a muralium osseum.



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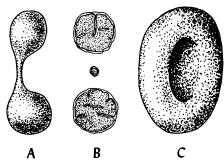


Fig. 10. (A) Previous interpretation of the three-dimensional shape of a mitochondrion as shown in section in Fig. 9A. (B) Expected sections through a mitochondrion as postulated. (C) Real shape of the same kind of mitochondrion.

sheets. This type of bone, which we have learned to call a muralium osseum, had been called spongy because these long stripes were assumed to be longitudinal sections of "spicules." Again, the cause for this case of erroneous identification of structure was the histologist's habit of identifying a section with the thing itself.

Dumbbell-Shaped Mitochondria

Mitrochondria are among the very few organelles, if not the only ones, which, although subserving the same function, are extremely varied in shape. Their pleomorphism is particularly evident in phase-microscopic time-lapse cinematography. Electron microscopists, however, see only their sections; and many of them have struggled with the identification of their three-dimensional shapes. One shape of mitochondria has attracted particular attention. Figure 9A shows a characteristic section through a mitochondrion which has been described as dumbbell-shaped. This presumed shape is sketched in Fig. 10A. Two oval "lobes" were thought to be connected by a thin, filamentous bridge. If this assumption were correct, sections such as seen in Fig. 9A would be extremely rare, because only by almost miraculous luck would the knife pass longitudinally through such a dumbbell-like structure. More likely would be sections such as seen in Fig. 10B, where the two alleged "lobes" would not look different from sections through oval or rod-shaped mitochondria. The section through the supposed bridge (Fig. 10B) would be so small that it would probably remain unnoticed. The theory of the dumbbellshaped mitochondrion was presented in 1964 at a scientific meeting (10). During the discussion a man in the audience expressed doubt about it. He pointed out that it was more likely that a mitochondrion of that kind had the shape of an erythrocyte, that is, a torus (doughnut-like ring) with a membrane closing the hole (Fig. 10C). The speaker was impressed but not entirely convinced. Therefore he went through the very time-consuming and difficult labor of producing serial sections for electron microscopy. From them he reconstructed a few mitochondria by means of Born's classical wax plate method (11, 12). The result was exactly as predicted. Mitochondria whose profiles appeared dumbbell-shaped had, indeed, the three-dimensional form of an erythrocyte, a torus with a thin

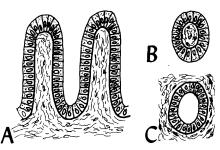


Fig. 13. Diagram of sections of villi and pits (foveolae).

diaphragm closing the central hole. This immense labor was entirely unnecessary. For this shape is evident, if one observes the sections with a critical eye for three-dimensional space. But a single section of that kind would not be sufficient for shape determination. The opinion formed must be verified. If these mitochondria have the postulated shape of a torus with a central diaphragm, then one should find, occasionally, ring-shaped profiles. Since such profiles do, indeed, occur as seen in Fig. 9B, the assumed shape is almost proved. It is not entirely proved, because Fig. 9B could also derive from a torus without diaphragm.

In spite of the rarity of erythrocyteshaped mitochondria, this case is important from a psychological point of view. Figure 11 shows profiles of exactly the same shape as Fig. 9. As any person familiar with electron microscopy sees at once, they are sections of mammalian erythrocytes. Everyone also "knows" that in three-dimensional space the erythrocyte has the shape of a torus with a central diaphragm, a shape shown in Fig. 10C. Why is it

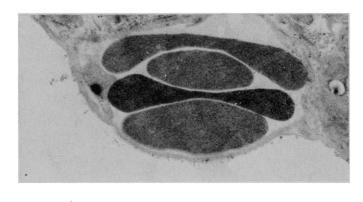
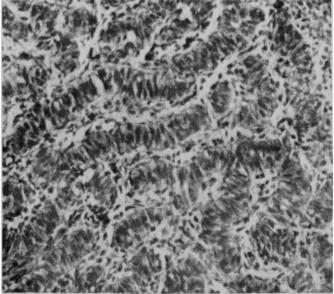


Fig. 11 (left). Sections of erythrocytes in rat's lung. Fig. 12 (right). Section through the testicle of an 18-mm-long human embryo.



that the same shape is interpreted correctly in one case and incorrectly in another? Simply because the threedimensional shape of the erythrocyte has been known since Leeuwenhoek, more than 100 years before the invention of the microtome. The discoverer of the "dumbbell-shaped" mitochondrion, although he had seen hundreds of sections through erythrocytes like those in Fig. 11, did not notice the similarity of shape of Figs. 9A and 11.

Sex "Cords"

The gonads of human male embryos, 15 to 25 mm long, can be distinguished from the female gonads by the presence, in section, of long, crooked, branching stripes (Fig. 12). These have been identified as "cords," that is, cylinders, for at least seven decades. The concept was transmitted from textbook to textbook. The marvelous photomicrographs in a recent monograph (13) show these long stripes beautifully and provide evidence that the objects cut are not cords, but thick sheets. Nevertheless, in the text, the authors describe them as cords. As we have seen above, the presence of long, crooked stripes in sections is evidence for the existence of curved sheets or plates in space. This truism has been proven by quantitative stereological methods and by reconstruction (14).

In fact, the embryonic testicle in this age interval contains one single, highly folded sheet which has some cylindrical processes at its edges and whose parts are connected by a few cylindrical bridges.

Gastric Pits versus Intestinal Villi

For the beginning student in histology it is difficult to distinguish a section of stomach from one through the small intestine. He knows, of course, from reading and lectures that the stomach has pits and the small intestine villi.

This knowledge derives from gross anatomical studies and the use of simple magnifiers. There is a simple way of distinguishing pits (foveolae) from "villi" (fingerlike, cylindrical processes) in sections. Figure 13A is a diagram of a section of an unknown portion of the gastrointestinal tract normal (perpendicular) to the wall of the organ. This point is illustrated by drawings rather than photomicrographs to avoid identification of the part through cellular structure known to the reader. It

is impossible to tell whether the two upward projections are longitudinal sections of villi or of folds which surround a pit in the center. Such exact normal sections are rare. It is a more frequent occurrence for villi or pits to be cut obliquely. A cross section through a villus would show a central core of connective tissue covered by epithclium, which, in turn, would be surrounded by empty space, as in Fig. 13B. An oblique section through a pit would show a central cavity (lumen) lined by epithelium which, in turn, would be surrounded by connective tissue (Fig. 13C). Unfortunately, such simple ways of identification are not taught in histology courses.

Since the small intestine of man and some other mammals is studded with villi (fingerlike, cylindrical projections), it is tacitly assumed that villi are characteristic of the small intestine of the vertebrates. Sections normal to the wall of the small intestine of a guppy seem to confirm this concept (Fig. 14A). However, a tangential section of the mucous membrane of the same viscus (Fig. 14B) reveals a quite different structure. The elevations are long ridges forming a beautiful pattern. Long, narrow grooves (sulciform glands) run between them.

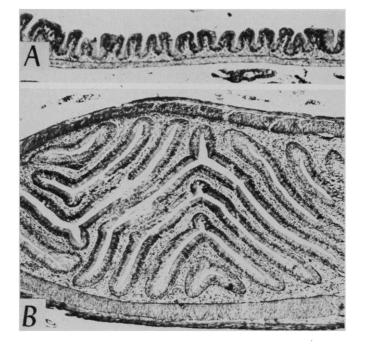


Fig. 14 (left). Sections of guppy intestine; (A) normal to wall; (B) parallel to wall.

Fig. 15 (right). Cross section through the ampulla of a human oviduct.



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Human Oviduct and Seminal Vesicle

Finally, two examples of well-known structures will be used to show what can be accomplished by a very simple commonsense approach without the use of mathematics. The structure of the human oviduct (fallopian tube) and of the seminal vesicle have been known through dissection and viewing with simple lenses, before the advent of the compound microscope and of the microtome. Let us assume in the following discussion that their structures were unknown and that we depended for their correct description on single sections seen in the compound microscope. Figure 15 shows a cross section of a human oviduct. Figure 16A is from a section through a seminal vesicle. At first sight, these two images look very much alike. Both show stripes of connective tissue covered on both sides by epithelium. The stripes are connected with the outer wall of the organ. Persons not a priori familiar with the structure of these organs might be inclined to think that both organs contain connective tissue cylinders or cords covered by an epithelial layer. The same kind of thinking encountered among persons describing the liver for 100 years could have lead to an identification of structure very much like that of the supposed netlike liver. In fact, Fig. 16B, a tangential section through the wall of the seminal vesicle, looks just like a section of liver, except that the branching and connected "cords" are made of material different from "liver cords."

Now familiar with the principle of dimensional reduction, we know immediately that the stripes in these three last illustrations cannot be sections of cylindrical cords; but they must be sections of flat sheets. For nowhere can a cross section of a cord (which would be round and surrounded by "empty" space) be seen. Thus from what we have learned above we can conclude that both organs contain extensive flat sheets.

But there is an essential difference between these flat sheets which are so much alike in histological texture. The sections of sheets in the oviduct (Fig. 15) arise from its wall and branch in a treelike fashion. They all taper into free ends. There are no cross connections between the sheets. The conclusion is that the mucous membrane of the oviduct consists of branching folds. They all run lengthwise; and so do the trenches between the folds. There are no closed pockets with blind ends. This arrangement of folds favors the ascent of spermatozoa and the descent of the egg. If one points with the tip of his pencil into what appears a blind end in the section, he can draw a line from that spot into the central cavity of the oviduct without crossing a mucosal "stripe." On the other hand, the con-

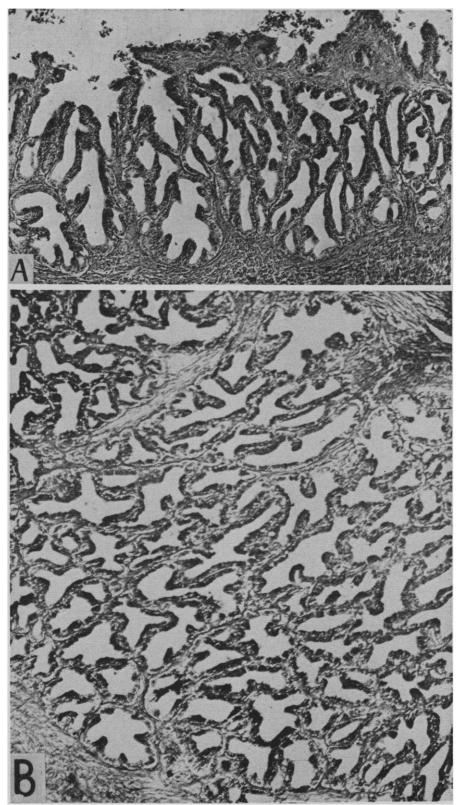


Fig. 16. (A) Section perpendicular to the wall of a human seminal vesicle. (B) Tangential section through the mucosa of a human seminal vesicle.

nective tissue stripes of the seminal vesicle (Fig. 16, A and B) are multiply connected. If one points with a pencil into almost any space between the stripes close to the outer wall, it is impossible to draw a line which reaches from that spot into the inner cavity without crossing several stripes. Yet at a very few places this is possible. We conclude that the mucous membrane of the seminal vesicle is a system of spaces separated by many interconnected walls and that some of these spaces communicate with the internal cavity. This is as far as we can go by mere examination of the image as a geometrical pattern. The pattern alone does not tell us whether all the spaces communicate, however indirectly, with the central cavity or whether some of them or many of them or most of them are completely closed. If we add to this shape analysis a physiological thought, the correct solution is inevitable.

Let us assume, hypothetically, that some of the spaces were completely closed off from the central cavity and then consider what the consequences might be. We may now turn to a high power objective and examine the epithelium (not illustrated). We find that the epithelium shows evidence of secretory activity everywhere. If one of the spaces were completely closed, secretion would accumulate in it. It would balloon out and form a spherical cyst. The complete absence of cysts is evidence that there must be a path, however crooked and indirect, for secretory material to flow away.

Since we do not find sperms in these spaces we can further conclude that the seminal vesicle is not a storage organ for semen, but a gland with a secretory function. Neither reconstruction from serial sections, nor mathematical stereological methods were needed to arrive at a correct identification of the structure of this organ.

Complicated Shapes

For simple shapes, such as ellipsoids, cylinders, and lenses, there are easy stereological methods of shape determination summarized in 1971 (15). One assumes that many structures of approximately equal shape are randomly distributed in space. Methods for the determination of complicated shapes from single sections are now in the process of being worked out. These methods involve measurements and classification of ratios of length to width, tangent counts for surface curvature determination by DeHoff's method (16), and counts of Y-shaped profiles for quantification of connectivity among tissue elements. No mathematical method is available yet for determination of shapes of objects as pleomorphic as mitochondria in liver cells. But I hope to have shown that mathematical procedures are not necessary for the identification of shape in many cases.

There are things of utterly complicated shapes which, at first, seem to defy description, objects which cannot be reconstructed by serial sections because of their size. An example is the podocyte in the kidney. Hall (17) described their shape successfully by looking at numerous micrographs and then building a model which he thought might resemble such a cell. He cut the model with a knife in various directions and obtained images resembling his original micrographs. Fifteen years later his concept of the shape of podocytes was confirmed by scanning electron microscopy (18).

Summary and Conclusions

Errors in the identification of objects have been made frequently because of faulty interpretation of their flat images or sections. Such errors are perpetuated through a strange psychological chain reaction.

1) The first author who observes sections of an object, although presenting faithful pictures of sections of it, identifies its shape incorrectly. Such an initial mistake may be due to identification of the flat image with the object itself or to failure to consider the shape of the image as a function of the shape of the real object and the angle and level of cutting.

2) The first author describes verbally his personal concept of the object.

3) The reader reads the text of a publication before or without examining the pictorial evidence.

4) The reader's belief in the authority of the printed word immunizes him against critical evaluation of the evidence.

5) The reader regards a published opinion as a "fact."

6) A mechanism of suppression of new evidence is set up in the brain of the reader in favor of previously published, verbalized concepts. His brain unconsciously rejects new concepts that might arise intracerebrally. The printed word supersedes visual evidence.

7) A secondary mechanism parallels steps 3 to 6. An observer notices an unfamiliar figure in the microscope. Following established procedures for scientific investigations, he refrains from forming an opinion about his observation. Instead he rushes to the library searching for similar, published observations. If he finds a previous report about a similar shape, he accepts it as a "fact" and he "confirms" the previously printed viewpoint. Let me interject a personal experience concerning this mechanism. I investigated the arrangement of blood vessels in the human liver by means of corrosion preparations. The work was divided between an assistant and me. He was assigned the task of preparing drawings of two specimens. In his drawings he showed a structure which was absent from the specimens but had been described in a previous publication.

This article shows simple ways for correct initial identification of shape and structure and for the breaking of the reverberating circuit of erroneous thinking.

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