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SYMBIOSIS AND EVOLUTION

Author(s): Lynn Margulis

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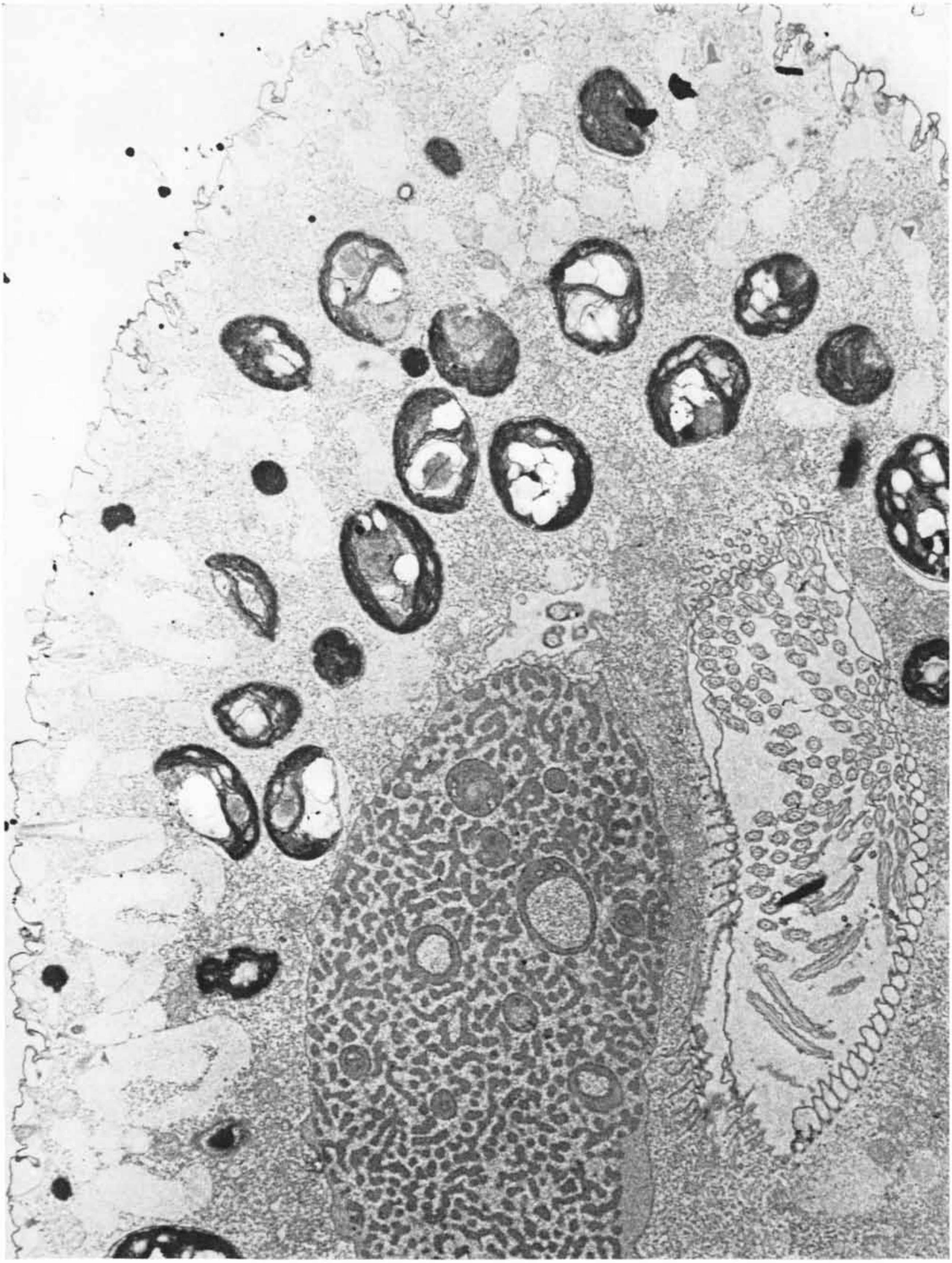


HEREDITARY SYMBIOSIS between photosynthetic green algae of the genus *Chlorella* (*scattered dark ovals*) and a single-celled animal host is characteristic of the species *Paramecium bursaria*, seen magnified 8,000 times in this electron micrograph. Even when the host is kept close to starvation, its guest symbionts satisfy its basic food requirements as long as sunlight is available. The chloroplasts in photosynthetic cells may once have been similar free-living alga-like organisms that eventually became guest symbionts.

SYMBIOSIS AND EVOLUTION

The cells of higher plants and animals have specialized organelles such as chloroplasts and mitochondria. There is increasing reason to believe that these organelles were once independent organisms

by Lynn Margulis

Every form of life on earth—oak tree and elephant, bird and bacterium—shares a common ancestry with every other form; this fact has been conclusively demonstrated by more than a century of evolutionary research. At the same time every living thing belongs primarily to one or another of two groups that are mutually exclusive: organisms with cells that have nuclei and organisms with cells that do not. (An exception is viruses and virus-like particles, but such organisms can reproduce only inside cells.) How can both of these facts be true? Why does so profound a biological schism exist? Ideas put forward and discarded some decades ago hinted at one explanation: Cells without nuclei were the first to evolve. Cells with nuclei, however, are not merely mutant descendants of the older kind of cell. They are the product of a different evolutionary process: a symbiotic union of several cells without nuclei.

The cells of the two classes of organisms are called prokaryotic ("prenuclear") and eukaryotic ("truly nucleated"). The two classes are not equally familiar to us. Most of the forms of life we see—ourselves, trees, pets and the plants and animals that provide our food—are eukaryotes. Each of their cells has a central organelle: a membrane-enclosed nucleus where genetic material is organized into chromosomes. Each has within its cytoplasm several other kinds of organelle. Prokaryotes are far less prominent organisms, although they exist in huge numbers. In the absence of a membrane-enclosed nucleus their genetic material is dispersed throughout their cytoplasm. Such primitive simplicity is characteristic of the blue-green algae and of all the myriad species of bacteria.

The relatedness of living things is fundamental. Organisms as apparently dissimilar as men and molds have almost identical nucleic acids and have similarly identical enzyme systems for utilizing the energy stored in foodstuffs. Their proteins are made up of the same 20 amino acid units. In spite of a bewildering diversity of forms, in these fundamental respects living things are the same. Yet we are left with the equally fundamental discontinuity represented by the two different classes of cells.

Varieties of Symbiosis

Symbiosis can be defined as the living together of two or more organisms in close association. To exclude the many kinds of parasitic relationships known in nature, the term is often restricted to associations that are of mutual advantage to the partners. One frequently cited instance of symbiosis is the partnership sometimes observed between the hermit crab and the sea anemone. The anemone attaches itself to the shell that shelters the crab; this provides its partner with camouflage, and stray bits of the crab's food nourish the anemone. An example that is more pertinent here is the relationship between the leguminous plants and certain free-living soil bacteria. Neither organism can by itself utilize the gaseous nitrogen of the atmosphere. The roots of the plants, however, develop projections known as infection threads that transport the soil bacteria into the root structure. Once present in the cytoplasm of the root cells, the bacteria (transformed into "bacteroids") combine with the host cells to form a specialized tissue: the root nodule. Inert atmospheric nitrogen is utilized by nodule cells as a nutrient. At the same time the nodules manufacture a substance—a pinkish protein known as leghemoglobin—that neither the plant nor the bacteria alone can produce. Because the bacterial symbionts live within the tissue of the plant host the partnership is classified as "endosymbiosis."

Neither of these relationships is necessarily hereditary. The hermit crab will never give rise to the anemone, nor the anemone to the hermit crab. Nor in most instances does a pea or an alfalfa seed contain bacteria; each new generation of plants must establish its own association with a new generation of bacteria. On the other hand, there is one plant—*Psychotria bacteriophila*—that contains the bacterial symbiont in its seed. Thus its offspring inherit not only chromosomes and cytoplasm from the parent plants but bacteria as well. This constitutes hereditary endosymbiosis.

Hereditary symbiosis is surprisingly common. In many instances the host—plant or animal—cannot manufacture its own food and the guest belongs to the family of organisms that can synthesize nutrients by absorbing sunlight. Hosts of this kind are heterotrophs: "other-feeders." Among plants the fungi fit into this group; so do most forms of animal life. Their guests are autotrophs: "self-feeders." The process that nourishes them is the familiar one we call photosynthesis.

An instance of such a relationship is provided by lichens, the characteristically flat, crusty plants that can survive in harshly dry and cold environments. Microscopic study long ago demonstrated that a lichen is a symbiotic partnership between an alga (the autotroph) and a fungus (the heterotroph). Vernon Ahmadjian of Clark University has managed to dissociate the partners that form lichens of the genus *Cladonia,* and he has succeeded in raising the two components independently.

Endosymbiosis has been characterized as swallowing without digesting. One protozoan symbiont—*Paramecium bursaria,* commonly known as the green paramecium—provides an apt illustration. This protozoon has been studied intensively by Richard Siegel of the University of California at Los Angeles and Stephen Karakashian of the State University of New York at Old Westbury. It is green because numerous photosynthetic green algae inhabit its single cell. The photosynthetic guests, given adequate light, can keep the host alive under near-starvation conditions. When the host is deprived of its guests, it will survive only if extra nutrients are added to its medium. The guests (members of the genus *Chlorella,* a common green alga) will also survive when they are removed from the host.

When the organism is reconstituted in the laboratory by bringing the isolated paramecium and the algae together, an interesting thing happens. Once back inside the host, the algae multiply, but only until the normal, genetically regulated number of algae per paramecium is attained. The multiplication then stops. Should the protozoon encounter free-living *Chlorella,* they are promptly digested. Its own algal partners, however, are totally immune. Somehow the paramecium recognizes its symbiont, although even with the electron microscope it is not easy to see any morphological difference between the free-living *Chlorella* and the symbiotic one.

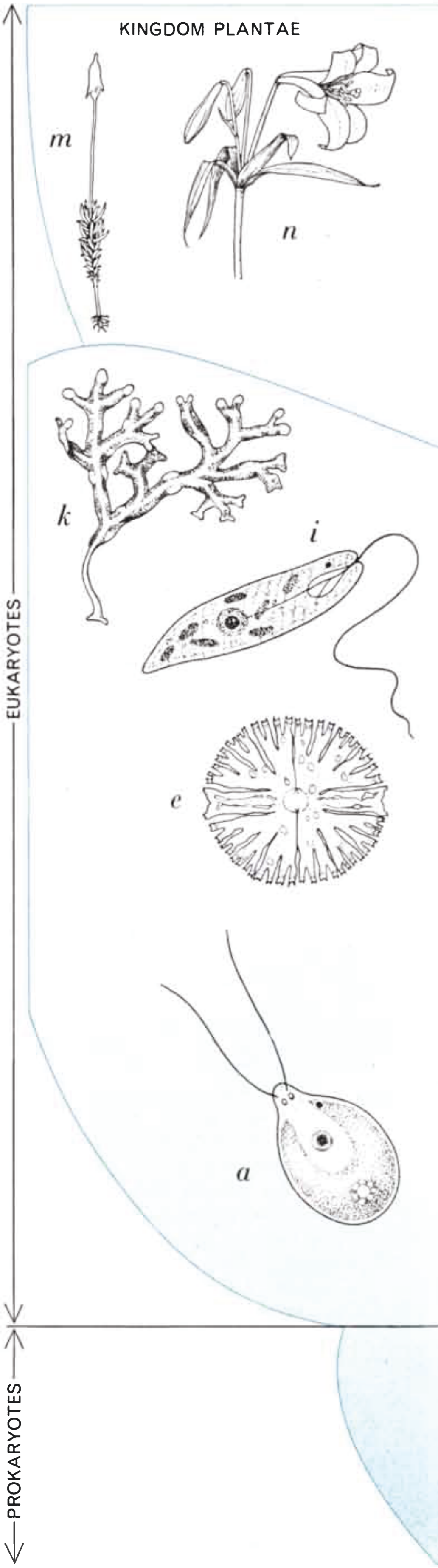
The relationships described thus far involve hosts whose guests all belong to a single species. Far more complex kinds of symbiosis are known. There is one protozoon, for example, that is itself a symbiont and at the same time is the host of three other symbionts. This is the flagellate *Myxotricha paradoxa,* a large, smooth-swimming single-celled organism that seems to be covered with hairlike flagella of various sizes. *Myxotricha* lives in the gut of certain Australian termites; it contributes to the insects' survival by helping them digest the pulverized wood that comprises their food. When *Myxotricha* was first described, it was thought to be just another multiflagellate protozoon with an unusual mode of swimming.

A detailed study by A. V. Grimstone of the University of Cambridge and L. R. Cleveland of the University of Georgia revealed that *Myxotricha* actually had only a few normal flagella at one end. What were mistaken for flagella elsewhere on the organism were spirochetes—a kind of elongated motile bacterium—that were living symbiotically on the surface of the protozoan host. This was not all; each spirochete was associated with another kind of symbiotic bacterium that was also attached to the host's surface, and still a third kind of symbiotic bacterium lived inside *Myxotricha* [*see illustration on page* 52]. As Grimstone and Cleveland have noted, the protozoon "glides along uninterruptedly" through the gut of the termite "at constant speed and usually in a straight line," with its symbiotic spirochetes undulating vigorously.

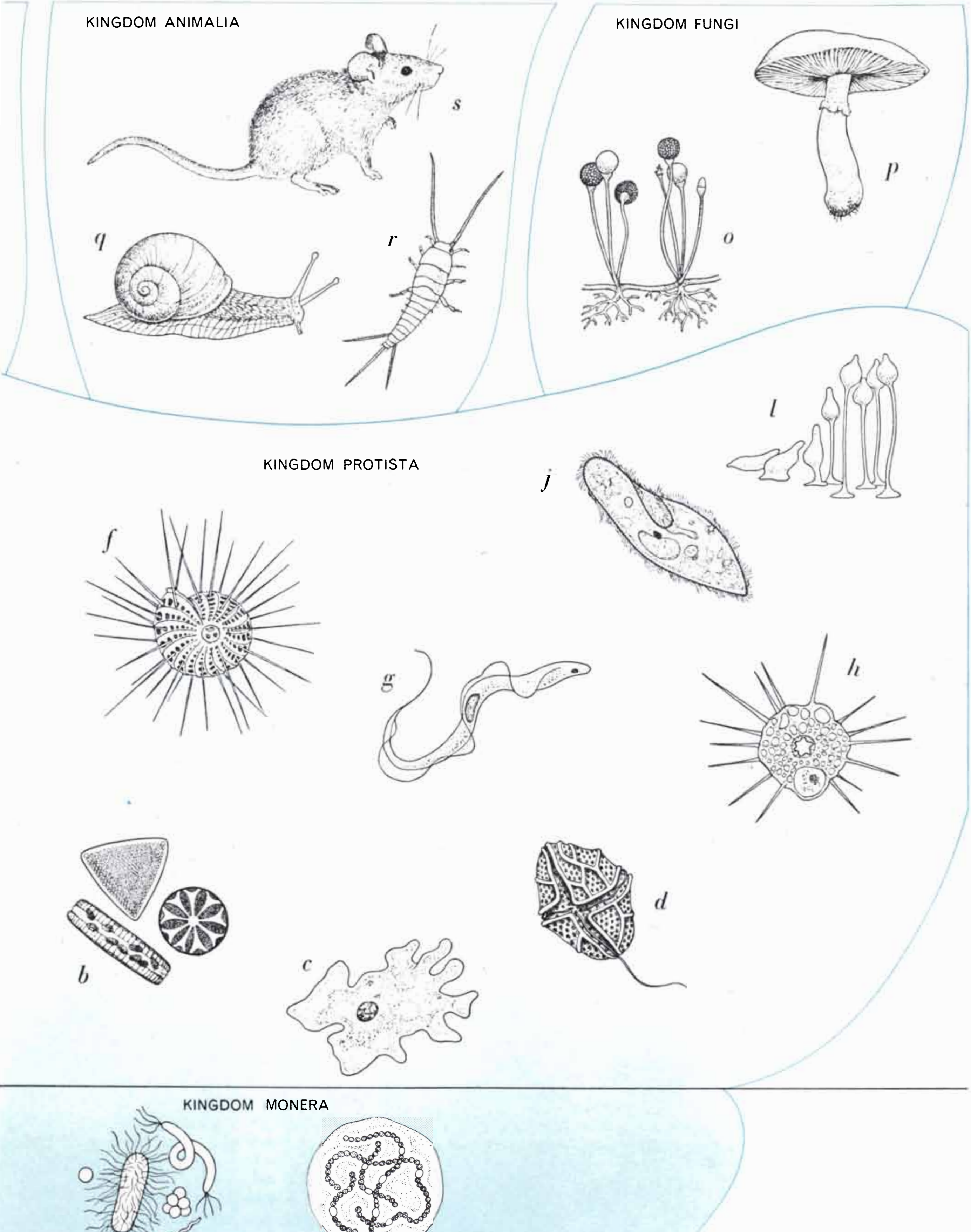
Organelles of the Eukaryotic Cell

Having seen how many different kinds of independent organism can enter into symbiotic partnerships and how some of these partnerships can be perpetuated on a hereditary basis, we now turn to the eukaryotic cell. When we examine such a cell under the microscope, we see that it contains not only a nucleus but also other organelles. In the eukaryotic cells of a green leaf, for example, there are tiny green chloroplasts, where the chemical events of photosynthesis take place. In the cells of both plants and animals there are mitochondria, where foodstuffs are oxidized to produce ATP (adenosine triphosphate), the universal fuel of biochemical reactions. These are only two of several types of organelle.

Could these organelles have originated as independent organisms? One kind



"FIVE-KINGDOM" CLASSIFICATION of terrestrial life, proposed by R. H. Whittaker of Cornell University to solve the dilemma posed by the conventional classification of organisms as either plants or animals, is shown as modified by the author. The life forms comprise two unambiguous and mutually exclusive groups: prokaryotes, the organisms with cells that lack membrane-enclosed nuclei, all within the kingdom Monera, and the eukaryotes, the organisms with truly nucleated cells, which include the populations of the other four. Organisms representative of major phyla are illustrated. In the kingdom Monera these are various bacteria (*left*) and a blue-green alga, *Nostoc* (*right*). In the kingdom Protista are *Chlamydomonas*, one of the chlorophyta (*a*), diatoms (*b*), an amoeba (*c*), a dinoflagellate (*d*), a desmid (*e*), a foraminiferan (*f*), a trypanosome (*g*), a sun animalcule (*h*), a euglena (*i*), a paramecium (*j*), a brown seaweed (*k*) and a cellular slime mold (*l*). The two phyla in the kingdom Plantae, a group nourished by photosynthesis, are represented by a haircap moss (*m*) and a lily (*n*). In the kingdom Fungi, a group characterized by absorptive nutrition, are a bread mold (*o*) and a mushroom (*p*). In the kingdom Animalia, characterized by ingestive nutrition, the representatives are a mollusk (*q*), arthropod (*r*) and chordate (*s*).


KINGDOM ANIMALIA
s
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KINGDOM MONERA

of evidence immediately suggests such an origin: the existence of what are known as cytoplasmic genes. When we speak of genes, we usually have in mind the hereditary material—the DNA—in the chromosomes of the cell nucleus. Yet genes are also found outside the nucleus in the cytoplasm, notably in association with chloroplasts and mitochondria.

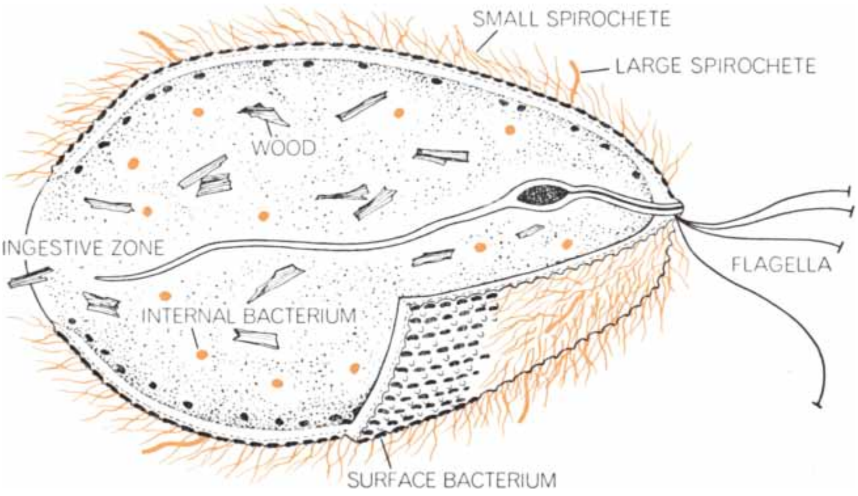
Chloroplasts belong to a group of organelles collectively known as plastids. Plastids have their own unique DNA—a DNA unrelated to the DNA of the cell nucleus. As has been abundantly demonstrated over the past two decades, DNA is the replicative molecule of the cell. It encodes the synthesis of the proteins required for the doubling of the cell material before cell division. It has also been demonstrated that chloroplasts have their own ribosomes: the bodies where protein is synthesized. The present picture of cellular protein synthesis is that the hereditary information encoded in DNA is transcribed in "messenger" RNA, which then provides the ribosome with the information it needs to link amino acids into a particular protein. In the process each amino acid molecule temporarily combines with a specific molecule of another kind of RNA: "transfer" RNA. Chloroplasts also contain specific transfer RNA's and other components necessary for independent protein synthesis.

Mitochondria also contain DNA that is not related to the DNA of the cell nucleus. The mitochondria in animal cells apparently have only enough DNA and the associated protein-synthesizing machinery to produce a fraction of the structural protein and enzymes needed by these organelles in order to function. Nonetheless, the machinery is there: DNA, messenger RNA, special mitochondrial ribosomes and so forth. The presence of DNA associated with protein synthesis implies that the mitochondria have a functional genetic system.

Here, then, are two organelles of eukaryotic cells that have their own genes and conduct protein synthesis. When one considers that almost all the protein synthesis in the eukaryotic cell is under the direction of nuclear DNA and that the synthesis is accomplished by ribosomes in the cytoplasm external to both the mitochondria and the plastids, it is natural to wonder why these organelles carry duplicate equipment. Does their ability to grow and divide within the cell and to make some of their own protein under the direction of their own genes imply that they were once free-living organisms? A number of investigators have thought so.

When the plastids of eukaryotic algae were studied under the microscope in the 19th century, it was remarked that they resembled certain free-living algae, and it was suggested that they had originated as such algae. A similar origin for mitochondria was proposed in the 1920's by an American physician, J. E. Wallin. On the basis of microscopic observations, of reactions to stains and of assertions (subsequently refuted) that he had grown isolated mitochondria in the laboratory, Wallin maintained that mitochondria were bacteria that had come to live symbiotically within animal cells. In his book *Symbioticism and the Origin of Species* he argued that new species arise as a result of this kind of symbiosis between distantly related organisms. As can happen to people obsessed by a novel concept, Wallin overstated his case and used doubtful data to defend it. His book fell into disrepute.

What is known today about the biochemical autonomy of mitochondria goes a long way toward rehabilitating Wallin's basic concept. It now seems certain that mitochondria were once free-living bacteria that over a long period of time established a hereditary symbiosis with ancestral hosts that ultimately evolved into animal cells, plant cells and cells that fit neither of these categories. The same history evidently holds true for plastids, which were originally free-living algae. I believe that still a third group of organelles, the flagella and cilia, became associated with the eukaryotic cell in much the same way.



COMPLEX SYMBIONT, the protozoon *Myxotricha paradoxa*, lives as a guest in the gut of certain Australian termites and plays host to three symbionts of its own. These are surface bacteria of the spirochete group (*color*), which observers first mistook for flagella, other surface bacteria (*black*) and still other bacteria (*color*) that live inside the protozoon.

Flagella and Cilia

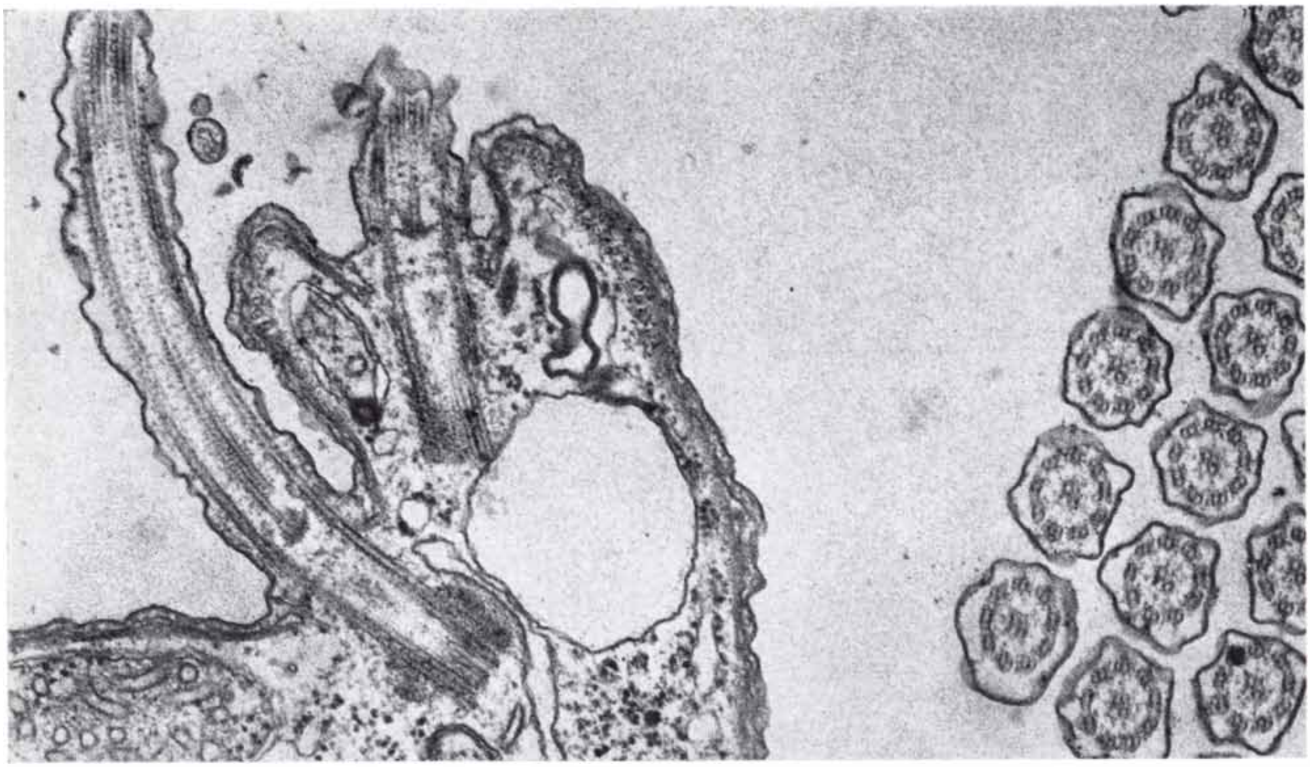
Flagella and cilia are really the same. If these hairlike cell projections are long and few, they are called flagella; if they are short and many, they are called cilia. Their motion propels the cell through its medium or, if the cell is fixed in place, moves things past it. In the tissues of higher animals some flagella and cilia have been drastically modified to serve other functions. The light receptors in the eye of vertebrates are such structures. So are the smell receptors of vertebrates. Among prokaryotes the analogous structures are much simpler. They are small, single-stranded and consist of a protein called flagellin.

The flagella and cilia of eukaryotic cells are much larger than those of prokaryotes. Their basic structure is strikingly uniform, whether they come from the sperm of a fern or the nostril of a mouse. Seen in cross section, each consists of a circle of paired microtubules surrounding one centrally located pair. If the structure is motile, there are always two microtubules in the middle and always nine more pairs surrounding them; the pattern is known as the "9 + 2 array" [*see illustrations on page 54*]. Microtubules from any kind of eukaryotic flagella and cilia are composed of related proteins called tubulin.

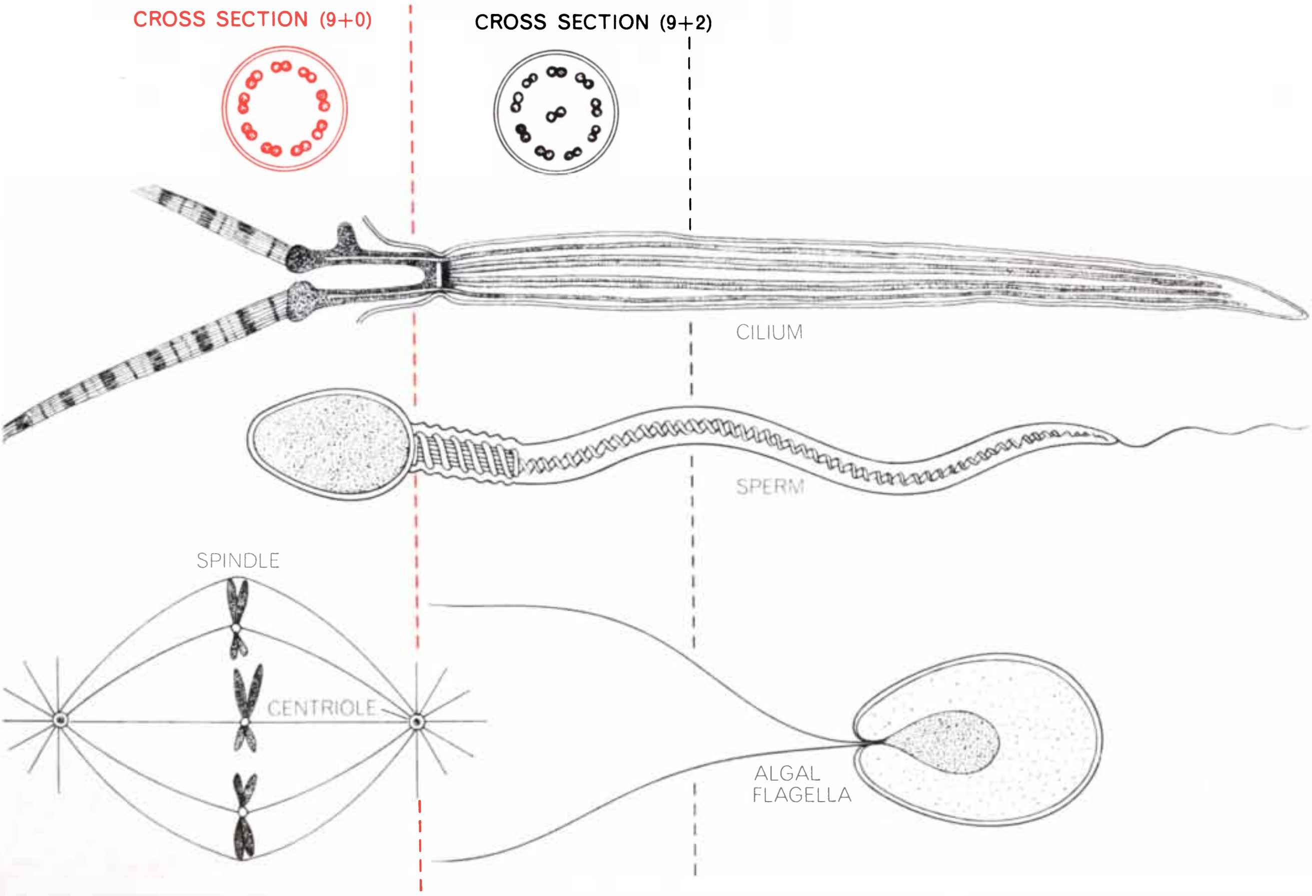
At the base of every eukaryotic flagellum and cilium is a distinct microtubular structure: the basal body. The architecture of the basal body is identical with that of the centriole, a structure found

SURFACE OF *MYXOTRICHA* appears at the bottom in transverse section in this electron micrograph by A. V. Grimstone of the University of Cambridge. In the "hollow" to the left of each surface "peak" lies one of the bacterium guests of the protozoan host. Two symbiotic spirochetes are visible at right with their basal ends attached to the host membrane. Other spirochetes whose attachments are not in the plane of focus are partially visible elsewhere in the micrograph (*top*). The theory proposing that eukaryotic cells are the products of similar symbiotic relationships suggests that the first symbionts were free-living bacterium-like prokaryotes.

PROKARYOTIC GUESTS, identifiable by their array of concentric photosynthetic membranes as the blue-green alga *Cyanocyta*, are enlarged 15,000 times in this electron micrograph by William T. Hall of the National Institutes of Health. They are inside protozoan hosts of the species *Cyanophora paradoxa*. Similar hereditary symbioses between various photosynthetic alga-like prokaryotes and large, more advanced eukaryotic hosts from the kingdom Protista is suggested as the step leading to evolution of the plant kingdom.



STRUCTURE OF FLAGELLA is shown in transverse section (*right*) and longitudinal section (*left*) in an electron micrograph by R. D. Allen of the University of Hawaii. In the part of the flagellum extending beyond the basal body a circle of paired microtubules surrounds a central pair in what is known as a "9 + 2 array." In the basal body the central pair of microtubules is absent and the array is "9 + 0." Such organelles are found only among the eukaryotes and may originally have been free-living cells.



MICROTUBULES comprise a variety of structures, including the motile flagella of certain algae (*bottom right*) and of sperm, the cilia of tracheal membrane and the centrioles and the spindle structure that mediates halving of the nucleus in mitotic division.

at opposite poles of the eukaryotic cell nucleus. Centrioles come into particular prominence during mitosis, the process by which eukaryotic cells divide. (Centrioles are found in nearly all animal cells and in the cells of many eukaryotic algae but not in certain fungi and in most higher plants).

The structural array of the basal body and the centriole is "9 + 0": the central pair of microtubules is absent. In cells that possess mitotic centrioles the centrioles left over from earlier cell divisions often grow projections that become flagella or cilia as the new cell differentiates. Thus not only are basal bodies and centrioles identical in structural pattern but also centrioles can become basal bodies. Moreover, the mitotic spindle, the characteristic diamond-shaped structure that lies between the centrioles during cell division, is an array of microtubules composed of tubulin.

A further finding requires that we now ask two fundamental questions. When the plant alkaloid colchicine is added to tubulin, derived either from flagella or cilia or from spindles, the alkaloid is bound to the protein. The reaction is characteristic of tubulin from the cells of all animals and all eukaryotic plants, but it has never been observed with the flagellin from prokaryotic cells. Nor, for that matter, have microtubules ever been observed in either bacteria or blue-green algae.

The first question is this: What differentiates animals from plants? At the macroscopic level the differences are obvious; for example, most animals move around in order to feed themselves, whereas most plants stand still and nourish themselves by photosynthesis. At the microscopic level distinctions of this kind become meaningless. Many kinds of single-celled organism sometimes nourish themselves by photosynthesis and at other times swim about ingesting food particles. Some organisms crawl like an amoeba at one stage in their development but later stop, sprout stems and disperse a new generation in the form of spores. Further examples are almost innumerable.

Generations of biologists have been troubled by the need to force such organisms into the plant or animal kingdom. A far less ambiguous dichotomy is the division between prokaryotes and eukaryotes. Notable dissenters from the plant-animal classification are Herbert F. Copeland of Sacramento State College, G. Evelyn Hutchinson of Yale University and most recently R. H. Whittaker of Cornell University. In what follows I have modified Whittaker's "five-kingdom" classification, which takes the fundamental prokaryote-eukaryote dichotomy fully into account [*see illustration on pages 50 and 51*]. The answer to the first question, then, is that there are not just two basic kinds of organism but five.

This brings us to the second question: How did five kingdoms arise? I have already suggested that eukaryotic cells, which are characteristic of all higher forms of life, came into existence through an evolutionary advance of a kind fundamentally different from discrete mutation. Specific answers to the second question will appear in the following hypothetical reconstruction of the origin of eukaryotic cells. The reconstruction traces the rise of the more advanced four of Whittaker's five kingdoms from their origin in the least advanced one. That kingdom is the kingdom Monera: the prokaryotic single-celled organisms that were the first living things to evolve on the earth. The reader should be warned that my presentation of the theory here is necessarily brief and oversimplified.

The First Cells

All life on the earth is believed to have originated more than three billion years ago during Lower Precambrian times in the form of bacterium-like prokaryotic cells. At that time there was no free oxygen in the atmosphere. The cells that arose were fermenting cells; their food consisted of organic matter that had been produced earlier by the action of various abiotic processes. Under pressures of natural selection directly related to the depletion of this stock of abiotic nutrients, there arose among the first fermenting bacteria many metabolic traits that are still observable among bacteria living today. These traits include the ability to ferment many different carbohydrates, to incorporate atmospheric carbon dioxide directly into reduced metabolic compounds, to reduce sulfate to hydrogen sulfide as a by-product of fermentation, and so on.

As the ammonia available in some parts of the environment became depleted, certain bacteria evolved metabolic pathways that could "fix" atmospheric nitrogen into amino acids. Other fermenters developed into highly motile organisms that foreshadowed such highly mobile living bacteria as spirochetes. All these fermenting bacteria were "obligate anaerobes," that is, for them oxygen was a powerful poison. Through various detoxification mechanisms the fermenters were able to dispose of the small amount of this deadly element present in the environment as a result of abiotic processes. Finally, many if not all of the various fermenting bacteria were equipped with well-developed systems for the repair of DNA. Such systems were necessary to counteract the damage done by ultraviolet radiation, which at that time was intense because there was no ozone (O_3) in the atmosphere to filter it out.

All these bacteria were heterotrophs; they had not evolved the photosynthetic mechanisms that would have enabled them to nourish themselves in the absence of abiotic organic compounds. In time some of them developed metabolic pathways that led to the synthesis of the compounds known as porphyrins. It is a purely fortuitous property of porphyrins that they absorb radiation at the visible wavelengths; nonetheless, this property was eventually put to use by the evolution of bacterial photosynthesis. The process of photosynthesis requires a source of hydrogen. Bacteria can utilize such inorganic substances as hydrogen sulfide and gaseous hydrogen as well as various organic compounds of the kind that would have been present in the environment as by-products of fermentation. These first anaerobic photosynthesizers appeared in Lower Precambrian times.

When the new photosynthetic bacteria became well established, a process that may have taken millions of years, a second kind of photosynthesis was able to make its appearance. In the second process the uptake of hydrogen was accomplished by the splitting of water molecules; as a result increasing quantities of lethal free oxygen entered the atmosphere as a waste product. The evolution of this mode of photosynthesis led to the appearance of the blue-green algae, the first organisms on the earth that were adapted to the presence of free oxygen. Since they were active photosynthesizers of the newer type, they accelerated the increase in atmospheric oxygen.

The blue-green algae, whose Precambrian success is attested by the massive calcium-rich rock formations they left behind, presented a profound threat to all other forms of life. The other organisms were forced to adapt or perish. Some of the anaerobes adapted simply by retreating into the oxygen-free muds where their fellows are found today. Others developed new mechanisms of oxygen detoxification; still others, it is safe to assume, merely disappeared. In any case, one result of the success of the blue-green algae was the evolution of new kinds of bacteria that utilized free oxygen in their metabolic processes: aerobic respirers, oxidizers of sulfide and ammonia, and the like. As atmospheric oxygen continued to accumulate, the stage was set for the initial appearance of eukaryotic cells.

The First Eukaryote

The first advanced cell came into existence when some kind of host, perhaps a fermenting bacterium, acquired as symbiotic partners a number of smaller oxygen-respiring bacteria. As atmospheric oxygen continued to increase, selection pressure would have favored such a symbiosis. Eventually the small aerobic bacteria became the hereditary guests of their hosts; these were the first mitochondria. The host symbionts, in turn, evolved in the direction of amoebas, so that a new population of large aerobic cells evolved and faced the problem of finding nutrients.

In due course the partners were aided in their quest for food: a second group of symbionts, flagellum-like bacteria comparable to modern spirochetes, attached themselves to the host's surface and greatly increased its motility. If this hypothetical triple partnership begins to resemble the termite symbiont *Myxotricha,* it is with good reason; I believe that just such a *Myxotricha*-like symbiotic association, formed in Precambrian times, was a universal ancestor to all eukaryotic organisms. With the appearance of this supercell the kingdom Monera gives rise, in a manner consistent with Whittaker's taxonomic system, to the kingdom Protista.

The internal guests, then, served as mitochondria and the external ones as flagella. The spirochete-like guests, however, slowly evolved another role. The specialized basal body of the flagellum and its associated microtubules came to serve the additional function of mediating the process of cell division. Respectively the centriole and the mitotic spindle, they were responsible for dividing the parent cell's genes evenly between daughter cells.

Mitotic cell division was the crucial genetic step toward further evolutionary advance. One would not expect it to have developed in a straight-line manner, starting with no mitosis and concluding with perfect mitosis. There must have been numerous dead ends, variations and byways. Evidence of just such uncertain gradualism is found today among the lower eukaryotes, for example the slime molds, the yellow-green and golden-yellow algae, the euglenids, the slime-net amoebas and others. Many of their mitotic arrangements are unconventional. The perfection of mitosis may have occupied as much as a billion years of Precambrian time.

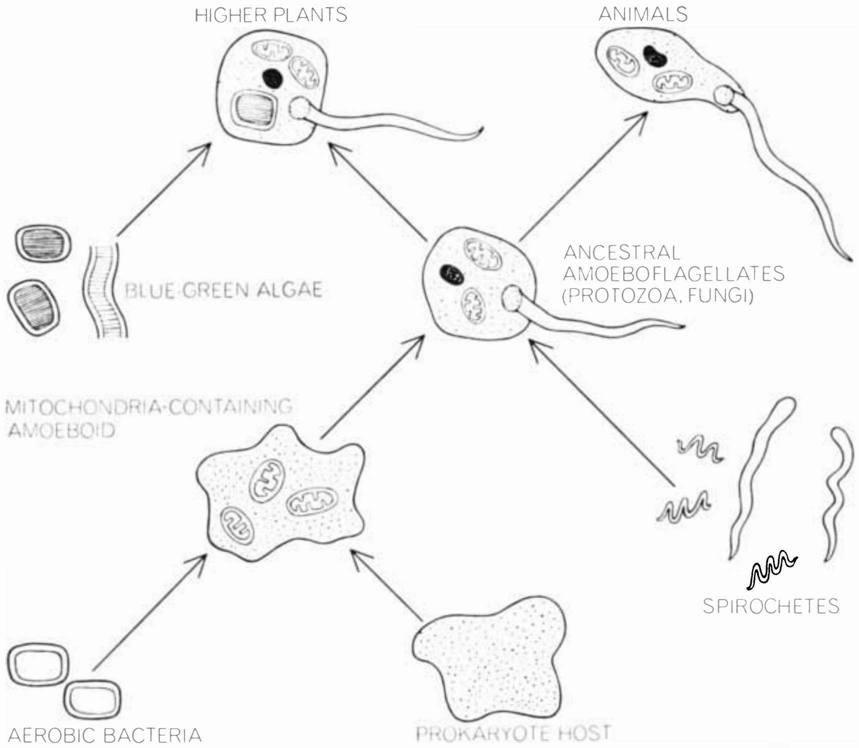
Mitosis, however, was the key to the future. Without mitosis there could be no meiosis, the type of cell division that gives rise to eggs and sperm. There could be no complex multicellular organisms and no natural selection along Mendelian genetic lines. As mitosis was perfected the kingdom Protista gave rise to three other new kingdoms.

Plant-like protists probably appeared several times through symbiotic unions between free-living, autotrophic prokaryote blue-green algae and various heterotrophic eukaryote protists. After much modification the guest algae developed into those key organelles of the plant kingdom, the photosynthetic plastids. Some of the original symbiotic organisms are represented today by the eukaryotic algae that eventually evolved into the ancestors of the plant kingdom. Both algae with nucleated cells and higher plants have of course evolved a great deal since they first acquired photosynthetic guest plastids more than half a billion years ago. Their evolutionary progress, however, involves neither the origin nor any fundamental modification of the photosynthetic process. This heritage from their anaerobic prokaryote ancestors they received fully formed at the close of the Precambrian.

The group of organisms that we know as the fungi—molds, mushrooms, yeasts and the like—are also thought to derive directly from protists that relinquished flagellar motility in exchange for mitosis. This suggestion is consistent with Whittaker's classification. He splits the fungi from the plant kingdom and recognizes that these fundamentally different organisms deserve a domain of their own. The evolution of the animal kingdom, in turn, is considered a straight-line consequence of natural selection acting on the multicellular, sexually reproductive organisms that, like the fungi, did not happen to play host to plastids in Upper Precambrian times.

Testing the Hypothesis

Compared with what had gone before, however, all this seems to be virtually modern history. It is more pertinent at this juncture to see if the theory of



SYMBIOSIS THEORY is summarized in the three steps illustrated here. Union between two members of the kingdom Monera, a newly evolved aerobic bacterium (*bottom left*) and a larger host, possibly a fermenting bacterium (*bottom right*), brought into existence an amoeboid-like protist whose several guests became mitochondria. A second hereditary symbiosis, joining the amoeboid to a bacterium of the spirochete group (*center right*), brought into being an ancestral "amoeboflagellate" that was the direct forebear of two kingdoms: Fungi and Animalia. When the same amoeboflagellate went on to form another relationship, with algae that became plastids, the fifth kingdom, Plantae, was founded.

FREE-LIVING MONERAN, a bacterium of the spirochete group, is seen magnified 55,000 times in this electron micrograph. It is an anaerobic bacterium found in the human mouth. Organisms like this may have given rise to the eukaryotic flagella through symbiosis.

eukaryotic-cell origin through hereditary symbiosis offers useful answers to further outstanding questions.

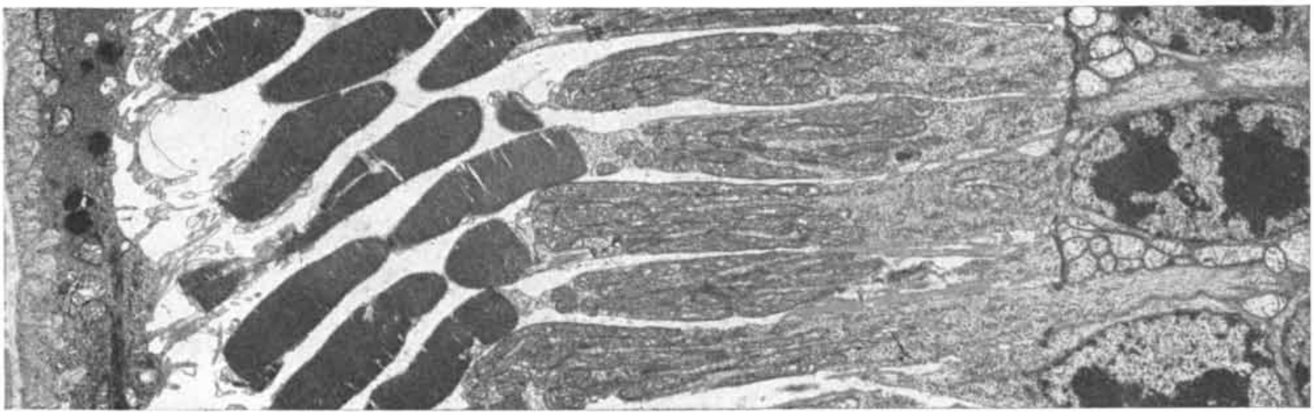
Why are there genes outside cell nuclei? Some cytoplasmic genes may have arisen in other ways, but the symbiosis theory holds that the genes associated with chloroplasts and mitochondria demonstrate that these two kinds of organelle were once free-living organisms.

Why does evidence for photosynthesis appear in Middle Precambrian times, even though no higher plants appear in the fossil record until a mere 600 million years ago? The theory proposes that the higher plants are the result of a symbiosis between animal-like hosts and photosynthetic blue-green-alga-like guests whose partnership could not have evolved until relatively recent times, when mitosis had been perfected.

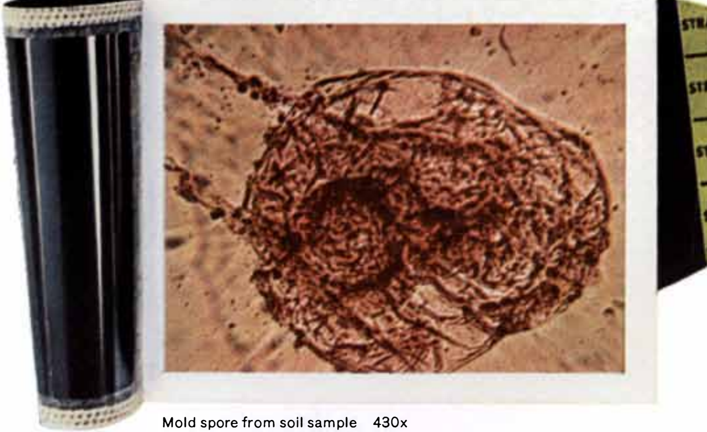
Why should there be any connection between, on the one hand, the basal body and the flagellum and, on the other, the centriole and the mitotic spindle? The proposal is that the original free-living organism that once accounted only for the function of motility was ancestral to the organelles that came to mediate the equal partition of genetic material between daughter cells during mitosis.

Obviously many other questions remain to be answered. Can the synthesis of DNA and of messenger RNA be detected in association with the reproduction of the basal body and the centriole? Can evidence be found of a unique protein-synthesis system associated with these bodies? Without such evidence the case for these organelles having once been free-living organisms is weak. How and when did meiosis evolve from mitosis? Which organisms were the initial hosts to the guest bacteria that became mitochondria? Were guest plastids of different kinds—red, brown, golden-yellow—acquired independently by the various kinds of eukaryotic algae? One related question is profoundly social. Can botanists, invertebrate zoologists and microbiologists, with their widely different backgrounds, agree on a single classification and a consistent evolutionary scheme for the lower organisms?

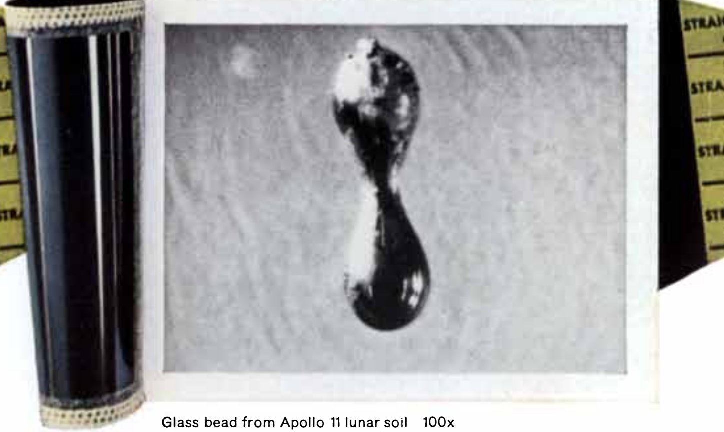
Conclusive proof that the symbiosis theory is correct demands experiment. The symbiotic partners will have to be separated, grown independently and then brought back into the same partnership. No organelle of a eukaryotic cell has yet been cultivated outside the cell. The function of a theory, however, is to make reasonable predictions that can be proved or disproved. The predictions of the symbiosis theory are clear.



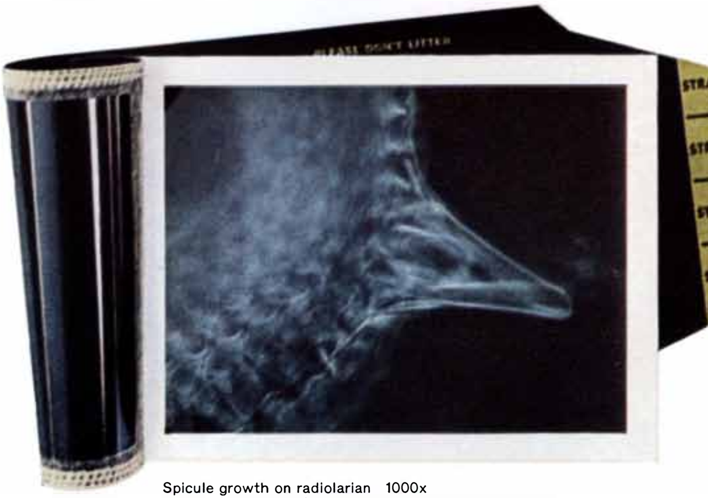
SPECIALIZED FLAGELLA, shown enlarged 3,900 times in an electron micrograph by Toichiro Kuwabara of the Harvard Medical School, are visual receptors in the retina of a rabbit. The darker structures at left are the outer segments of the visual receptors.



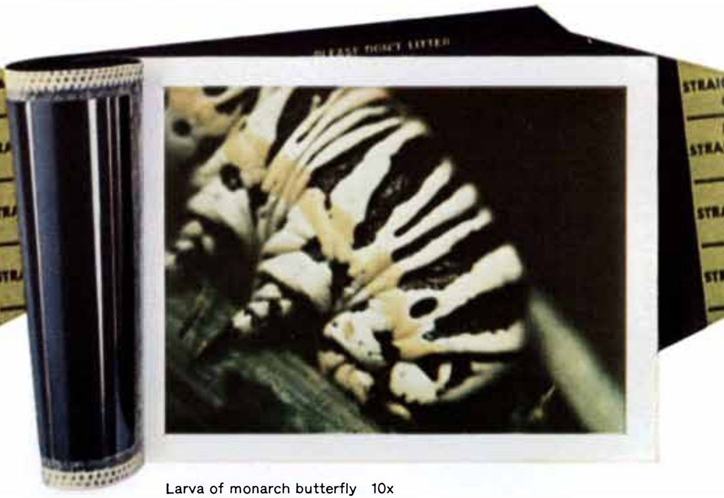
Mold spore from soil sample 430x
David McCurdy, Middletown, N.J.



Glass bead from Apollo 11 lunar soil 100x
Dr. W. D. Ehmann, University of Kentucky

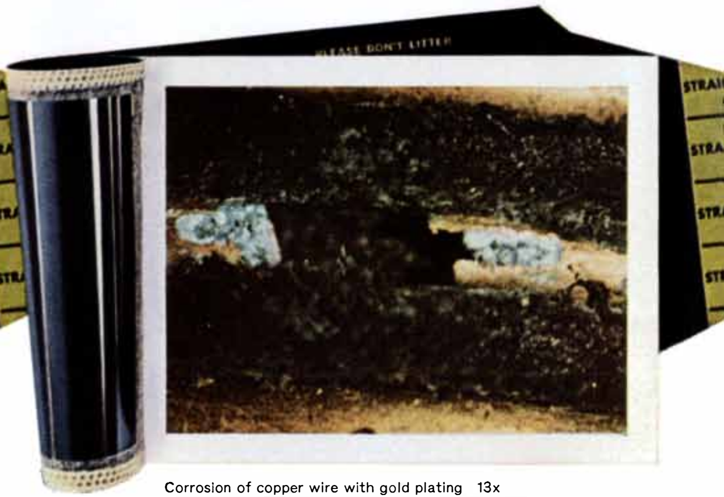


Spicule growth on radiolarian 1000x
Selwyn R. Mather, Elmhurst, Ill.

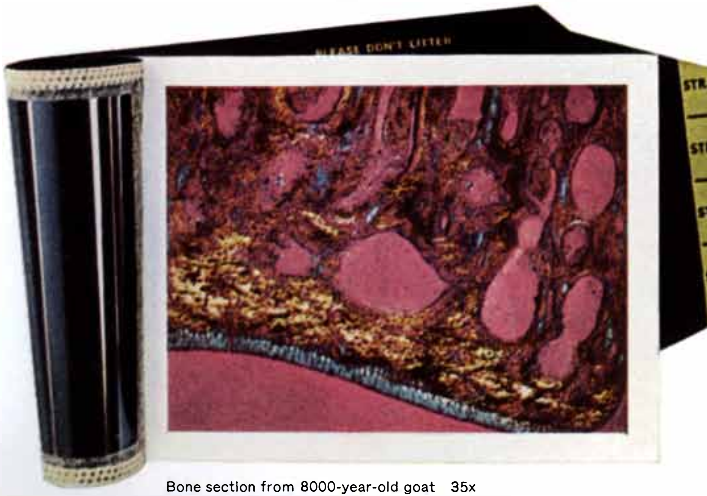


Larva of monarch butterfly 10x
J. Roger Matkin, Santa Ana, Calif.

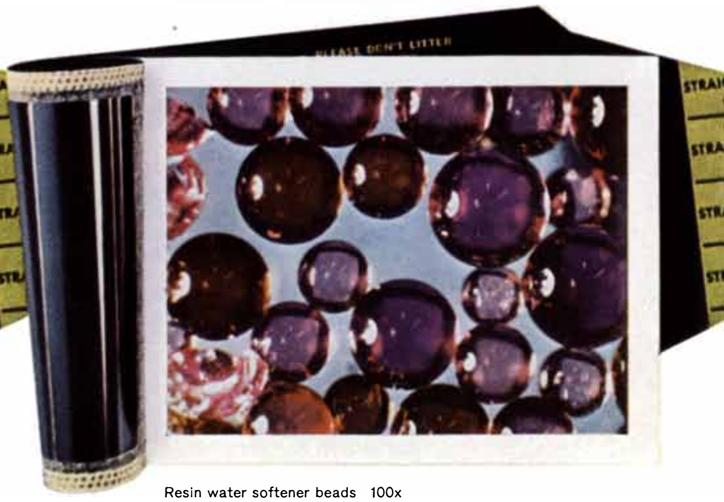
Freshwater copepod cyclops 80x
Robert J. Western, Kailua, Hawaii



Corrosion of copper wire with gold plating 13x
Walter R. Banzhaf, Ledyard, Conn.

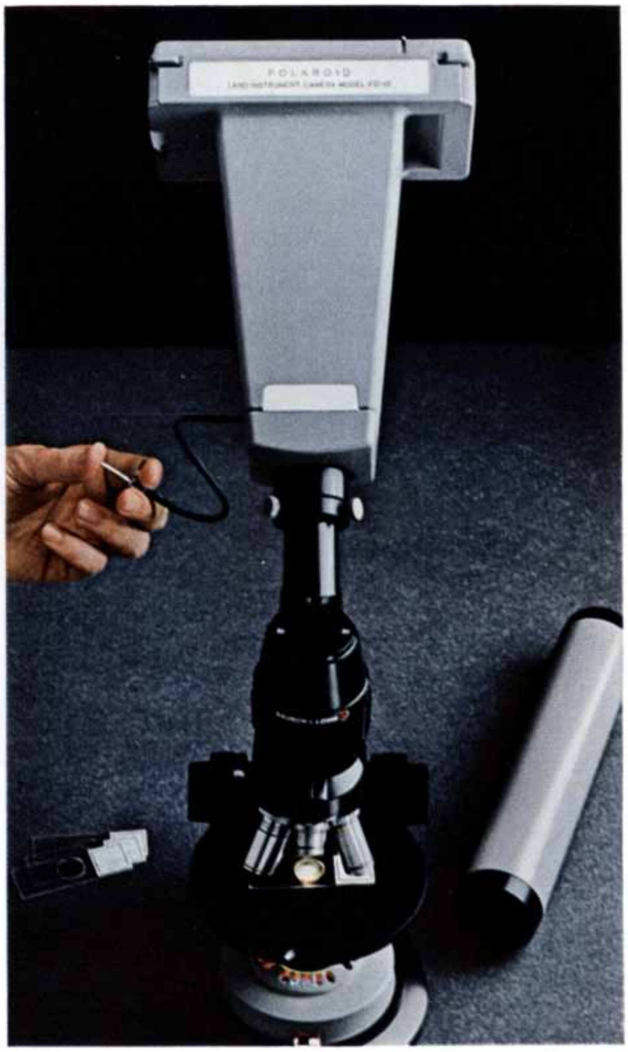


Bone section from 8000-year-old goat 35x
Dr. Isabella M. Drew, Sackler Lab., Columbia University



Resin water softener beads 100x
Benjamin B. Bonadio, Madison, Ind.

All it takes is a microscope, a minute, and less than $70.



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It's well worth looking into.

The Polaroid Land Instrument Camera.