CENGAGE

SEVENTH EDITION

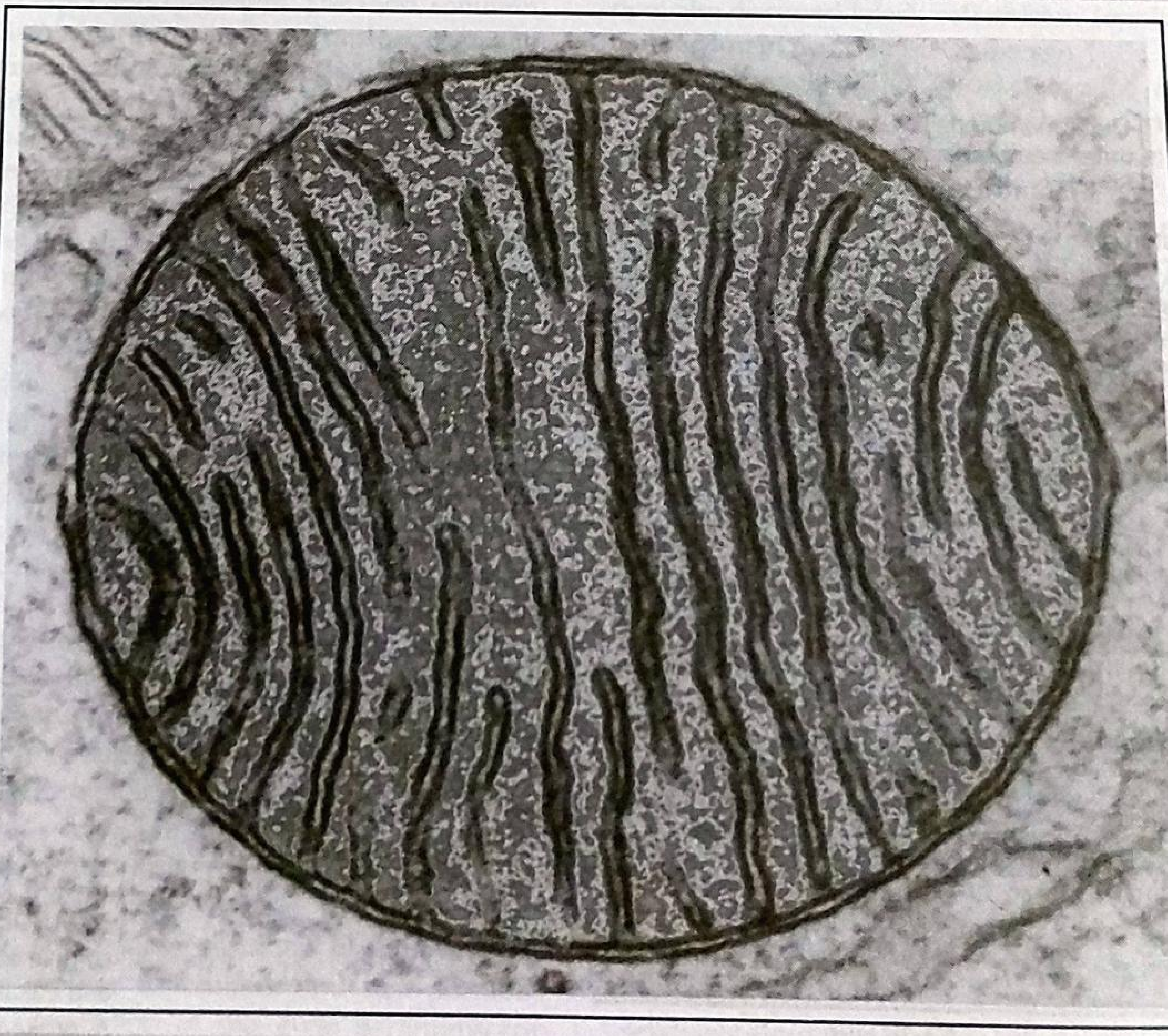
# INVERTEBRATE ZOOLOGY

## A Functional Evolutionary Approach

RUPPERT • FOX • BARNES

# 2 Introduction to Protozoa





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The unicellular **eukaryotes**—cells with a membrane-enclosed nucleus—are the atoms of the invertebrate world. Each cell is a complete organism adapted to meet the challenges of life, but some form colonies of cells, and from these evolved the world's multicellular organisms (fungi, algae, plants, animals). The entire assemblage of unicellular eukaryotes is known as Protista, and a large subgroup of mostly motile forms is called protozoa. The protozoa and its taxa will be discussed in Chapter 3. The purposes of this chapter are to describe the structure, function, and evolution of the eukaryotic cell with an emphasis on animal cells. As eukaryotes, protozoans have the same cellular components found in the cells of animals, plants, and fungi, but as cell-organisms, protozoans have specialized these parts into the functional equivalents of tissues and organs. These uniquely protozoan organelles and other structures will be described in Chapter 3. This chapter discusses the basic tool kit of eukaryotic cells and how it evolved.

# EUKARYOTIC CELL STRU

Eukaryotic cells contain **organelles**, functi... ulated compartments surrounded by one... (Fig. 2-1). One organelle, the **nucleus**, conta... is surrounded by a double membrane... genomic compartment from the metabolic... cytoplasm. Other organelles include mito... plasts, both of which are enclosed in two... **dria** contain DNA and the enzymes for... **Chloroplasts** also have DNA and are the site...

Apart from the cell membrane itself... eukaryotic cells has an **internal membr...** includes the endoplasmic reticulum, Golgi... somes (Fig. 2-1). Arising from the outer... the **endoplasmic reticulum** is a mazelike... network that functions in the synthes... lipids, and, when ribosomes are present... **body** is a stack of flattened vesicles that...

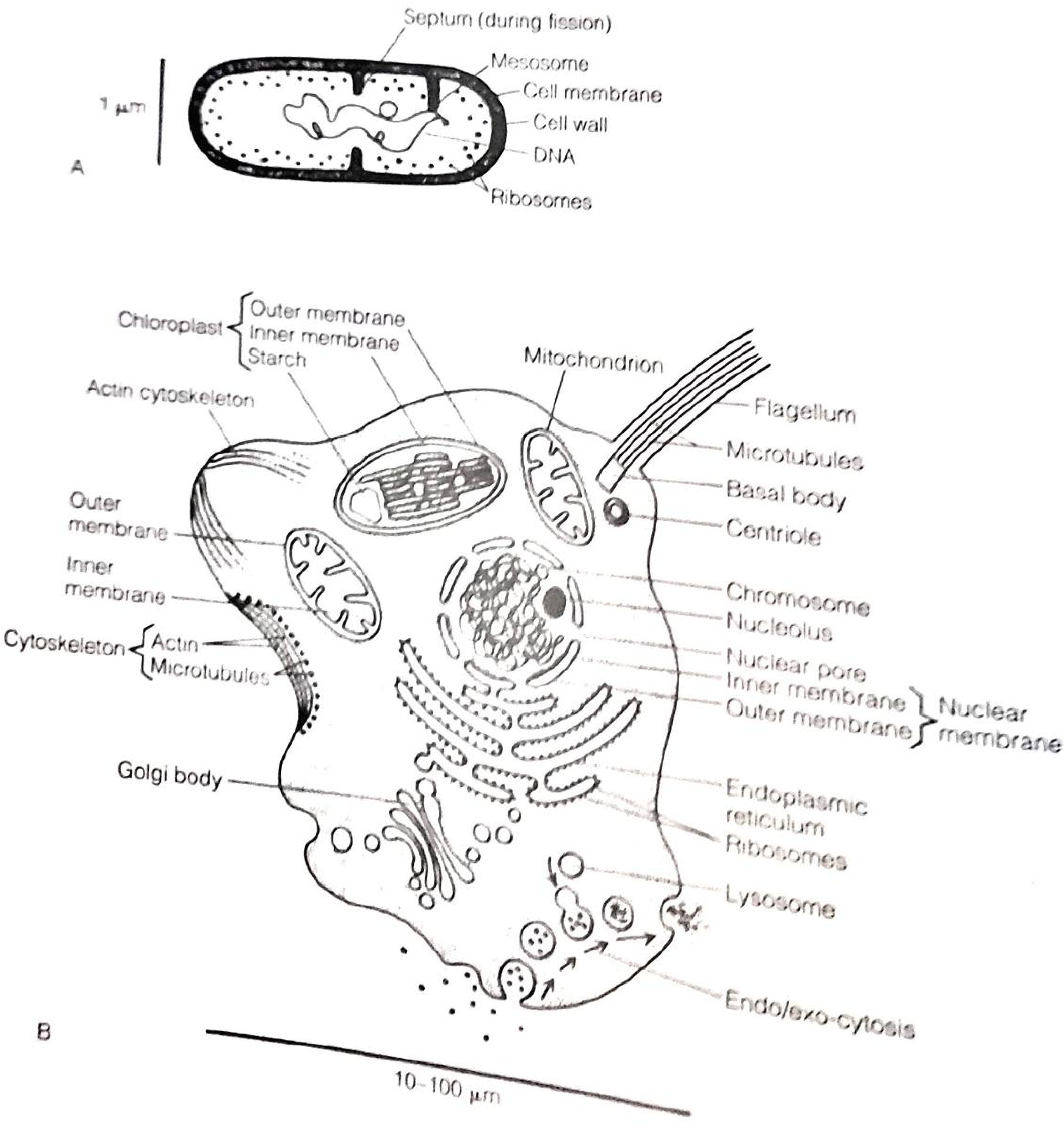


FIGURE 2-1

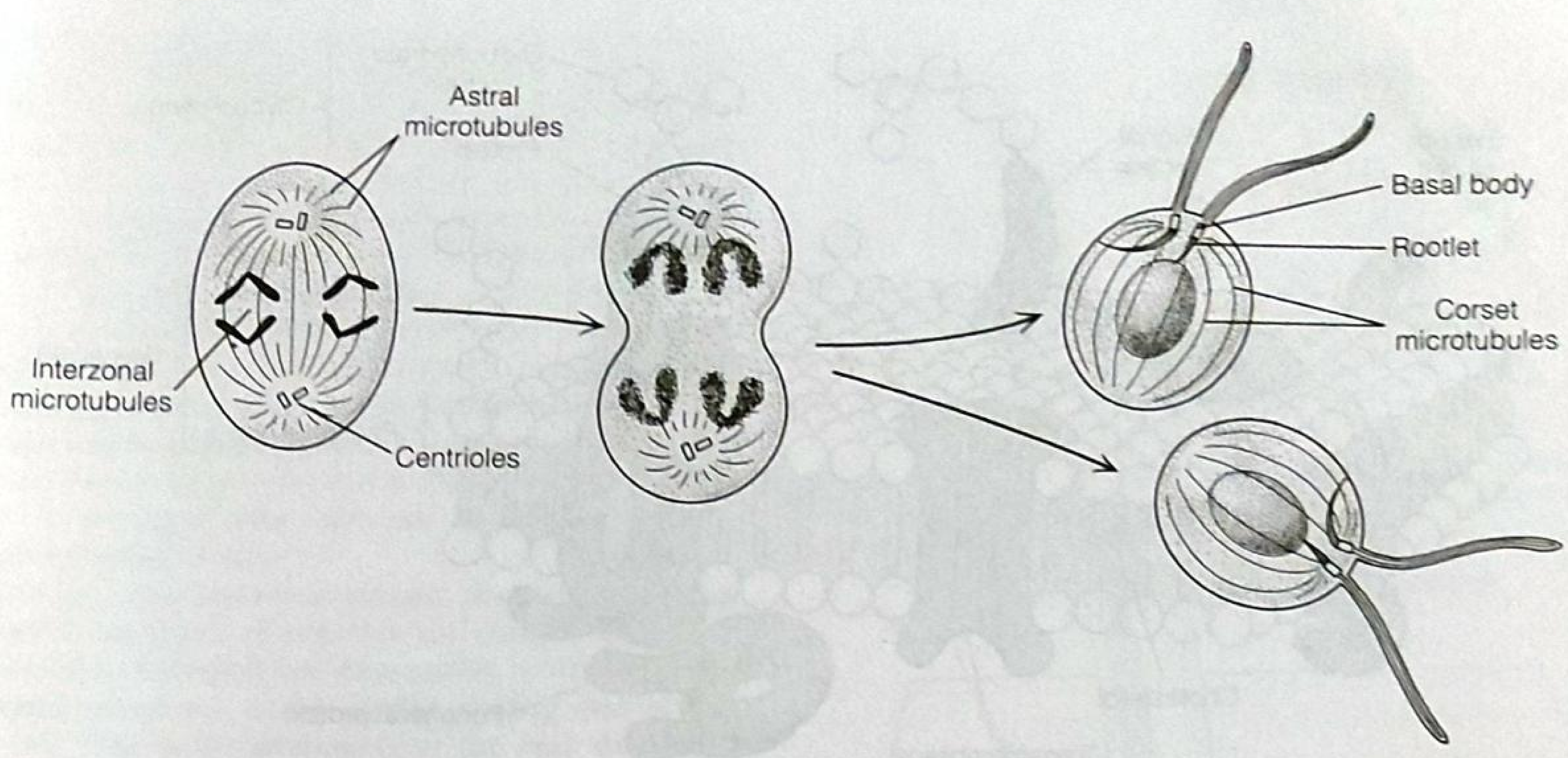


**FIGURE 2-2** Eukaryotic cell structure. Relationship of centrioles and mitotic spindle fibers (astral and interzonal microtubules) to flagellar basal bodies and cytoskeleton (corset microtubules).

the endoplasmic reticulum, then modifies and releases them in vesicles for transport elsewhere, often to the surface of the cell. **Lysosomes** are Golgi-derived, membrane-bound vesicles that contain enzymes for intracellular digestion.

Unlike prokaryotes (bacteria), which support themselves with a cell wall, the eukaryotic cell has a **cytoskeleton** of protein filaments of different types and diameters. The most common of these are **actin** filaments (6 nanometers [nm] in diameter, also called **microfilaments**) and **microtubules** (15 nm in diameter; Fig. 2-2). Microfilaments are polymers of monomeric actin and microtubules are cylindrical polymers of the protein tubulin. The cytoskeleton typically has the form of a three-dimensional network and is responsible for the maintenance of cell shape. Often, it is well developed just below the cell membrane, where it strengthens the cell surface. The cytoskeleton, however, is not always a static or permanent fixture, but rather can be dynamic and temporary. Because polymerization of the cytoskeleton is reversible, the filaments or tubules can be locally assembled or disassembled to provide scaffolding for special structures, such as the transient spindle apparatus associated with mitosis (Fig. 2-2) or the outgrowth of semipermanent cilia and flagella from the cell surface (Fig. 2-1, 2-5).

The eukaryotic cytoskeleton is also essential for **cell motility.** As is true of other skeletons (see Chapter 4), the cytoskeleton can transmit force from one part of the cell to another, resulting in cell movement, or its filaments can serve as tracks along which vesicles and other structures are transported. In either case, the force for movement is generated by so-called **motor molecules,** such as myosin and dynein, which change shape in the presence of ATP. Typically, a motor molecule that is attached securely to one structure attaches temporarily to the cytoskeleton and flexes, moving the structure with respect to the skeleton (Fig. 2-5). The motor molecule then withdraws from its original attachment site, forms another attachment at a new position, and flexes once again. Repetition of this cycle is reminiscent of walking on a treadmill, and is referred to as **treadmilling. Dynein,** the motor molecule associated with microtubules, is important for the movement of cilia and flagella as well as for shuttling vesicles inside of the cell. **Myosin** binds to actin as well as to other structures and is responsible for ameboid movement (discussed later), streaming, and cyclosis (cytoplasmic circulation, also discussed later), cell division (cytokinesis), and muscle contraction in metazoans (Chapter 6).

The organelles and cytoskeleton of the eukaryotic cell are surrounded by a fluid **cytoplasm.** Cytoplasm, in turn, is enclosed by the **cell membrane,** a phospholipid bilayer that separates the internal environment of the cell from the exterior (Fig. 2-3). In doing so, it regulates the biochemical conditions of the cell's interior for the processes of life. The cell membrane controls what may enter and leave the cell, the responsiveness of the cell to external stimuli, the selectiveness with which the cell binds to other cells or to a substratum, and the maintenance of cell shape. The bilayered structure of the cell membrane results from the opposing phospholipids that compose it (Fig. 2-3). Proteins are also important membrane constituents and may span it or be attached to the inner or outer surfaces. The exposed outer surfaces of membrane proteins and lipids may have attached to them carbohydrates that radiate into the surrounding medium like tails. Together, these tails and especially their extracellular peripheral proteins form a surface coat, or **glycocalyx,** outside the cell. The glycocalyx is an important physiological barrier; it forms a template on which the exoskeleton is secreted and regulates binding to signal molecules and to surfaces, such as other cells. Membrane proteins may receive and transmit signals to the interior of the cell and serve as points of anchorage for cytoskeletal fibers. The cell membrane itself can also play a skeletal role. If the membrane lipids are largely unsaturated, like some vegetable oils used in cooking, the membrane is relatively fluid and flexible. If, on the other hand, the lipids

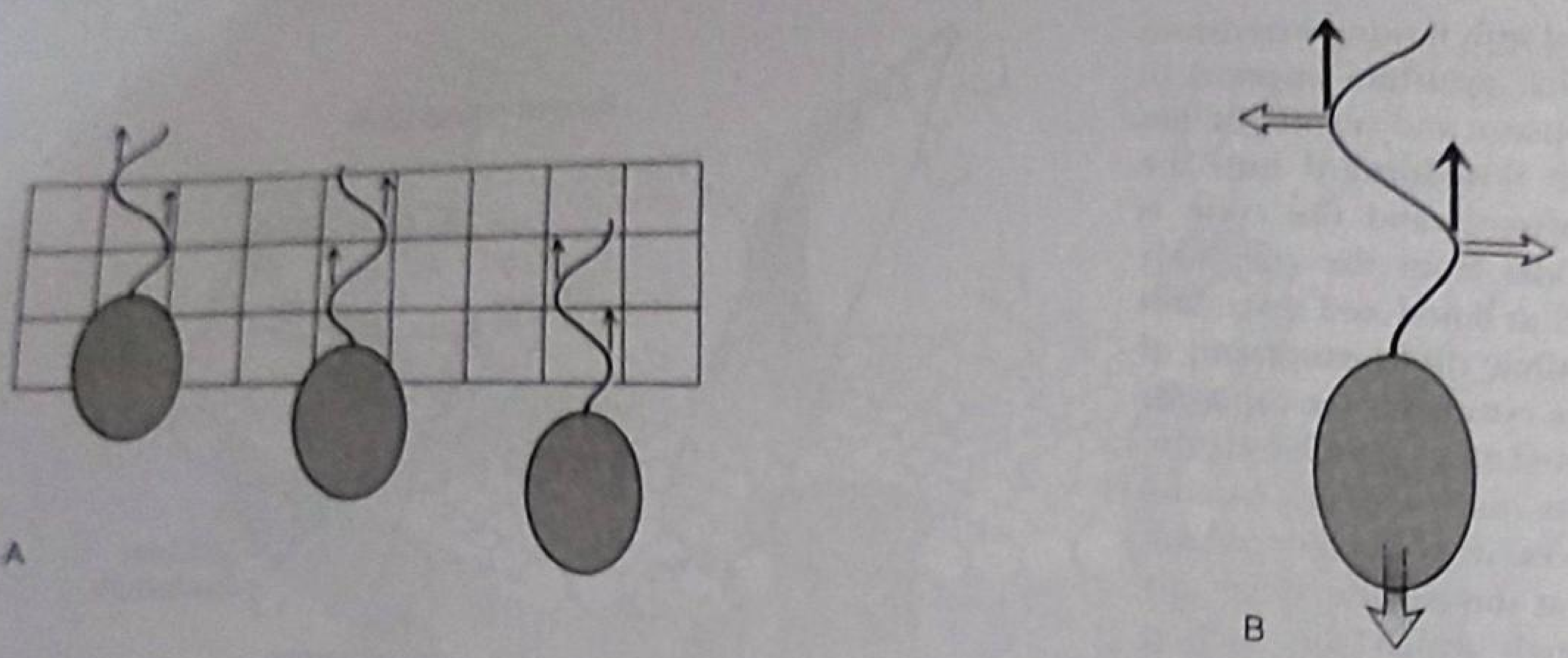


**FIGURE 2-6** Cell motility: flagellar propulsion in a pro... **A,** base-to-tip wave propaga... **B,** forces generated by base-to... wave propagation. Lateral for... (outlined arrows) cancel each other. Longitudinal forces (solid arrows) combine to produce thrust.

(Fig. 2-2). A region around basal bodies and centrioles called the **microtubule organizing center (MTOC)** controls the polymerization of microtubules while the basal body is the template on which developing axonemes are organized.

In most protozoan and metazoan cells, the flagellum propagates an undulatory wave from the cell to the flagellar tip that pushes the cell in the direction opposite the flagellum or drives water away from the flagellar end of a stationary cell (Fig. 2-6). (We will encounter some exceptions later, in Chapter 3.) As an undulatory wave moves along the flagellum, the advancing wavefront, like a wave approaching a beach, generates a *longitudinal* pushing force (Fig. 2-6B). In the meantime, the sideways undulations of a flagellum generate *lateral* forces. Because the lateral undulations are usually symmetrical, the left-directed ... cancel the right-directed forces, and only the longitudinal ... remains to move the cell.

Cilia are short, commonly numerous, densely ar... and especially well represented in the ciliate pro... such as *Paramecium* and related genera (Fig. 2-7A). Dur... effective stroke, the cilium is outstretched stiffly and ... in an oarlike fashion, perpendicular to the cell surface ... 2-7B). In the recovery stroke, the cilium flexes and ... forward parallel to the cell surface. As the organism ... through the medium, the ciliary beat is coordinated ... surface of the cell. The cilia in any cross row are all ... same stage of the beat cycle, while those in front are in ...

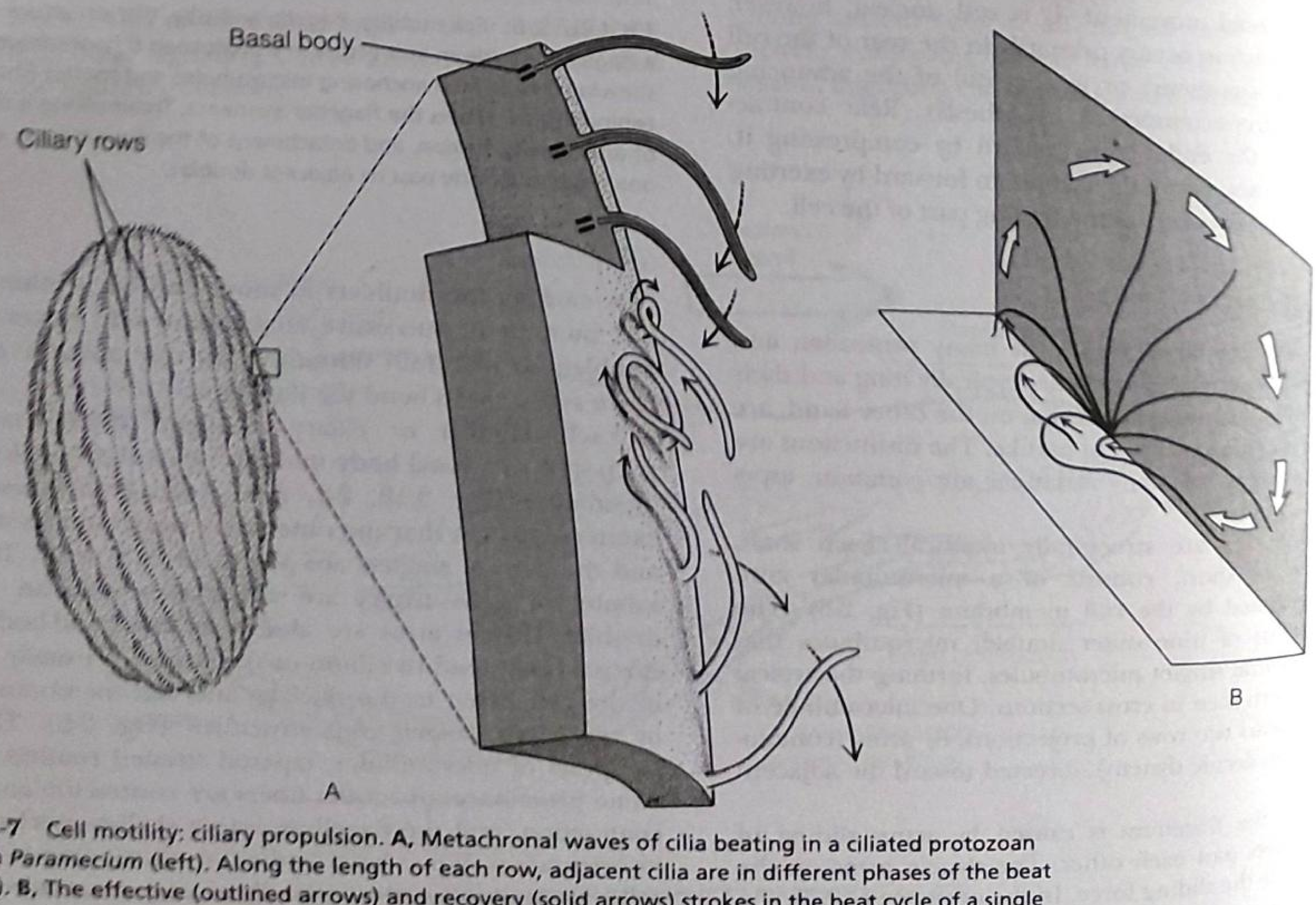


**FIGURE 2-7** Cell motility: ciliary propulsion. **A,** Metachronal waves of cilia beating in a ciliated protozoan related to a *Paramecium* (left). Along the length of each row, adjacent cilia are in different phases of the beat cycle (right). **B,** The effective (outlined arrows) and recovery (solid arrows) strokes in the beat cycle of a single cilium.

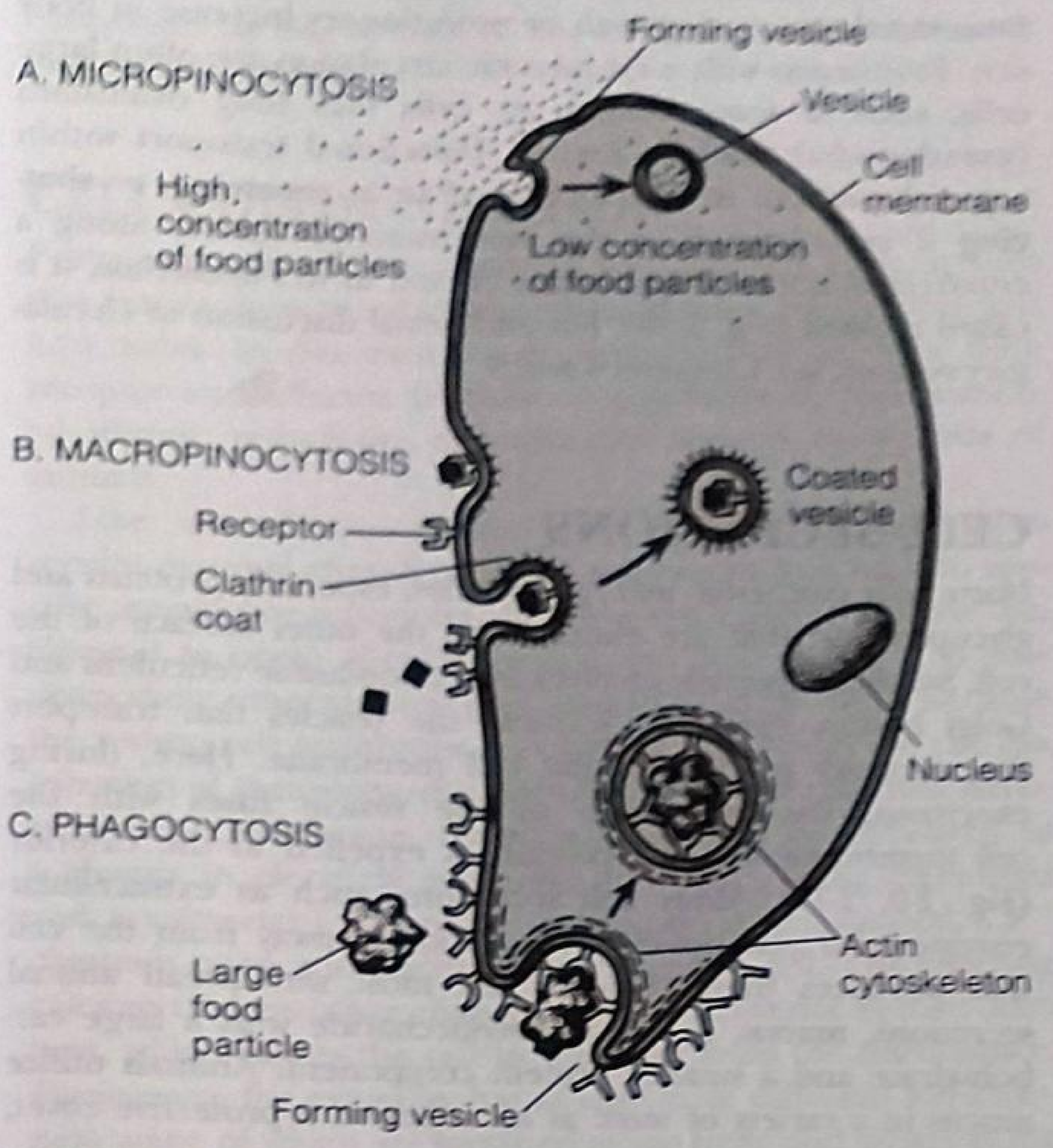


**FIGURE 2-8** Endocytosis. **A,** micropinocytosis; **B,** macropinocytosis; **C,** phagocytosis.

lier stage and those behind are in a later stage (Fig. 2-7A inset). This phase shift is seen as waves, called **metachronal waves,** that pass over the surface of the cell like wind passes in waves over a wheat field.

## UPTAKE BY CELLS

Substances enter the cells of protozoans and other eukaryotes in a variety of ways. The protein channels of the cell membrane provide for the passive diffusion of water, ions, and small molecules, such as sugars and amino acids. Some function as energy-requiring pumps, actively transporting certain molecules or moving ions in or out against their concentration gradient.

Some extracellular materials enter a cell in minute pits on the cell's membrane that later pinch off internally—a process called **endocytosis** (Fig. 2-8). **Micropinocytosis** is a nonspecific form of endocytosis in which the rate of uptake is in simple proportion to the external concentration of the material being absorbed (Fig. 2-8A). Water, ions, and small molecules may be taken in by micropinocytosis. **Macropinocytosis** brings in proteins and other *macro*molecules at a rate greater than predicted by the concentration gradient. These substances may or may not bind to, and be concentrated on, specific membrane receptors before they are internalized in vesicles, which are coated with a protein called clathrin (Fig. 2-8B). Larger particles, such as bacteria and protozoans, are taken up in large vesicles **(food vacuoles)** by **phagocytosis** (Fig. 2-8C). Phagocytosis requires binding of a particle to membrane receptors and dynamic alteration of the cell membrane involving the actin cytoskeleton.

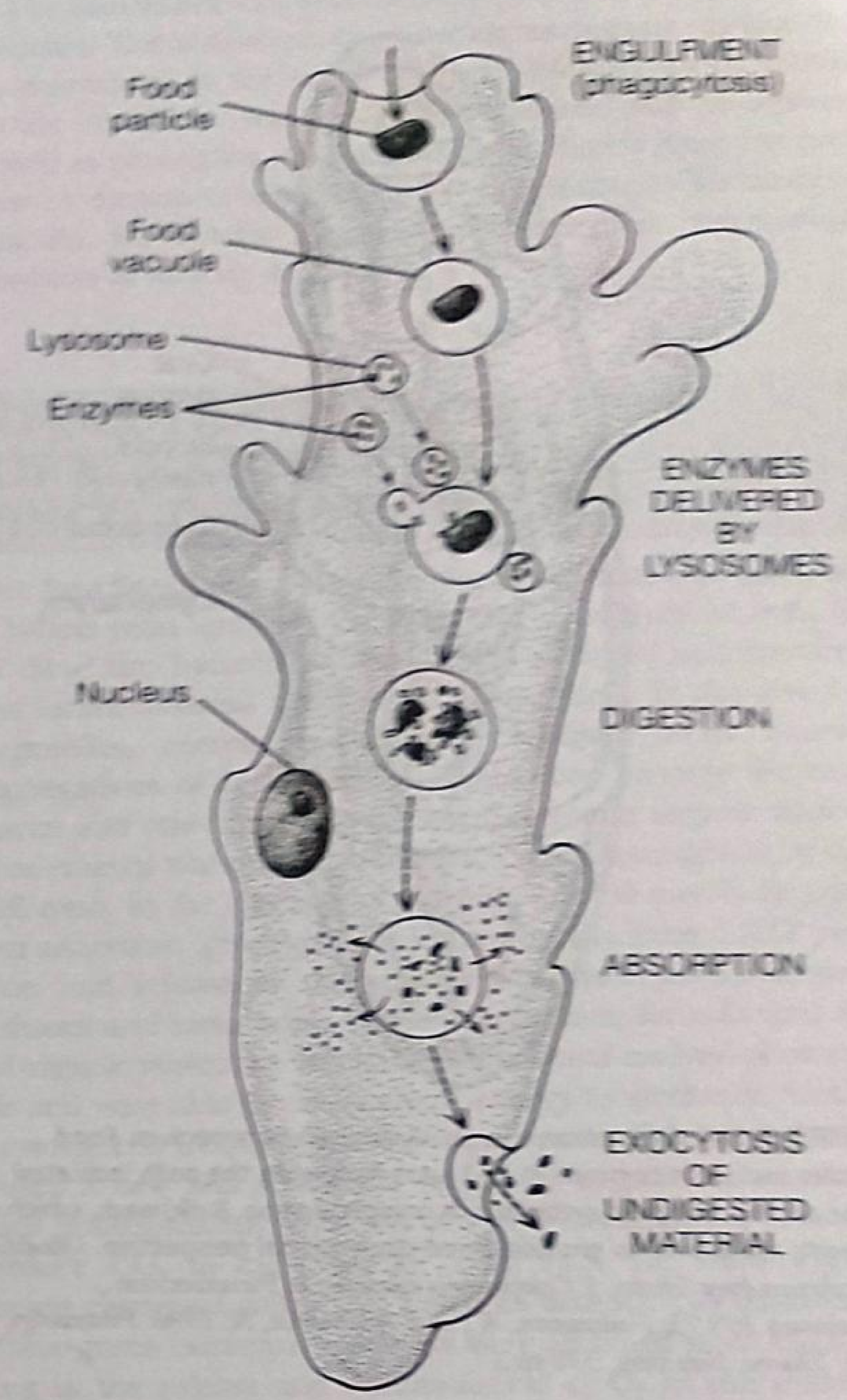


**FIGURE 2-9** Intracellular digestion in an ameba-like protozoan.

## INTRACELLULAR DIGESTION

Once food enters the cell, lysosomes fuse with the endocytic vesicles or food vacuoles. Lysosomes are membrane-enclosed organelles that originate from Golgi bodies and contain acids and hydrolytic enzymes (Fig. 2-9). Release of those biomolecules into the food vacuole initiates digestion. Eventually, the products of intracellular digestion diffuse across the vacuole membrane into the cytoplasm of the cell, where they may be used in metabolism or stored, after undergoing synthesis, in forms such as glycogen and lipids. Indigestible material is released from the cell to the exterior by fusion of the residual vacuole with the cell membrane in a process called **exocytosis** (Fig. 2-9).

## CIRCULATION IN CELLS

Some protozoans have a definite cytoplasmic circulation. In general, circulatory systems are required when the supply of a substance by simple diffusion cannot keep pace with the metabolic demand for it. This limit is often reached as an organism becomes large, regardless of whether that results

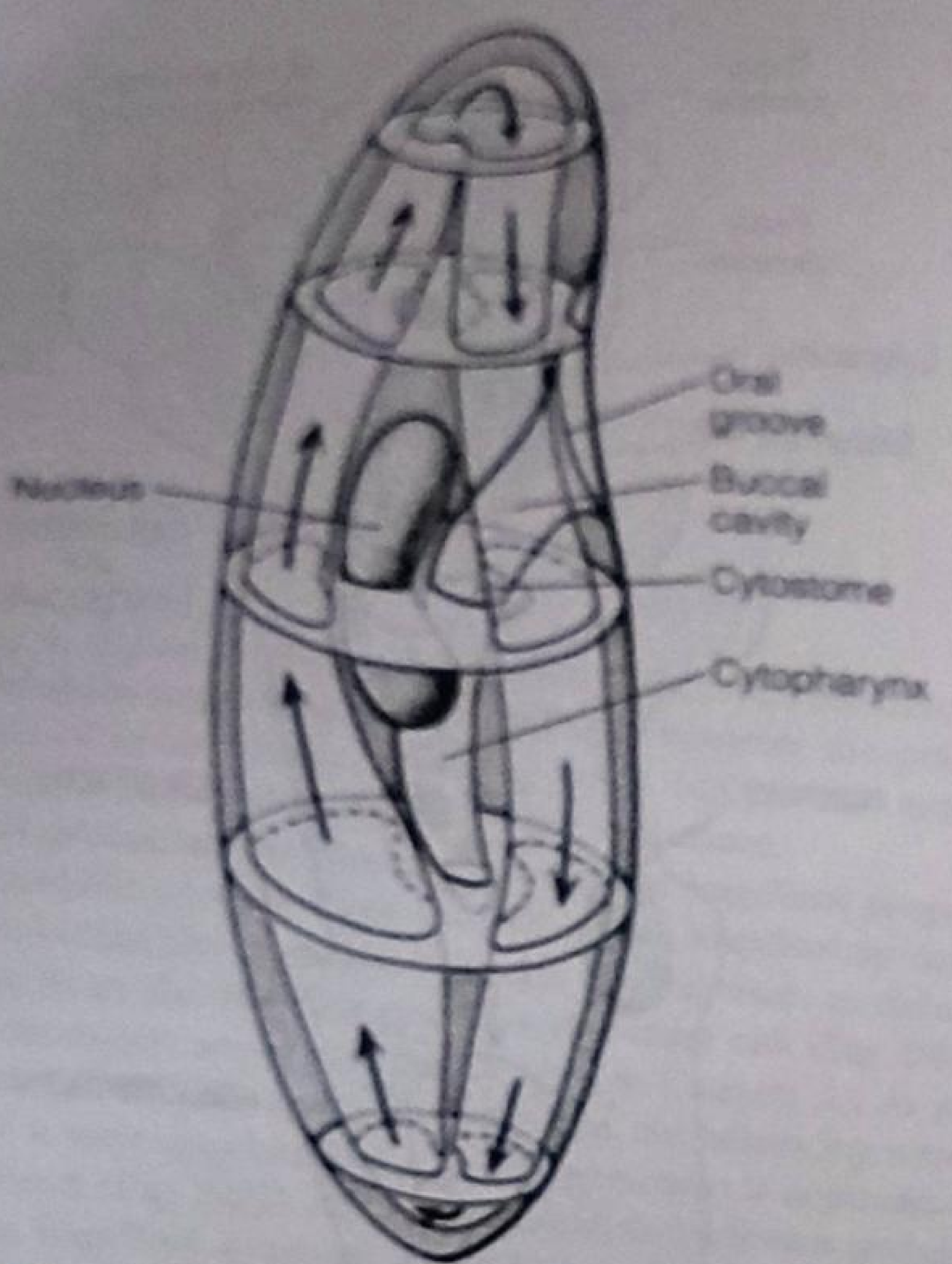


**FIGURE 2-10** Circulation in cells. Cyclosis in *Paramecium*. Food vacuoles and vesicles move at 2–3 µm/s following the path indicated by the arrows. Stippled cytoplasm is noncirculating. Bulkheads, which do not exist, are drawn to provide three-dimensional perspective. *(Modified and redrawn from Sikora, J. Cytoplasmic streaming in Paramecium. Protoplasma 109:57; Hausmann, K., and Hülsmann, N. 1996. Protozoology. Georg Thieme, New York. 338 pp.)*

from developmental growth or evolutionary increase in size. Protozoans with a cytoplasmic circulation are … cells, such as some ciliates, or cells with long … (pseudopodia), such as forams. Directional transport … a pseudopodium or cell is referred to as **streaming** … **fling** if in reference to the movement of vesicles … cytoskeletal track. If flow is in a circuit, as in *Parame…* called **cyclosis** (Fig. 2-10). For additional discussion … tory systems, see Chapters 4 and 9.

## CELL SECRETIONS

Many cells synthesize macromolecules, especially pro… glycoproteins, that are exported to the outer surface … cell. Synthesis typically involves the endoplasmic retic… Golgi bodies, the latter forming the vesicles that … the secretory product to the cell membrane. Dur… exocytosis, the membrane of the vesicle fuses … cell membrane and the product is expelled to the … (Fig. 2-9, 2-11). Many cell secretions, such as … enzymes and pheromones, are exported away from … that produces them. One of the most widespread … secretions, **mucus**, is a mucopolysaccharide with … bohydrate and a smaller protein component. … mucus in a variety of ways: as an adhesive, a protec… and a lubricant.

Some cell secretions remain associated with the … surface of the cell membrane to form extracellular … materials (Fig. 2-11), of which **chitin** is a good … Chitin is a cellulose-like polysaccharide that … an exoskeleton around the bodies of some protozoa … example, the protective retreat of the marine … *culina*, cysts of amebas) as well as metazoans …

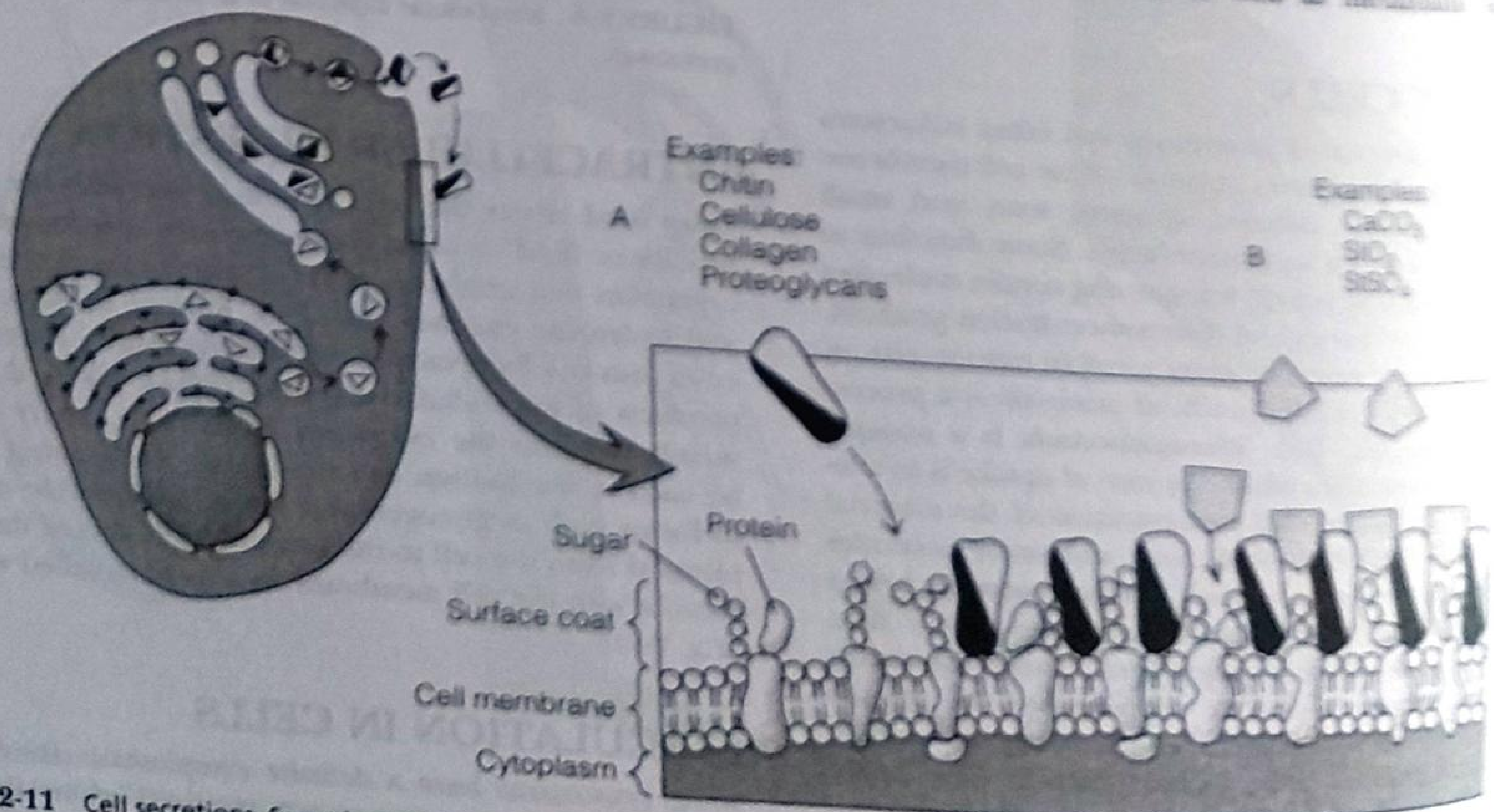


**FIGURE 2-11** Cell secretions. Secretion of extracellular skeletal materials involves the nucleus (coding and transcription), ribosomes (black dots on endoplasmic reticulum; translation, protein synthesis), endoplasmic reticulum (addition of components), Golgi body (addition of components, packaging in vesicles for release at surface), and, following exocytosis, self-assembly of the exoskeleton. **A**, organic secretions; **B**, mineral secretions.

insect exoskeleton). Chitin and its associated proteins are exocytosed at the surface of the cell, where they assemble into the exoskeleton.

## CELL COMMUNICATION

Protozoans respond to chemical and physical cues in ways that enable them to avoid adverse conditions, locate food, and find mates. In this sense, each protozoan cell must be both receptor and effector. In their receptiveness to environmental stimuli, protozoans resemble the sensory nerve cells of animals.

Like animal sensory receptor cells, protozoans often receive external stimuli as signal substances that bind to specific membrane molecules. Binding can cause a specific ion channel to open, allowing ions (often $Na^+$ and $K^+$) to flow down their concentration gradients ($Na^+$ in, $K^+$ out). Because the resting cell membrane is polarized with respect to the distribution of these ions, the opening of the ion channels depolarizes the membrane. (Depolarization can be measured as a change in electrical potential, or voltage, using electrodes and a voltmeter.) When the membrane is depolarized, $Ca^{2+}$ channels open and calcium ions enter the cell. The entering calcium triggers other changes, such as a reversal in the ciliary beat, which causes the cell to withdraw from the disturbance. *Paramecium*, for example, has at least nine different ion channels, some of which are localized at the front and others at the rear of the cell. Such localized receptor fields differentiate "head" from "tail" and are thus analogous to the localization of receptor cells and organs in many metazoans. Intercellular chemical signaling (pheromones) in protozoans, in fact, often involves signal molecules, such as serotonin, β-endorphin, acetylcholine, and cyclic-AMP, which in animals function as neurotransmitters and internal messengers.

## SYMBIOSIS BETWEEN CELLS

Animal-like eukaryotic cells (heterotrophs) often establish an endosymbiotic relationship with photosynthetic cells (autotrophs) to the benefit of both partners. The photosynthetic partner may be either a eukaryote or a prokaryotic cyanobacterium. When the photosynthetic symbionts are green unicellular algae or diatoms, they are referred to as **zoochlorellae** (both *os* in *zoo-* are pronounced), but the most commonly occurring symbionts are yellow or brown and are known as **zooxanthellae** (Fig. 7-11). These zooxanthellae are a nonmotile stage of flagellated protozoans called dinoflagellates, which will be described in Chapter 3. The photosynthetic member of the partnership is generally located intracellularly within a vesicle in the host cytoplasm, although in a few metazoans, it is found between cells.

This symbiosis has its evolutionary origin in the phagocytosis of photosynthetic cells by heterotrophic cells. Delayed digestion by the larger cell may have resulted in the captured cells continuing to live and photosynthesize. Use of any excess photosynthate by the larger partner would have created a positive selective pressure for it to maintain the autotroph alive within its cytoplasmic vesicle. This symbiosis evolved numerous times, considering the different sorts of autotrophs and their symbiotic partners.

The benefits of this symbiosis are probably similar wherever it occurs. The autotroph provides excess organic carbon from photosynthesis to the larger partner, which in return provides certain nutrients, such as $CO_2$, nitrogen, and phosphorus, as well as protection, to the autotroph. Rarely does the protozoan or metazoan rely entirely on its autotrophs for nutrition; typically, the benefits of symbiosis supplement heterotrophic nutrition to varying degrees.

## EVOLUTIONARY ORIGIN OF EUKARYOTIC CELLS (INCLUDING PROTOZOA)

Our best hypothesis is that life began on an anoxic Earth some 3 billion years ago with the evolution of prokaryotic cells. Each of these tiny bacterium-like cells was enclosed in a membrane, but lacked internal membranes (organelles). In the absence of organelles, compartmentalization resulted from functional aggregations of biomolecules. Their food (energy for maintenance and reproduction) consisted of simple organic molecules that entered the cell and were distributed throughout by simple diffusion. In the absence of $O_2$, their central metabolic pathway was anaerobic (glycolysis), which resulted in limited ATP production and release of the energy-rich waste products, such as ethanol and lactic acid. As the competition for a limited supply of organic molecules intensified, some taxa evolved photosynthesis and were able to use sunlight energy to synthesize food from atmospheric $CO_2$ and $N_2$. The appearance of photosynthesis provided a new and renewable supply of organic molecules. The first photosynthetic microbes probably obtained the electrons to reduce $CO_2$ to carbohydrate from $H_2S$, the waste byproduct being elemental sulfur (S). Later, in taxa such as Cyanobacteria (blue-green bacteria), electrons were obtained from $H_2O$, resulting in the release and accumulation of $O_2$ in the atmosphere (Fig. 2-12). This newly available atmospheric $O_2$ set the stage for the evolutionary adoption of aerobic respiration, which enabled the complete breakdown of food for maximal ATP production and the release of the waste products $CO_2$ and $H_2O$.

Eukaryotic cells evolved about 1.5 billion years ago, nearly 2 billion years after the first prokaryotes and 1 billion years before the first animals. How did eukaryotic cells evolve from an ancestral prokaryote? As already noted, the small cells of prokaryotes lack internal membranes, except for the photosynthetic membranes of cyanobacteria and a fingerlike invagination of the cell membrane called a **mesosome,** to which the DNA is attached (Fig. 2-1A). In general, the cells of eukaryotes are 10 times larger than those of prokaryotes and may have required another level of compartmentalization to operate effectively. That new level, beyond the organized cytoplasm, was the organelle. What was the evolutionary origin of these organelles? Some seem to have evolved by modification of preexisting prokaryotic structures and others from entire prokaryotic cells that were engulfed by another cell and became permanent residents. The establishment of one cell inside of another, for their mutual benefit, is called an **endosymbiosis** (Fig. 2-13). A possible scenario for the endosymbiotic origin of eukaryotic organelles follows.

As oxygen was liberated by photosynthesis on the early Earth, the anaerobic prokaryotes presumably were faced with

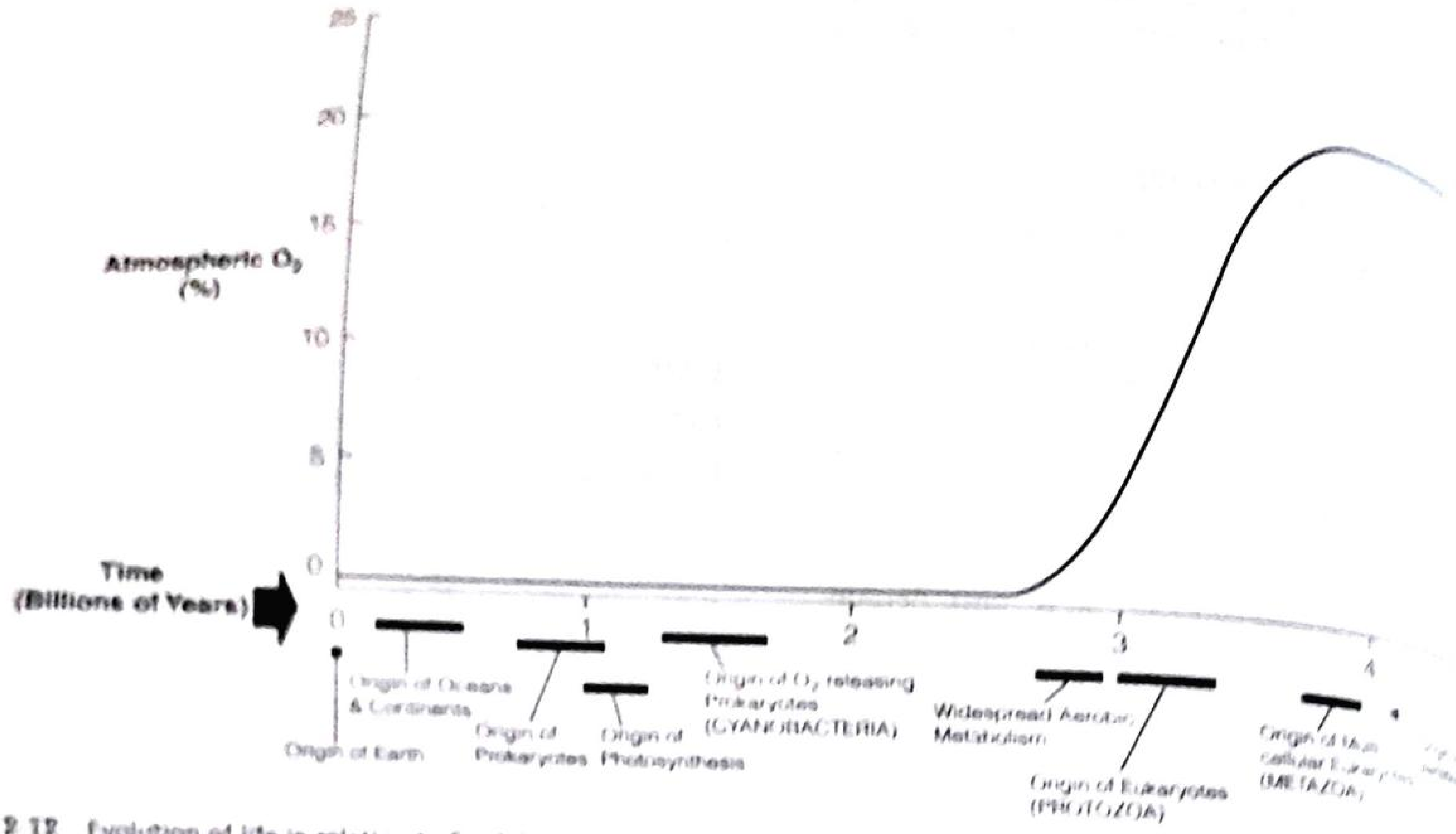


**FIGURE 2.12** Evolution of life in relation to Earth history and oxygen availability. Note the billion-year lag between the first oxygen-producing photosynthetic cyanobacteria and the rise of atmospheric oxygen. Geological deposits of massive amounts of iron oxide suggest that the first free molecules of oxygen combined with ferrous ions in the sea until these ions were depleted, presumably requiring a billion years. *(Modified and redrawn from Alberts, B., Bray, D., Lewis, J., Raff, M., and Watson, J. D. 2002. Molecular Biology of the Cell. Garland Publishing, New York. 1616 pp.)*

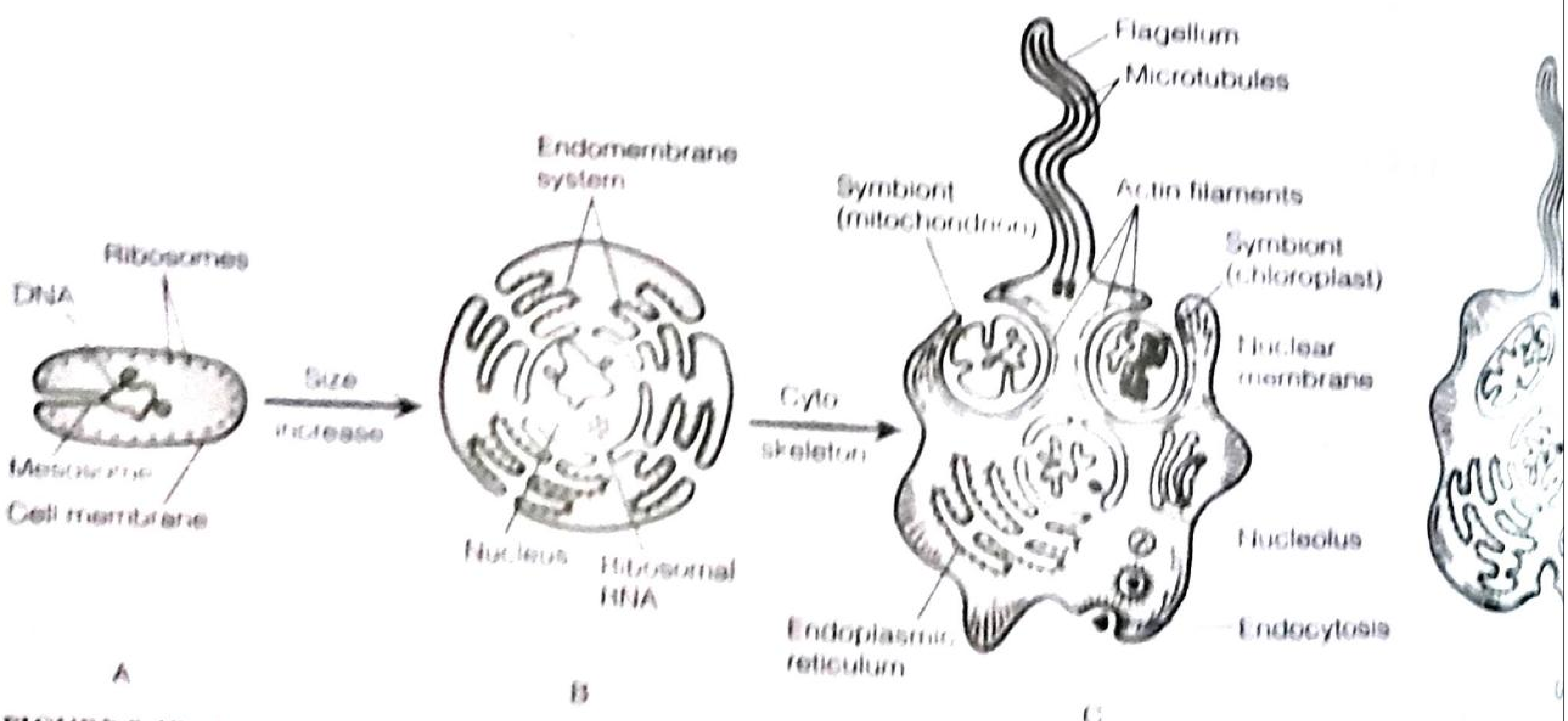


**FIGURE 2.13** Evolution of eukaryotic cells. A scenario for the evolution of a eukaryotic cell from a prokaryotic cell. **A,** A hypothetical ancestral prokaryote. **B,** Increase in cell size and the origin of internal membranes. The nuclear membrane and endomembrane system may have evolved from a series of mesosome-like invaginations of the cell membrane. The endomembrane system of eukaryotes increases the surface area on which proteins are synthesized (ribosomes). **C,** Origin of cytoskeleton (actin, microtubules) and motor molecules, allowing flagellar (ciliary) and ameboid motion, as well as endocytosis. Acquisition of mitochondrion by phagocytosis of a prokaryotic aerobe and chloroplast by phagocytosis of a photosynthetic prokaryote. **D,** A eukaryotic cell.

a challenge: Adapt to the presence of $O_2$ or face extinction. Undoubtedly, some found anoxic refuges, perhaps deep within waterlogged sediments, while others, through variation and natural selection, evolved aerobic respiration and took advantage of the newly available $O_2$. At this point, the competition between aerobes and anaerobes may have been intense, with the advantage going to the aerobes as $O_2$ levels rose. Perhaps during this time, some *anaerobic* cell with the capacity for phagocytosis engulfed an *aerobic* prokaryote that was not digested, but rather was permanently sequestered as an endosymbiont. The host cell retained its cytoplasmic anaerobic pathway (glycolysis), providing the end products (lactate, pyruvate) to the symbiont as food. Using aerobic respiration, the symbiont then converted that food-energy into ATP, which was shared with the host, eventually releasing $CO_2$ and $H_2O$ as waste products. The aerobic endosymbiont, of course, eventually became the mitochondrion (Fig. 2-13). Phagocytosis of a *photosynthetic* prokaryote, followed by the evolution of a mutualism, probably established the chloroplast.

The evidence for these hypotheses stems from several sources. One is that both mitochondria and chloroplasts are enclosed by two membranes. If the endosymbiotic hypothesis is correct, then the outer membrane should represent the membrane of the original phagocytic vesicle while the inner membrane should correspond to the original cell membrane of the prokaryote. In support of the hypothesis, the biochemistry of the outer membrane of mitochondria and chloroplasts resembles that of a eukaryotic cell membrane whereas the inner is similar to a prokaryotic cell membrane. Pharmaceutical evidence provides further support, as both mitochondria and chloroplasts are susceptible to antibacterial antibiotics. Mitochondria and chloroplasts also have DNA and ribosomes that are similar to those of prokaryotes. Further support is provided by *Pelomyxa palustris,* a large ameba that lacks mitochondria but has aerobic endosymbiotic bacteria that carry out oxidative metabolism. Although *Pelomyxa* is not the actual intermediate between the ancestral, mitochondria-free eukaryote and its descendants with typical mitochondria—it's an example of an evolutionary parallelism—it nevertheless indicates the plausibility of the endosymbiotic scenario.

Similar to mitochondria, the eukaryotic cell nucleus also is surrounded by a double membrane, but this does not seem to indicate an endosymbiotic origin for the nucleus. Instead, both nuclear membranes resemble a eukaryotic cell membrane. Perhaps the evolutionary origin of the nuclear membranes was by modification of one or more mesosome-like infoldings of the ancestral cell's surface (Fig. 2-13). If so, the blind ends of these infoldings may have expanded around the centrally located DNA, forming the nuclear envelope, while the infoldings themselves became a rudimentary endomembrane system from which the endoplasmic reticulum, Golgi bodies, and other structures eventually differentiated.

At present, a model for the evolution of eukaryotic cells is incomplete. Few plausible hypotheses, for example, have been formulated for the origin of the cytoskeleton and related structures. It is generally assumed, however, that the evolution of the microtubular mitotic spindle, including its centrioles, is closely linked with the origin of cilia and flagella, which use centrioles as basal bodies.

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### INTERNET SITES

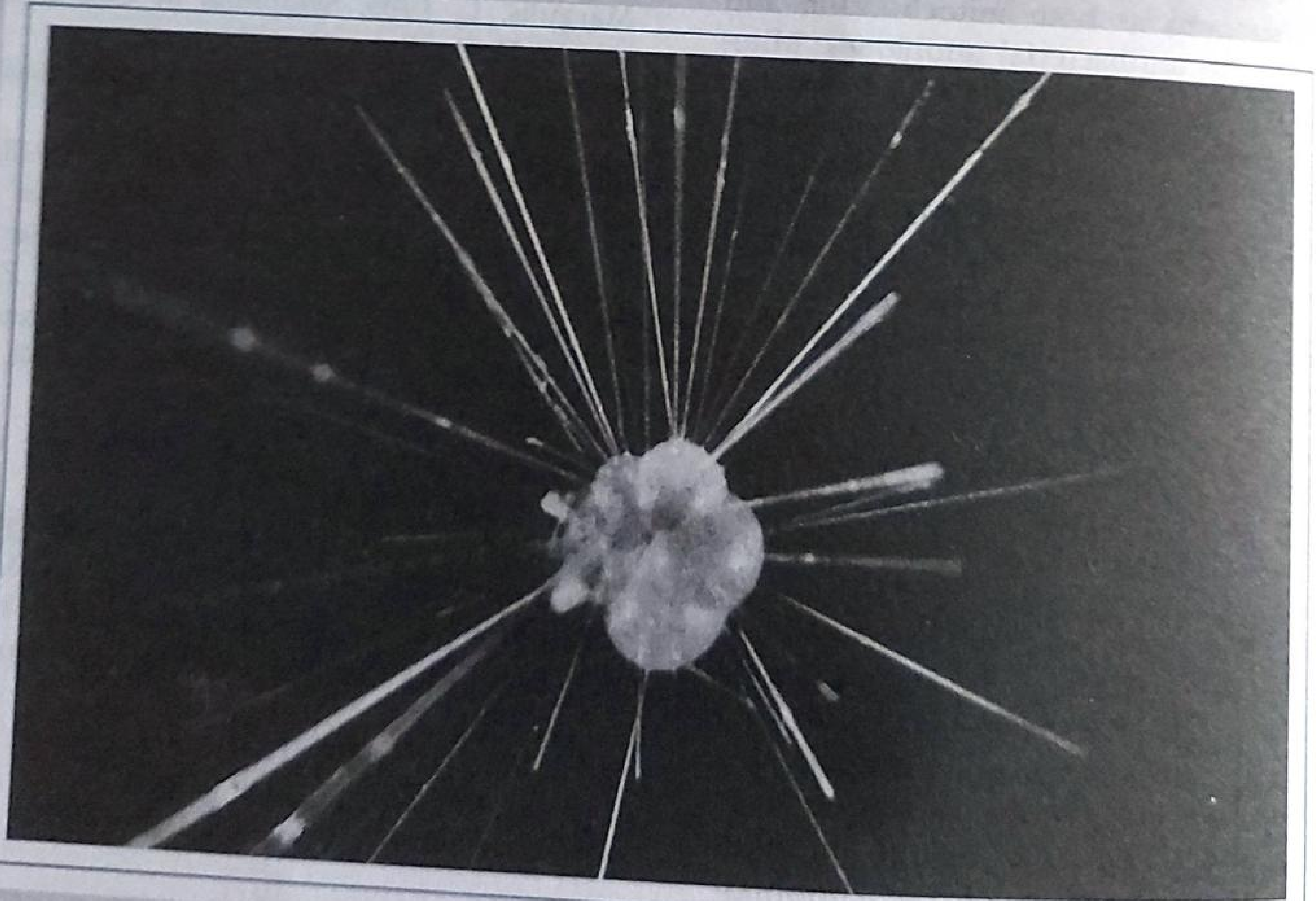

*www.cco.caltech.edu/~brokawc/Demo1/BeadExpt.html* (Image of microtubule sliding in an active flagellum of a sea urchin sperm.)

*http://cellbio.utmb.edu/cellbio/cilia.htm* (Transmission electron micrographs and diagrams of cilia/centriole structure.)

*http://cas.bellarmine.edu/tietjen/images/origin_of_mitochondria_in_eukary.htm* (Concise description of ideas and facts regarding the evolution of mitochondria.)

# 3 Protozoa





Formerly known as infusoria or animalcules, protozoans are motile, eukaryotic, unicellular organisms. United by the common possession of motility, an attribute that undoubtedly evolved independently in many groups, protozoa is a polyphyletic taxon with an unclear boundary. Historically, protozoa included nearly every group of what we now consider Protista—funguslike, animal-like, plantlike, and other unicellular eukaryotes. The name *protozoa* means "first animals," and it was natural for early biologists to seek the ancestor of Metazoa (animals) from among the free-moving protists. But it has now been established that only one protozoan taxon, the collared flagellates (Choanoflagellata), is the sister taxon of Metazoa and truly qualifies as the "first animal." The remaining protozoan taxa are either unique groups with no significant multicellular descendants or they are related closely to plants or fungi. Remarkably, one protozoan taxon, Myxozoa (formerly Myxosporidia), is actually a group of animals related to cnidarians (anemones and jellyfishes). Thus *protozoa* is the name for a grade within a scheme of organization, a loose confederation of eukaryotic taxa, rather than for a monophyletic taxon.

Protists exhibit astounding diversity and play a significant ecological role. The nearly 215,000 described species equal in number the vascular plants and are 10 times more plentiful than the number of bacterial and viral species combined. Of the total number of protist species, slightly less than half (around 92,000) are protozoans, one-quarter of which live as symbionts of other organisms. Protozoan parasites, for example, have an enormous impact on humans: Millions of people die yearly from malaria and other parasitic protozoans, and protozoans that sicken and kill livestock, poultry, fish, and wildlife cost economies several hundred million dollars annually. But the other face of protozoan ecology is beneficial. The mutualism between photosynthetic protozoans and corals underlies the coral-reef ecosystem, one of the most diverse on earth. Myriads occupy aquatic environments and soils and play essential roles in food chains, including the control of bacterial populations and the recycling of nutrients. The protists as a whole, including the photosynthetic protozoa, account for 40% of global primary productivity.

The great diversity of protozoa necessarily restricts coverage in this chapter to the most common and significant freshwater, marine, and parasitic taxa. Omitted are many "algal" taxa that other biologists consider to be protozoans. This chapter's goals are to provide an overview of protozoan diversity, to examine the functional adaptations of cells as organisms, and to identify living examples of how cell-organisms might have evolved into those multicellular creatures we call animals. One of the best models to illustrate that evolutionary transition is *Volvox* and its relatives. Although the multicellular *Volvox* is clearly a green alga related to land plants and thus provides only a parallel example for the evolution of multicellularity, it is included in this chapter because of its easy availability for study.

## FORM AND FUNCTION

The body of most protozoans consists of a single cell, although many species form colonies. Cell size ranges from approximately 10 μm, as in choanoflagellates, to several centimeters in some dinoflagellates, forams, and amebas.

The protozoan body is usually enclosed only by the cell membrane. The rigidity or flexibility of the body and its shape are largely determined by the cytoskeleton, which typically is located just below the cell membrane. The cytoskeleton and cell membrane together form the **pellicle,** a sort of protozoan "body wall." The **cytoskeleton** often is composed of protein filaments (actin, for example), microtubules, vesicles (such as alveoli), or combinations of all three. The protein filaments may form a dense mesh in the outermost cytoplasm (Fig. 3-1A) as in, for example, *Euglena*. More conspicuous cytoskeletal structures are pellicular microtubules that occur in flagellates, apicomplexans, and ciliates. They can be arranged as a microtubular corset (Fig. 3-1B) or, as in some flagellates, the microtubules can originate on the flagellar basal bodies and radiate rearward to the opposite extremity of the cell as a sort of axial skeleton (axostyle; Fig. 3-1C). Such microtubules resemble the

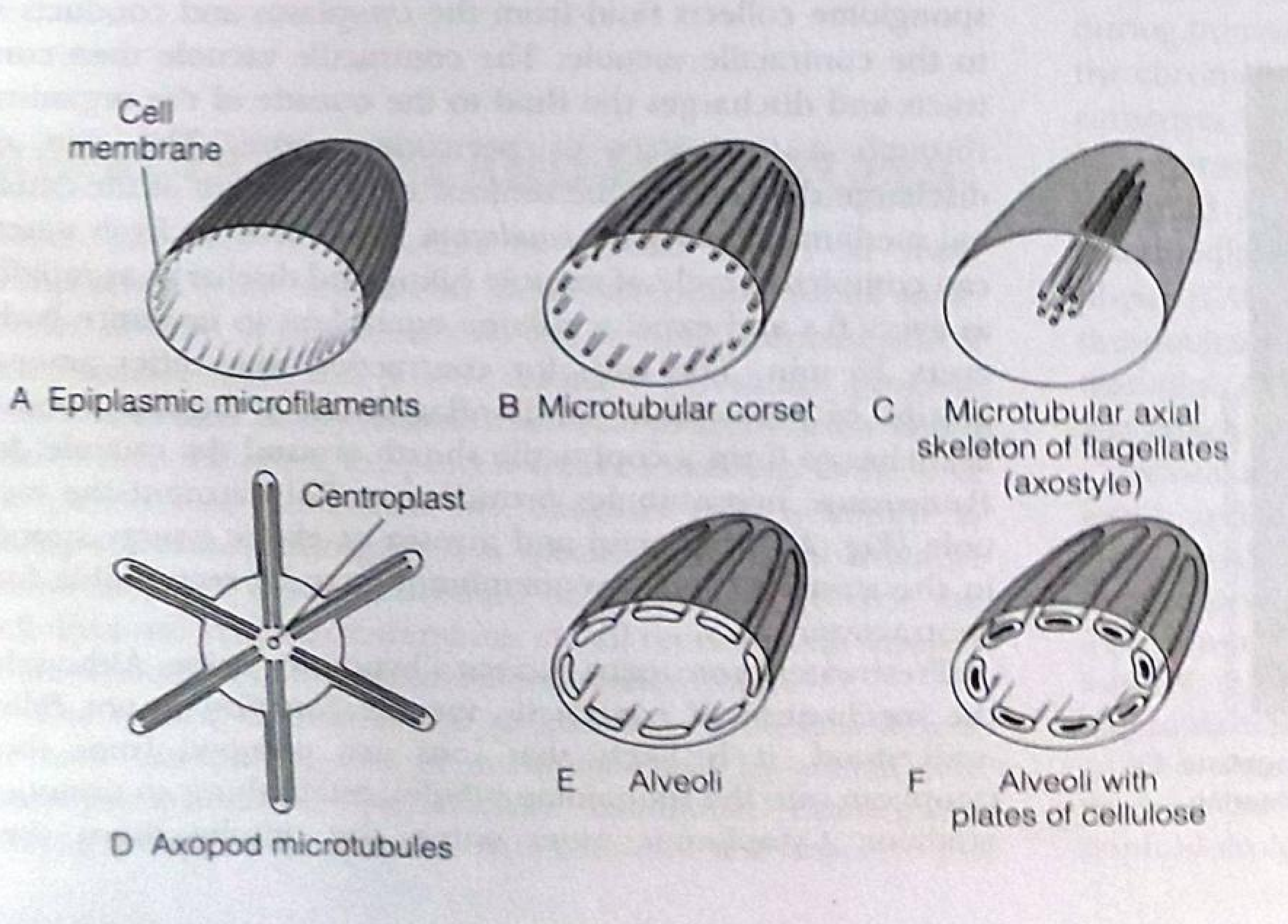



**FIGURE 3-1** Protozoa: Cytoskeletons of actin microfilaments, microtubules, and alveoli. Examples: **A,** amebas, euglenoids; **B,** euglenoids; **C,** axostylates; **D,** heliozoans; **E,** ciliates, apicomplexans; **F,** dinoflagellates.

microtubules of a mitotic spindle, which radiate from centrioles and form the mitotic apparatus (Fig. 2-2). In other protozoa, such as the spherical radiolarians and heliozoans, bundles of microtubules radiate from a centroplast (an MTOC) at the cell's center and then extend into and support a raylike projection of the cell's surface (axopod; Fig. 3-1D). The centroplast and its microtubules resemble the starlike asters that form around centrioles at the poles of the mitotic spindle.

Vesicles, known as **alveoli,** occur immediately below the cell membrane in many protozoans, such as dinoflagellates, apicomplexans, and ciliates (together forming the Alveolata). "Empty" alveoli, like those that occur in ciliates, may be turgid and help to support the cell, but they also store $Ca^{2+}$, which can be released to trigger cellular responses (Fig. 3-1E). In some dinoflagellates, plates of cellulose secreted into the alveolar vesicles form a rigid endoskeleton (Fig. 3-1F).

Protozoan skeletons, like those of metazoans, can also be endo- or exoskeletons. A skeleton that forms a more or less complete covering, whether internal or external, is called a **test** (or a lorica, theca, or shell).

The protozoan locomotor organelles may be flagella, cilia, or flowing extensions of the cell known as pseudopodia (described in Chapter 2). The undulatory waves of flagella pass from base to tip and drive the organism in the opposite direction (Fig. 2-6). The flagella of many protozoans bear fine lateral "hairs" called **mastigonemes** (Fig. 3-2). The mastigonemes cause the flagellum to pull rather than push as the flagellar waves pass from base to tip. Flagellar, ciliary, and pseudopodial specializations characterize many of the protozoan taxa.

All types of nutrition occur in protozoa. Some protozoa rely on photosynthesis, others absorb dissolved organic material from the environment, and many digest food particles or prey intracellularly in food vacuoles. Food enters the vacuole by phagocytosis, often at a definite cell mouth, or **cytostome.** The vacuole then may be shuttled to the interior along a specialized microtubular tract called a **cytopharynx.** Macromolecules enter by micro- and macropinocytosis, which may occur over the entire surface of the cell. Intracellular [illegible] been most studied in amebas and ciliates, and, [illegible] part, it follows the general pattern described in [illegible] Digestive specializations of ciliates will be described [illegible] this chapter.

Diffusion is important for internal transport [illegible] zoans and may be the sole mechanism in small [illegible] large protozoans and those with long pseudopodia [illegible] mechanisms of internal transport. The inner, fluid [illegible] of *Paramecium* circulates, via cyclosis, in a [illegible] (Fig. 2-10). In forams and actinopods, bidirectional [illegible] of vesicles occurs on tracks of microtubules in the [illegible] slender pseudopodium.

Most protozoans are aerobes that rely on diffusion [illegible] uptake of oxygen and release of $CO_2$. A few [illegible] however, are obligate anaerobes, especially those [illegible] symbionts in the digestive tract of animals. [illegible] associated with decomposing organic matter [illegible] tive anaerobes, using oxygen when it is present [illegible] capable of anaerobic respiration. In general, [illegible] availability of food and oxygen associated with [illegible] results in a successional sequence of protozoa [illegible] Because of their short generation time, protozoan [illegible] structure changes rapidly with environmental change [illegible] be used to monitor aquatic systems for pollution.

Many freshwater protozoa osmoregulate to [illegible] water (volume regulation) and to adjust the [illegible] and proportions of their internal ions (ionic [illegible] Excess water enters by osmosis when the [illegible] concentration exceeds that of the surrounding [illegible] tional water may enter with food in vacuoles [illegible] vesicles. For example, an ameba fed on a [illegible] imbibes, by macropinocytosis, a quantity of water [illegible] one-third of its body volume.

Osmoregulation is accomplished by active [illegible] the cell membrane and by a system of water- and [illegible] organelles called the **contractile vacuole** complex [illegible] The complex is composed of a large spherical [illegible] **contractile vacuole** proper—and, surrounding [illegible] cytoplasmic vesicles or tubules termed the spongiome [illegible] spongiome collects fluid from the cytoplasm and [illegible] to the contractile vacuole. The contractile vacuole [illegible] tracts and discharges the fluid to the outside of the [illegible] through a temporary or permanent pore. The [illegible] discharge depends on the osmotic concentration of the [illegible] nal medium. *Paramecium caudatum,* which lives in fresh [illegible] can complete a cycle of vacuole filling and discharge [illegible] as every 6 s and expel a volume equivalent to its [illegible] every 15 min. The basis for contraction may differ [illegible] groups of protozoans. In dinoflagellates, a flagellar [illegible] branches to form a contractile sheath around the [illegible] *Paramecium,* microtubules provide a scaffold around [illegible] uole (Fig. 3-3), but actin and myosin or elastic energy [illegible] in the stretched vacuolar membrane may be responsible [illegible] contraction.

Freshwater protozoans excrete a hypotonic urine [illegible] the mechanism of contractile vacuole function is [illegible] understood, it is likely that ions are pumped [illegible] cytoplasm into the spongiome tubules, establishing [illegible] gradient. Cytoplasmic water enters the tubules [illegible]

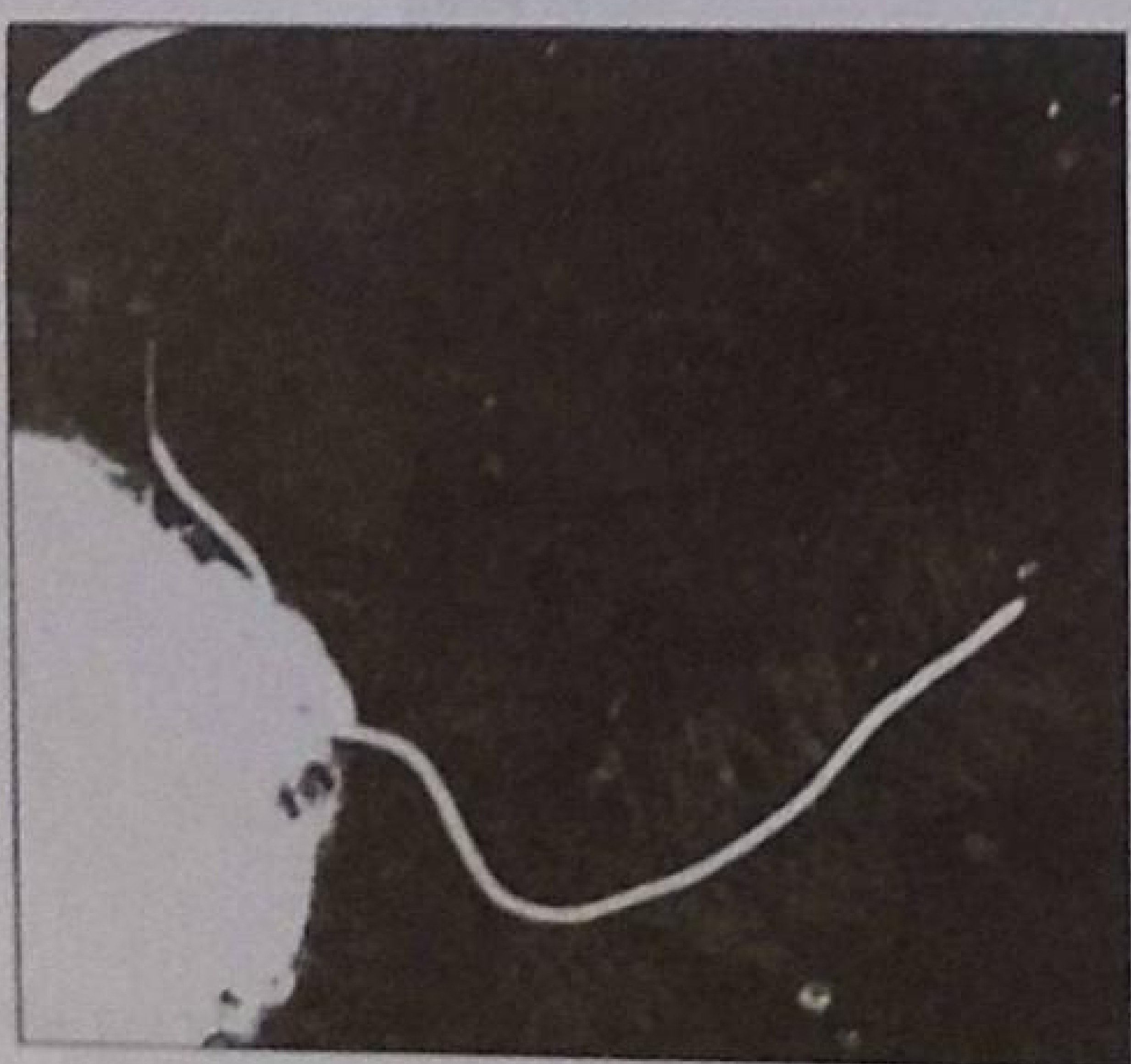


Image courtesy of BioPhoto Associates

**FIGURE 3-2** Protozoa: Flagellar mastigonemes. Phytoflagellate with one short smooth flagellum and one long flagellum bearing mastigonemes.

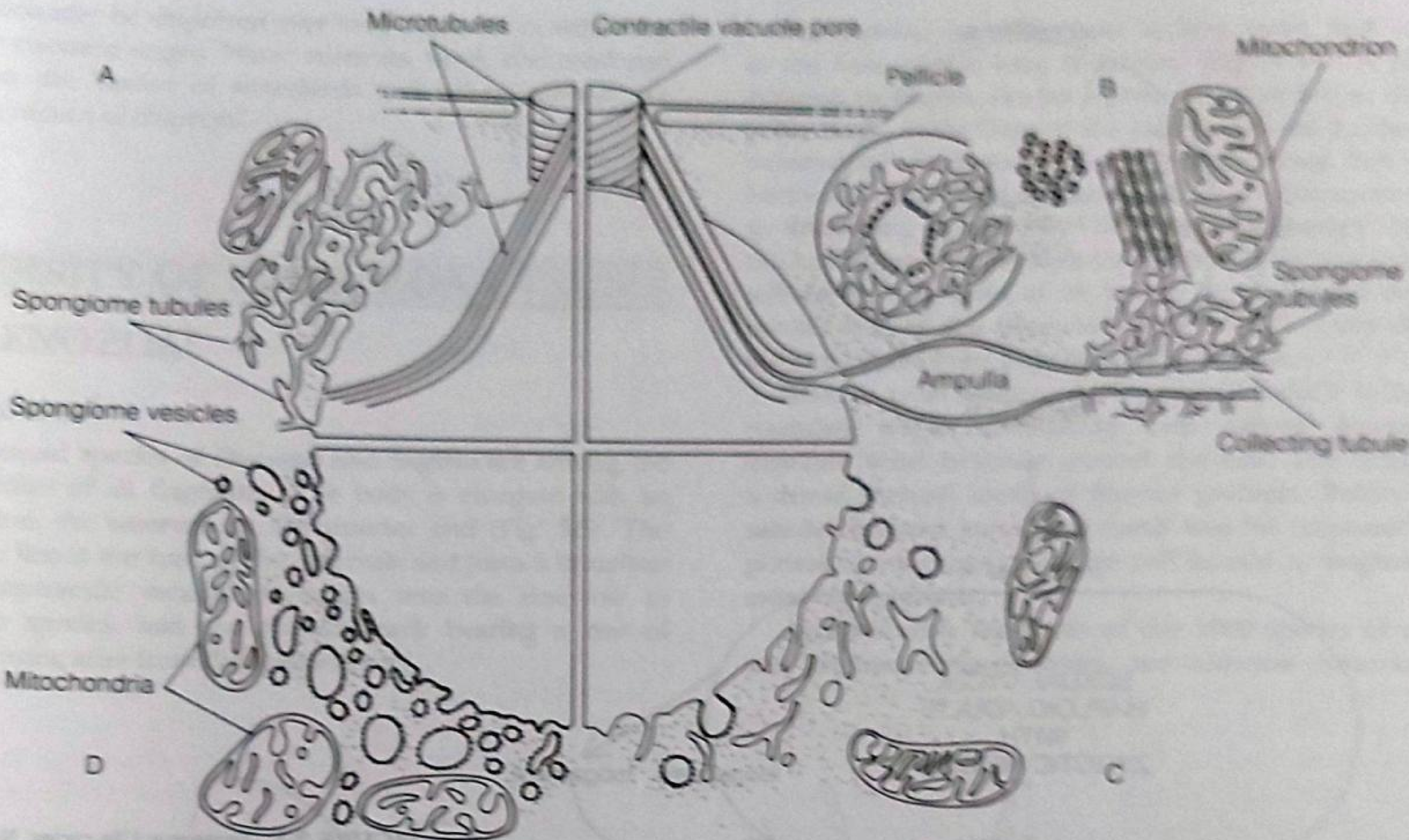



**FIGURE 3-3** Protozoa: Diagram of four types of contractile vacuoles. Types **A** and **B** are from ciliates, in which the spongiome is composed of irregular, fluid-filled tubules. Actin filaments (not shown) wind around the pore and extend over the vacuole surface. **A**, The network of spongiome tubules empties directly into the vacuole. **B**, The network of irregular tubules first empties into ampullae, which dilate and then contract, discharging fluid into the vacuole, as occurs in *Paramecium*. **C**, Typical of flagellates and small amebas, the spongiome contains small vesicles and tubules. **D**, Arrangement found in large amebas. *(After Patterson, D. J. 1980. Contractile vacuoles and associated structures; their organization and function. Biol. Rev. 55:1–46. © Copyright Cambridge University Press, reprinted by permission.)*

osmotic gradient. As water and ions flow along the tubules, ions and perhaps other substances are selectively reabsorbed before the urine is discharged to the exterior. The contractile vacuole system is of no particular significance in removing metabolic wastes, such as ammonia and $CO_2$, as these simply diffuse to the outside of the organism.

## REPRODUCTION AND LIFE CYCLES

Clonal (asexual) reproduction by mitosis occurs in most protozoa and is the only known mode of reproduction in some species. Division of the parent into two or more daughter cells is called **fission.** When this process results in two similar progeny cells, it is termed **binary fission;** when one progeny cell is much smaller than the other, the process is called **budding.** Division of the parent into more than two daughter cells is known as **multiple fission. Schizogony** is a specialized form of multiple fission in which repeated divisions of the nucleus precede the cell divisions. With few exceptions, clonal reproduction involves some replication of organelles before or after fission.

The mitotic division of the protozoan cell nucleus differs, in most cases, from that of an animal cell. In animal cells undergoing mitosis, the nuclear membrane disintegrates during mitosis as the chromosomes condense and attach to the mitotic spindle, located in the cytoplasm of the cell. Because the nuclear membrane breaks down, this form of mitosis is said to have an **open spindle.** Later in mitosis, after the chromosomes have separated, a new nuclear membrane is assembled around each nucleus. Among most of the protozoans described in this chapter, however, the nuclear membrane does not break down during mitosis and the spindle forms within the nucleus itself. As the chromosomes separate, the intact nucleus stretches and then constricts, pinching off two new nuclei. Protozoans with this arrangement have a **closed spindle.** The closed spindle is regarded as the primitive form of mitosis in eukaryotic cells. Intermediates between closed and open spindles occur in chlorophytes *(Chlamydomonas, Volvox)* and apicomplexans. In these taxa, the nuclear membrane remains largely intact, but breaks occur that allow cytoplasmic spindle microtubules to enter the nucleus and attach to the chromosomes.

Sexual reproduction is widespread but not universal in protozoans, and life cycles are diverse. Many well-studied protozoans lack sexual reproduction entirely. In some species this absence may be primitive, whereas in others it may be a secondary loss. The primitive protozoan life cycle may have been sex free: a haploid (N) individual reproduced solely by fission, as in the living kinetoplastids (Fig. 3-4A).

The three general forms of sexual life cycles in protozoans are haploid dominance, diploid dominance, and haploid-diploid codominance. A **haploid-dominant** life cycle

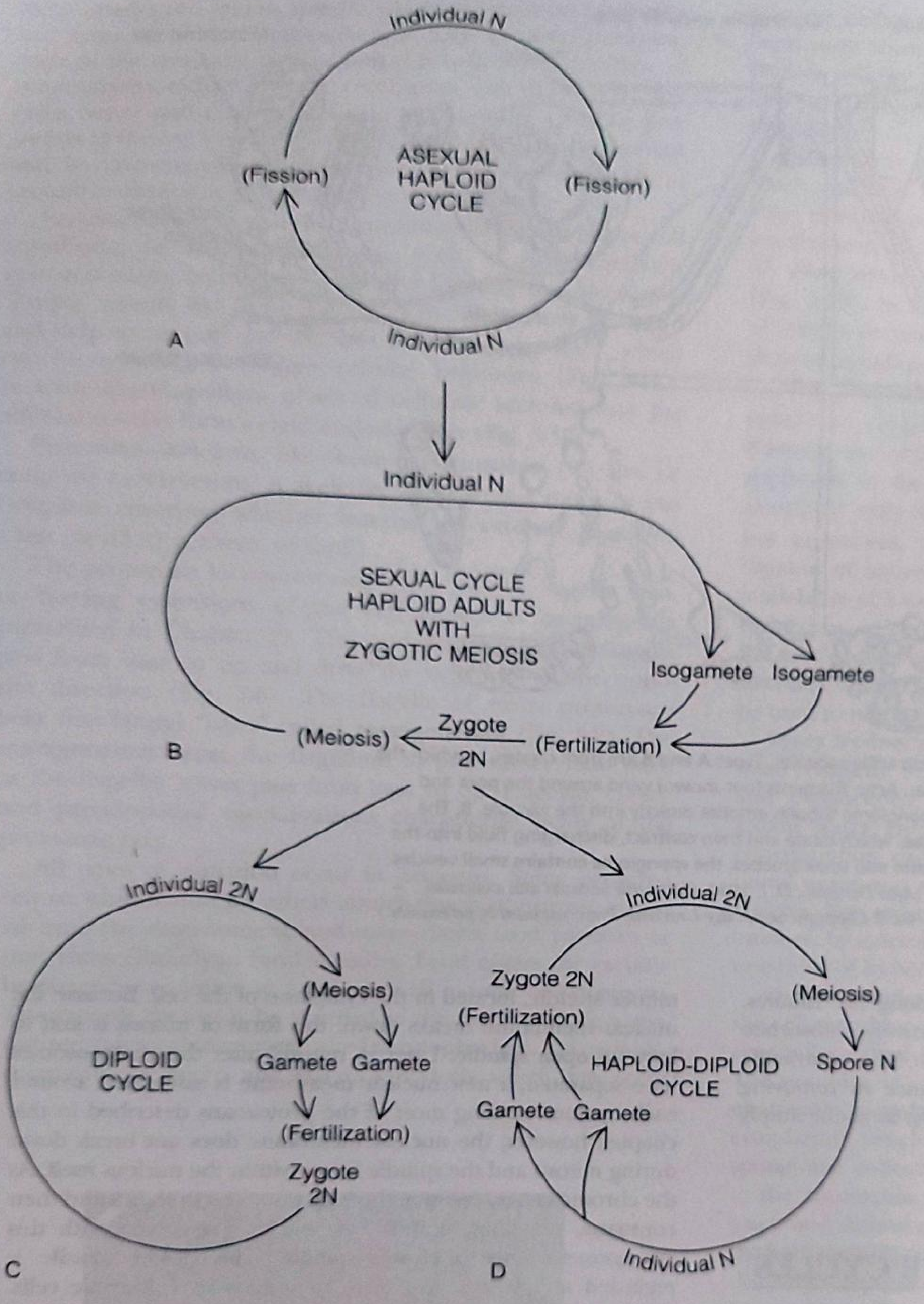



**FIGURE 3-4** Protozoa: Life cycles. N = haploid; 2N = diploid. A, Haploid asexual life cycle: individuals arise directly by fission (mitosis), as illustrated by the kinetoplastids. B, Haploid-dominant life cycle: Two N individuals mitotically produce isogametes, which fuse to form a zygote. The zygote then undergoes meiosis to form haploid individuals. Examples include Volvocida, many dinoflagellates, axostylates, apicomplexans (sporozoans). C, Diploid-dominant life cycle: 2N individuals meiotically produce N gametes, which fuse to restore a 2N individual, as happens in some axostylates, heliozoans, green algae, diatoms, and ciliates (and multicellular animals). Ciliates, however, do not form gametes, but exchange haploid nuclei, which fuse. D, Haploid-diploid codominant life cycle: 2N individuals meiotically produce N spores that develop into N individuals that mitotically produce N gametes that fuse to restore the 2N individual. This includes many forams, and many algae (and multicellular green plants).

includes haploid individuals that either transform into gametes or produce them by mitosis. Fusion of the haploid gametes results in a diploid zygote that soon undergoes meiosis to form four new haploid individuals (Fig. 3-4B). The haploid-dominant life cycle typifies apicomplexans. In a **diploid-dominant** life cycle, the 2N individuals undergo meiosis to produce N gametes (or gamete nuclei), which fuse into a 2N zygote individual (Fig. 3-4C). This type of life cycle occurs, for example, in ciliates (and animals). In the **haploid-diploid codominant** life cycle, an asexual generation (N or 2N) alternates with a sexual generation (2N or N; Fig. 3-4D). This pattern is characteristic of forams (and plants).

Encystment is characteristic of the life cycle of protozoa, including the majority of freshwater ... In forming a cyst, the protozoan secretes a thickened envelope about itself and becomes inactive. Depending on the species, the protective cyst is resistant to desiccation or low temperatures and encystment enables the ... pass through unfavorable environmental conditions ... simplest life cycle includes only two phases: an active and a protective, encysted phase. However, the complex life cycles are often characterized by ... zygotes or by formation of special reproductive ... which fission, gametogenesis, or other reproductive processes take place.

Protozoa may be dispersed over long distances in either the active or encysted stages. Water currents, wind, and mud and debris on the bodies of waterbirds and other animals are common means of dispersal.

# DIVERSITY OF PROTOZOA

## EUGLENOZOA[P]

### Euglenoidea[C]

The euglenoid species of *Peranema* and *Euglena* are among the most familiar of all flagellates. The body is elongate with an invagination, the **reservoir,** at the anterior end (Fig. 3-5). The cytostome lies at the base of the reservoir and joins a cytopharynx. A contractile vacuole discharges into the reservoir in freshwater species, and two flagella, each bearing a row of mastigonemes, arise from the reservoir wall.

In *Euglena,* one flagellum is very short and terminates at the base of the long flagellum (Fig. 3-5A). A pigmented **eyespot,** or stigma, shades a photosensitive bulge, the **paraflagellar body,** at the base of the long flagellum. In the colorless heterotroph *Peranema,* both flagella are long, but one trails backward and can be used to catch food or temporarily attach to something (Fig. 3-5B). The long locomotory flagellum is thickened, up to five times the normal flagellar diameter, and stiffened along most of its length by a **paraxial rod** located to one side of the axoneme (Fig. 3-5B,C). Only the mobile terminal end of the flagellum lacks the rod.

Seen in cross section, the euglenoid pellicle is thrown into rounded ridges alternating with narrow grooves, which together wind helically around the cell. The ectoplasm has a dense skeletal mesh of fibrous proteins. Pellicular microtubules situated below this mesh may be responsible for the peristaltic movements of the cell known as **euglenoid movement** (or metaboly).

Approximately two-thirds of the 1000 species of the marine and freshwater Euglenoidea are colorless heterotrophs and

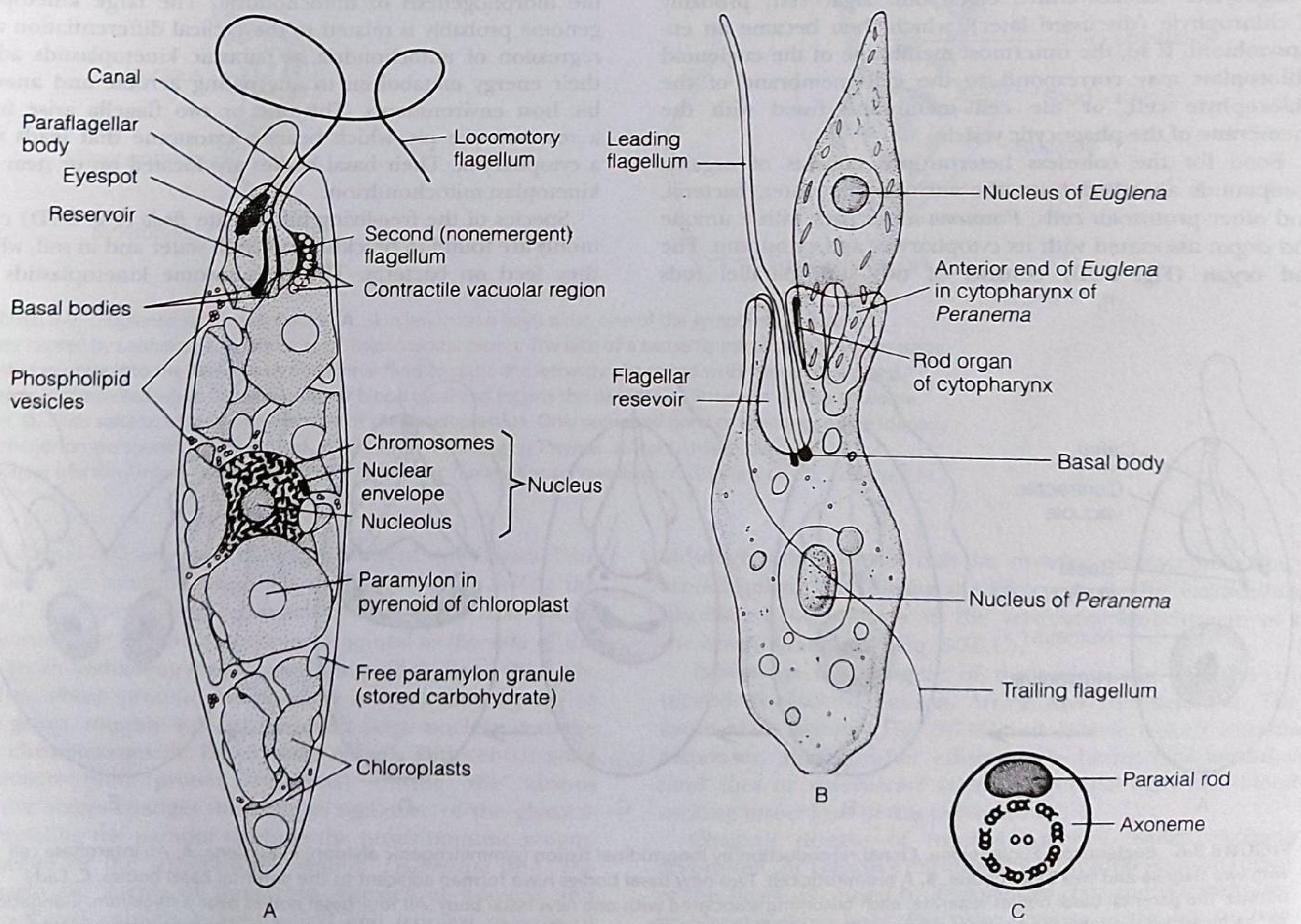



**FIGURE 3-5** Euglenozoa: Euglenoidea. **A,** Structure of the photosynthetic *Euglena gracilis.* **B,** The colorless heterotroph *Peranema* swallowing a *Euglena.* **C,** Cross section of leading flagellum of *Peranema* showing paraxial rod. *(A, From Leedale, G. F., 1967, Euglenoid Flagellates. Prentice-Hall, Inc. Englewood Cliffs, N.J.; B, Modified after Chen)*

one-third are green photoautotrophs, such as the species *Euglena*. The chloroplasts of photosynthetic species contain chlorophylls a and b. Photosynthetic euglenoids rotate around their longitudinal axis as they swim toward light. As long as they maintain this orientation, the photosensitive paraflagellar body receives constant illumination. But if they deviate from their head-on approach to a light source, the rotating eyespot periodically shades the paraflagellar body and elicits a course correction. The heterotrophic mode of nutrition is primitive in euglenoids. Chloroplasts were acquired secondarily within the taxon and independently of other photosynthetic flagellates.

The green, photosynthetic species such as *Euglena* store food energy as a unique starchlike carbohydrate called **paramylon.** Paramylon is synthesized in a specialized region, the pyrenoid, of the chloroplast, but stored as free granules in the cytoplasm (Fig. 3-5A). The large paramylon granules may also have a skeletal function, as in *Cyclidiopsis acus,* whose longitudinally aligned granules form an intracellular "backbone." The chloroplasts of euglenoids are surrounded by *three* membranes, not two as in green algae and plants. For this reason, euglenoids are believed to have acquired their chloroplasts by phagocytosis of an entire eukaryotic algal cell, probably a chlorophyte (discussed later), which then became an endosymbiont. If so, the outermost membrane of the euglenoid chloroplast may correspond to the cell membrane of the chlorophyte cell, or the cell membrane fused with the membrane of the phagocytic vesicle.

Food for the colorless heterotrophs consists of organic compounds absorbed from the surrounding water, bacteria, and other protozoan cells. *Peranema* seizes prey with a unique rod organ associated with its cytopharynx and cytostome. The **rod organ** (Fig. 3-5B) consists of two stiff, parallel rods (microtubule bundles) and other intracellular structures, "vanes." (*Euglena* has a rudimentary rod organ, an indication of its heterotrophic ancestry.) *Peranema* feeds on a wide variety of living organisms, including *Euglena*, and the cytostome is greatly distended to permit phagocytosis of large prey. During feeding, the rod organ is protruded, attaches to the prey, then retracts, pulling the prey into the cytostome and cytopharynx. (Fig. 3-5B). The prey is swallowed (phagocytosed) and digested in a food vacuole.

Sexual reproduction has not been observed in euglenoids, but clonal reproduction occurs by longitudinal binary fission (Fig. 3-6). The two flagella and their basal bodies, as well as the nucleus, replicate before the cell itself divides.

## Kinetoplastida[C]

Kinetoplastid flagellates are colorless heterotrophs. A few of the 600 species are free living, but most are important parasites. All share the flagellar paraxial rod with their euglenoid relatives, but uniquely have a conspicuous mass of DNA, a **kinetoplast,** located within a single, large mitochondrion (Fig. 3-7D). Most of the kinetoplast DNA sequences ... the morphogenesis of mitochondria. The large kinetoplast genome probably is related to the cyclical differentiation and regression of mitochondria as parasitic kinetoplastids adapt their energy metabolism to alternating aerobic and anaerobic host environments. The one or two flagella arise from a reservoir-like pit, which bears a cytostome that leads to a cytopharynx. Their basal bodies are located on or near the kinetoplast mitochondrion.

Species of the free-living biflagellate *Bodo* (Fig. 3-7D) commonly are found in brackish and fresh water and in soil, where they feed on bacteria. The trypanosome kinetoplastids

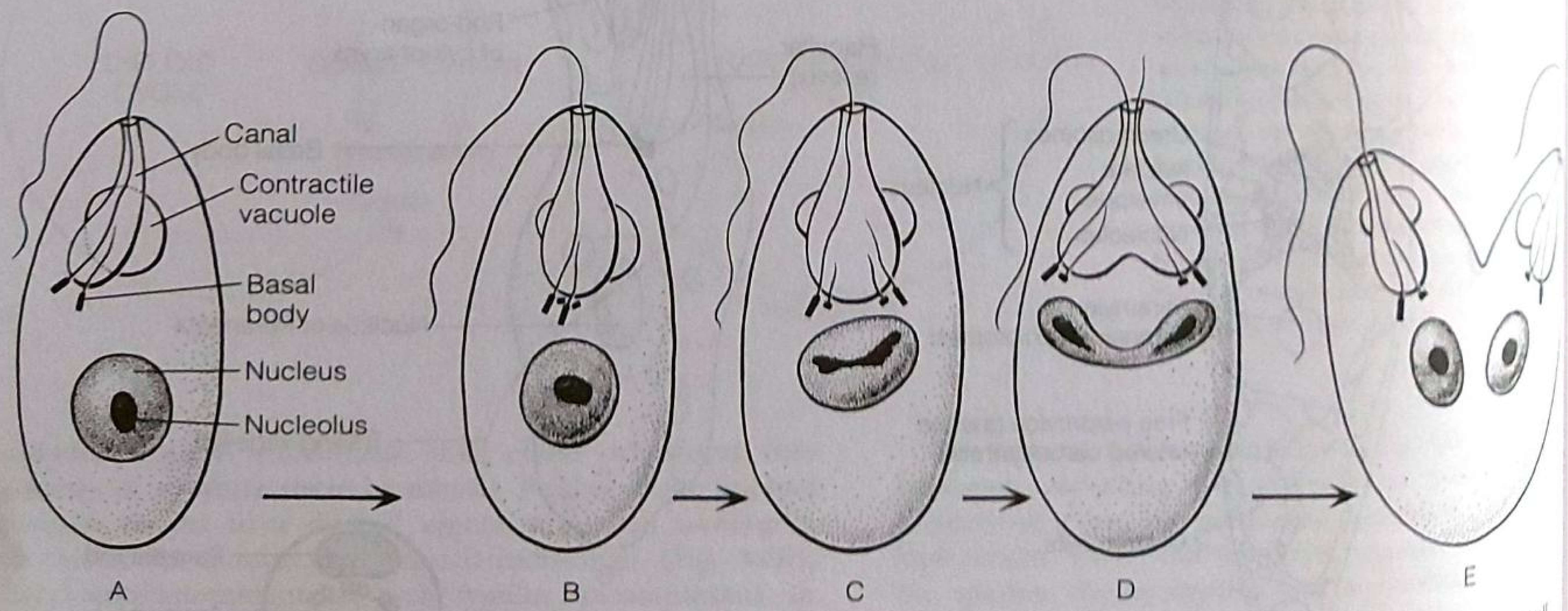



**FIGURE 3-6** Euglenozoa: Euglenoidea. Clonal reproduction by longitudinal fission (symmetrogenic division) in *Euglena*. **A,** An interphase cell with two flagella and two basal bodies. **B,** A premitotic cell: Two new basal bodies have formed adjacent to the parental basal bodies. **C,** Early mitosis: The parental basal bodies separate, each becoming associated with one new basal body. All four basal bodies bear a flagellum. Elongation of the nucleolus indicates the onset of nuclear division. Unlike mitosis of animal cells, the euglenoid nuclear membrane remains intact (closed spindle) during the entire division cycle and the flagella do not regress. **D,** Late mitosis: Each separate pair of flagella consists of a parental and a daughter basal body. The nucleus is dividing by constriction, the contractile vacuole has divided, and the reservoir (gullet) is undergoing division. **E,** The anterior end is dividing following duplication of organelles. *(Modified and redrawn from Ratcliffe, 1927, and Triemer, www.lifesci.rutgers.edu/~triemer/flagellar_appt/flagellarapparatus.html)*

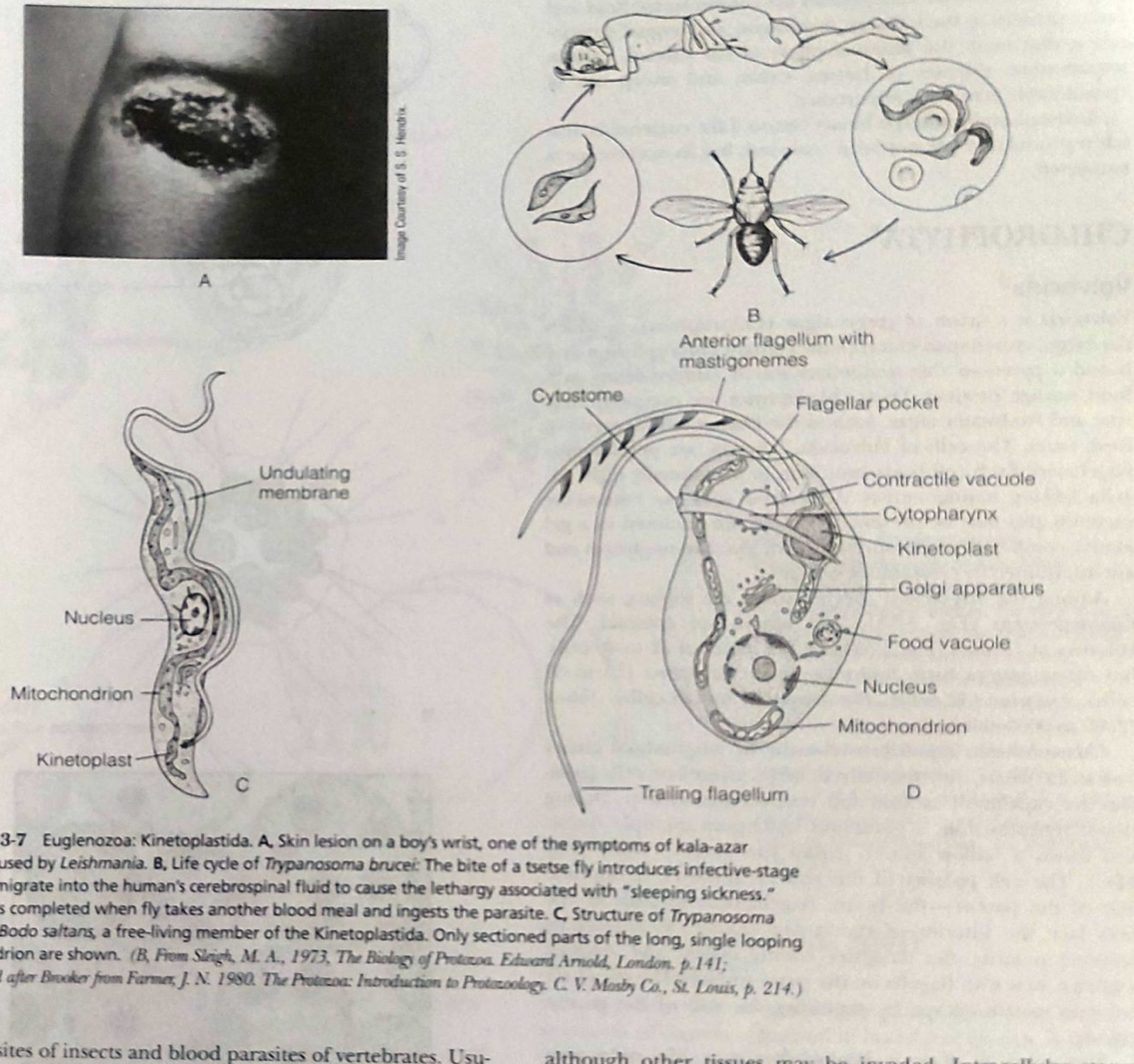



**FIGURE 3-7** Euglenozoa: Kinetoplastida. **A,** Skin lesion on a boy's wrist, one of the symptoms of kala-azar disease caused by *Leishmania*. **B,** Life cycle of *Trypanosoma brucei*: The bite of a tsetse fly introduces infective-stage cells that migrate into the human's cerebrospinal fluid to cause the lethargy associated with "sleeping sickness." Life cycle is completed when fly takes another blood meal and ingests the parasite. **C,** Structure of *Trypanosoma brucei*. **D,** *Bodo saltans*, a free-living member of the Kinetoplastida. Only sectioned parts of the long, single looping mitochondrion are shown. *(B, From Sleigh, M. A., 1973, The Biology of Protozoa. Edward Arnold, London. p.141; C, Modified after Brooker from Farmer, J. N. 1980. The Protozoa: Introduction to Protozoology. C. V. Mosby Co., St. Louis, p. 214.)*

gut parasites of insects and blood parasites of vertebrates. Usually only the anterior flagellum is present (Fig. 3-7C), the second flagellum being represented only by a basal body. Commonly, the flagellum trails and is joined to the side of the body by an **undulating membrane.** The pellicle has a thick glycocalyx, whose protein composition is controlled by up to 1000 genes, roughly 40% of the cell's large nuclear genome (120 chromosomes in *Trypanosoma brucei*). Differential gene expression (and protein synthesis) during the various infective stages changes the antigen signature of the glycocalyx, enabling the parasite to elude the host's immune system.

Species of the trypanosome genera *Leishmania* and *Trypanosoma* are agents of numerous diseases of humans and domesticated animals in subtropical and tropical regions of the world. Part of the life cycle is passed within or attached to gut cells of blood-sucking insects, mostly various kinds of flies, and another part of the cycle is spent in the blood plasma or in white blood cells and lymphoid cells of the vertebrate host, although other tissues may be invaded. Intracellular stages are aflagellate, but during the life cycle, motile, extracellular, flagellated stages occur in the vertebrate bloodstream or in the invertebrate host (Fig. 3-7B,C).

*Leishmania* is the agent of the widespread kala-azar and related diseases of Eurasia, Africa, and the Americas. They cause skin lesions (Fig. 3-7A) and interfere with immune responses, among other effects. Tiny biting flies known as sand flies or no-see-ums (Ceratopogonidae) are the blood-sucking insect host of this protozoan.

Chagas's disease of tropical America, which probably accounted for Darwin's chronic ill health following the voyage of the *Beagle*, is caused by *Trypanosoma cruzi* and is transmitted by blood-sucking bugs. Extensive damage to the human host occurs when the parasite leaves the circulatory system and invades the liver, spleen, and heart muscles.

*Trypanosoma brucei rhodesiense* and *T. b. gambiense* cause African sleeping sickness and are transmitted by the tsetse fly

(Fig. 3-7B,C). The parasite invades the cerebrospinal fluid and brain, producing the lethargy, drowsiness, and mental deterioration that mark the terminal phase of the disease. Various trypanosome diseases of horses, cattle, and sheep are of considerable economic importance.

Kinetoplastids undergo binary fission. Like euglenoids, sexual reproduction has not been observed, but its occurrence is suspected.

# CHLOROPHYTA[P]

## Volvocida[O]

Volvocida is a taxon of green algae (Chlorophyta), in which the large, cup-shaped chloroplasts contain chlorophylls a and b and a pyrenoid that synthesizes starch (amylopectin) as a food storage product. Many chlorophytes are nonmotile marine and freshwater algae, such as the filamentous *Spirogyra* of fresh water. The cells of Volvocida, however, are permanently flagellated: Each cell bears two, four, or occasionally eight flagella lacking mastigonemes. An eyespot and two contractile vacuoles also may be present. The cells are enclosed in a gel matrix composed of glycoproteins and glycoaminoglycans and are interjoined by cytoplasmic bridges.

Among the flagellated species, some are solitary, such as *Chlamydomonas* (Fig. 3-8A), and others are colonial. The colonies of *Gonium* (Fig. 3-8B) are flat plates of 32 to 40 cells, but other genera form hollow spheres: *Pandorina* (16 to 32 cells), *Eudorina* (32 cells), *Pleodorina* (64 to 128 cells), *Volvox* (2000 to 6000 cells).

*Chlamydomonas* reproduces clonally by longitudinal binary fission. In *Volvox*, only specialized, large, aflagellate cells **(gonidia)** are capable of asexual and sexual reproduction. During clonal reproduction, a gonidium undergoes multiple fission and forms a hollow sphere within the parent colony (Fig. 3-8C). The cell polarity of this sphere, however, is opposite that of the parent—the future flagella-bearing ends of the cells face the interior of the young colony. To correct its reversed polarity, the daughter colony inverts and reforms a sphere, now with flagella on the outer surface. The daughter colonies usually escape by rupturing the wall of the parent colony.

The volvocids have a haploid-dominant life cycle with postzygotic meiosis (Fig. 3-4B). In most species of *Chlamydomonas*, the two structurally identical cells act as gametes (isogametes), fuse, and form a zygote. Other species show the beginnings of sex differentiation by having gametes that differ slightly in size (anisogametes). In *Pleodorina*, the size distinction is pronounced, but the large macrogametes still retain flagella and are free swimming. Finally, in *Volvox*, true eggs and sperm develop from gonidia at the posterior of the colony. The egg is stationary and is fertilized within the parent colony by a sperm packet released from another colony. Colonies may be either hermaphrodites or one or the other sex.

Although closely related to plants and not to animals, *Volvox* nevertheless illustrates how multicellularity might have evolved in the first animals. Beginning as a single cell, subsequent mitoses result in a symmetrical colony composed of hundreds of cells. These cells then specialize functionally into somatic cells and reproductive cells (gonidia).

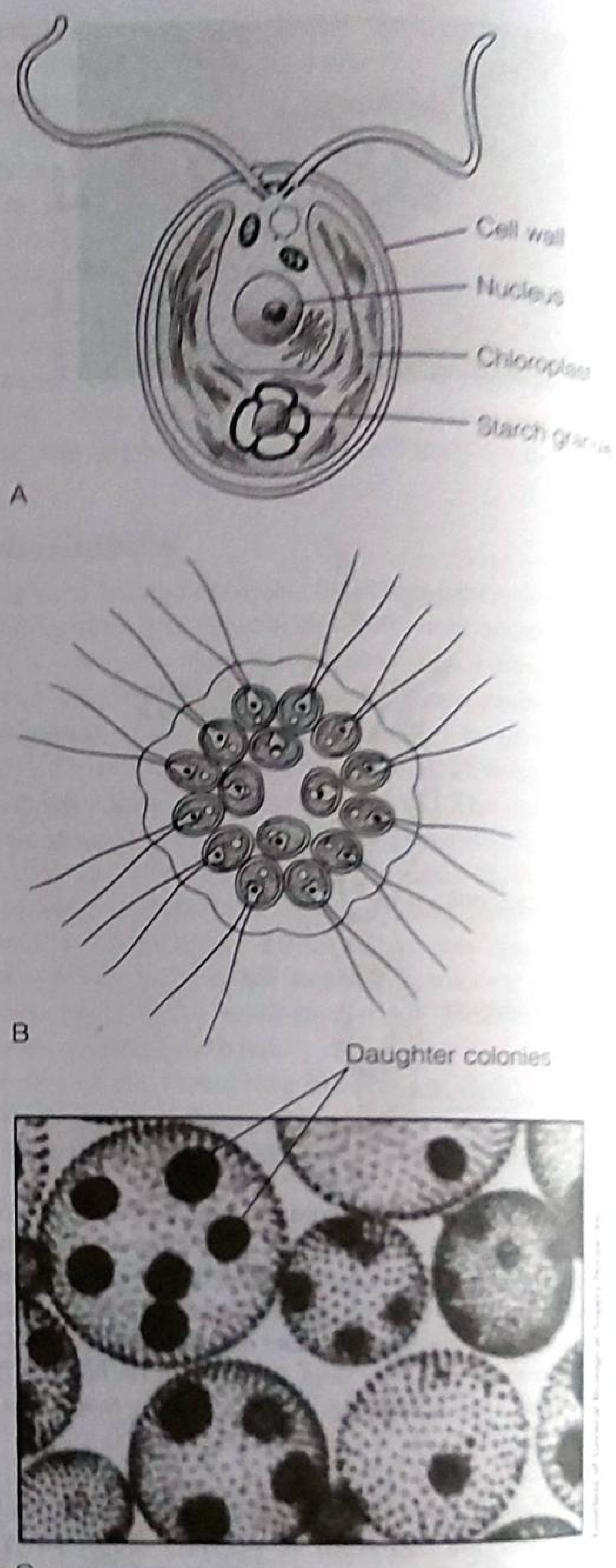



**FIGURE 3-8** Chlorophyta: Volvocida. **A,** *Chlamydomonas reinhar*... a noncolonial solitary species. **B,** *Gonium pectorale. Gonium* spe... form colonies in the form of a flat, square plate in which all cells ar... embedded in a common gelatinous envelope. **C,** *Volvox* colonies a... hollow spheres. Note daughter colonies within parent colonies. ... *Sleigh, M. 1989. Protozoa and Other Protists. Edward Arnold, London; ... B, Courtesy of General Biological Supply House, Inc.)*

# CHOANOFLAGELLATA[P]

Surprising as it may seem, the marine and fresh... choanoflagellates are the sister taxon of animals (Meta... Both choanoflagellate and primitive monociliated ... cells bear a single flagellum, which bears a bilateral va...

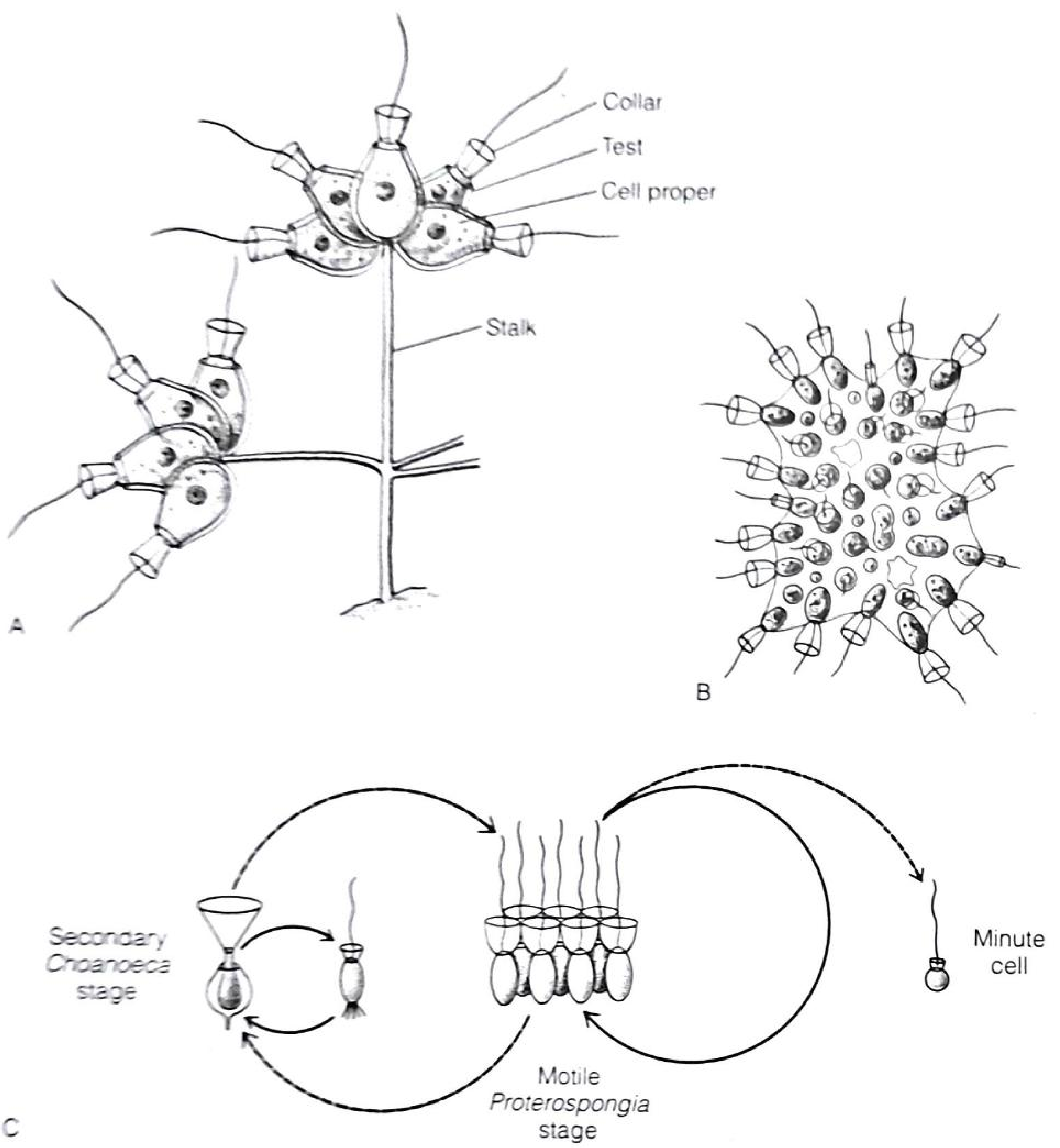



**FIGURE 3-9** Choanoflagellata. Choanoflagellates have one flagellum surrounded by a collar of microvilli. **A,** A stalked colonial species. The stalk is an extension of the vaselike test that surrounds each cell. **B,** *Proterospongia,* a colonial species with cells united in a gelatinous matrix. **C,** *Proterospongia choanojuncta* has both a sessile and planktonic stage. *(A, From Farmer, J. N. 1980. The Protozoa: Introduction to Protozoology. C. V. Mosby Co., St. Louis.; B and C, From Leadbeater, B. S. C. 1983. Life-history and ultrastructure of a new marine species of Proterospongia. Jour. Mar. Biol. Assoc. U.K. 63:135–160.)*

mastigoneme-like filaments and is surrounded by a cylindrical **collar** of microvilli (Fig. 4-2A). This synapomorphy, along with support provided by rDNA sequences, unites the choanoflagellates and metazoans as sister taxa in a monophyletic taxon (see Chapter 1 for cladistic terms and method).

The 600 species of choanoflagellates are mostly tiny and inconspicuous, usually not in excess of 10 μm in diameter (Fig. 3-9, 4-12A,B, 4-13A). While feeding, the flagellum creates a water current from which the collar filters bacteria and organic particulates. Bacteria trapped on the collar are ingested by phagocytosis.

Choanoflagellates may be solitary or colonial, attached or free swimming. Some sessile species are attached by a stalk, part of a vaselike test (Fig. 3-9A). The test is composed of interconnected, extracellular, siliceous rods. The individuals of colonial planktonic forms, such as species of *Proterospongia,* are united by a jellylike extracellular matrix or by their collars (Fig. 3-9B,C, 4-12A,B). In the latter case, the colony may resemble a plate, with all of the collars and flagella located on the same side, or a sphere on which the flagellated collars radiate from the surface (Fig. 4-12A). The marine *Proterospongia choanojuncta* was found to include both a colonial planktonic stage and a solitary, aflagellate attached stage (Fig. 3-9C).

## RETORTAMONADA[P] AND AXOSTYLATA[P]

These two taxa of heterotrophic flagellates have from four to thousands of flagella organized in functional groups. A few of the 700 species are free living (*Hexamita*) in anoxic habitats, but most live anaerobically in the guts of vertebrates and insects, especially wood roaches and termites. Because they live in oxygen-free environments, mitochondria are either absent or atypical, the cells being specialized for glycolysis rather than aerobic respiration. Even when mitochondria are absent, as in *Giardia,* certain mitochondrial genes and proteins do occur, suggesting that the lack of mitochondria is secondary rather than primary.

Retortamonads, such as *Giardia lamblia,* have four flagella, one of which trails behind the leading three and the cell body, and lack Golgi bodies as well as mitochondria. *Giardia lamblia,* which can cause a bloody diarrhea, is a common intestinal parasite in the United States. It frequently occurs in toddlers and child-care workers, but also can be acquired by drinking from seemingly pristine mountain streams. The axostylate *Trichomonas vaginalis* is a small parasite with four anterior flagella (Fig. 3-10A) that inhabits the urogenital tract of

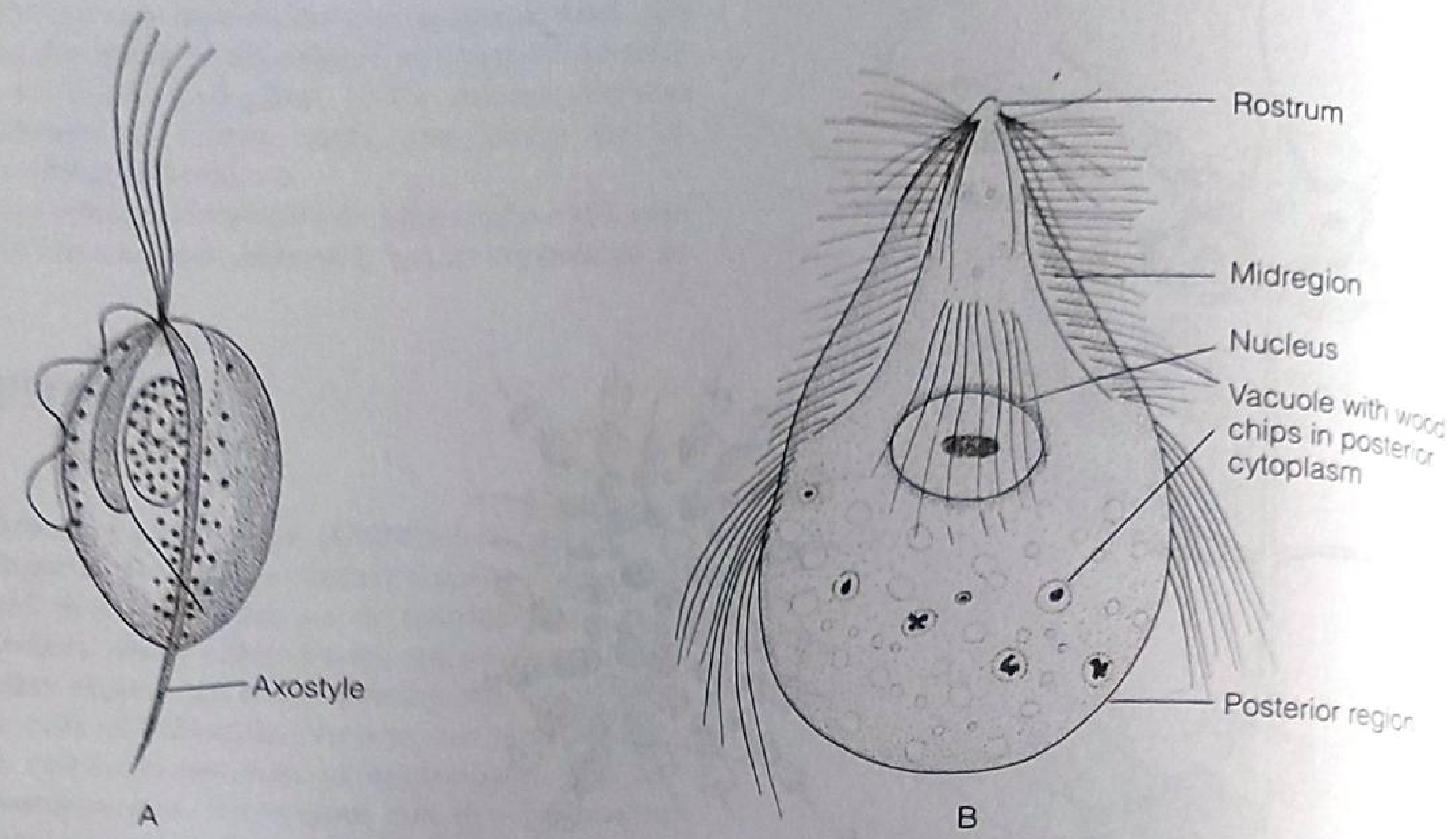



**FIGURE 3-10** Axostylata. **A,** *Trichomonas vaginalis,* a trichomonad parasite in the human vagina and male reproductive tract. In addition to the four anterior flagella, a trailing flagellum borders a looping undulating membrane. An axial skeleton, the axostyle, originates at the flagellar basal bodies, passes through the body of the cell, and protrudes posteriorly. **B,** The hypermastigid *Trichonympha campanula* lives in the gut of termites. *(A, After Wenrich; B, from Farmer, J. N. 1980. The Protozoa: Introduction to Protozoology. C. V. Mosby Co., St. Louis. p. 266.)*

humans and causes a widespread sexually transmitted disease. Living tissues can be invaded and the vaginas of seriously infected women produces a greenish yellow discharge.

The axostylates have a bundle of microtubules called an **axostyle** that extends the length of the cell. It most species, it is skeletal in function, like an intracellular backbone, but in some primitive species, it undulates and imparts a snaky motion to the cell. The derived axostylates, such as the hypermastigid mutualists in the gut of termites and wood roaches, have hundreds or thousands of flagella and astounding internal complexity; *Trichonympha* (Fig. 3-10B) is a good example. Most have a saclike or elongated body usually bearing an anterior rostrum. Axostylates lack mitochondria, but have Golgi bodies.

Many termites and wood-eating cockroaches are dependent on their hypermastigids for the digestion of wood. The flagellates, however, rely on intra- and extracellular bacteria and spirochetes for the actual breakdown of cellulose. The nutrients released from the wood are used by bacterium, flagellate, and insect. The termite host loses its gut mutualists with each molt of its exoskeleton, but by licking other individuals, by rectal feeding, or by eating cysts passed in feces (in the case of roaches), a new innoculation is obtained. In wood-eating cockroaches, the life cycles of the flagellates are closely tied to the production of molting hormones by the late nymphal insect.

## Diversity of Retortamonada

**Retortamonadea[C]:** Two or four anterior flagella, one of which is associated with the cytostome, which is elongate longitudinally as a body furrow; mitochondria are absent. *Chilomastix* sp. (plural, spp.) cause diarrhea in humans, poultry; *Retortamonas.*

**Diplomonadea[C]:** Cell with eight flagella, two two nuclei (twinned, diplozoic cell); mito absent. Free-living *Hexamita* and parasitic Giar attachment disc and long flagellar axonemes

## Diversity of Axostylata

**Oxymonadea[C]:** Four posterior flagella; no chondria, or Golgi bodies. Undulatory axost cellular bacteria and surface-attached spiro obes in the gut of termites and wood roache *Pyrsonympha.*

**Parabasalea[C]:** Cells have from a few to thous and aggregates of large Golgi bodies (para Axostyle is skeletal, single, replicated, or lost are absent; gut symbionts. Trichomonadida six flagella; a recurrent flagellum forms membrane; axostyle projects posteriorly to for ment site. *Trichomonas* and *Mixotricha parado* gut have surface-attached spirochetes whose the flagellate. Hypermastigida[O] has many fla anterior end of the cell (sometimes also else have surface-attached symbiotic bacteria. In termites and wood roaches. *Barbulanympha Trichonympha.*

# ALVEOLATA[P]

Three taxa, Dinoflagellata, Ciliophora, and (Sporozoa) constitute the Alveolata. Alveolates the basis of having similar ribosomal DNA pellicular alveoli.

## Dinoflagellata[sP]

Approximately one-half of the 4000 marine and freshwater species of dinoflagellates have chloroplasts and are important primary producers, especially in the sea. The xanthophyll pigment **peridinin** colors them red-brown or golden brown. Their chloroplasts are surrounded by three membranes and have chlorophylls a and c, but lack chlorophyll b. Dinoflagellate chloroplasts are diverse, having originated as endosymbionts from at least three different taxa of photosynthetic cells. Heterotrophic dinoflagellates lack plastids and are colorless. Like euglenoids, dinoflagellates originated as colorless heterotrophs that independently acquired chloroplasts by endosymbiosis, probably more than once. A few dinoflagellates are endoparasites of other protozoans, crustaceans, and fishes. The cell nucleus contains permanently condensed (thickened) chromosomes having relatively small amounts of protein, and each chromosome is permanently attached to the nuclear membrane.

Typical dinoflagellates have two flagella. One is attached a short distance behind the middle of the body, is directed posteriorly, and lies in a longitudinal groove **(sulcus)** (Fig. 3-11B). Its surface is smooth or it may have two rows of mastigonemes. The other flagellum is transverse and located in a groove **(cingulum)** that either rings the body once or forms a spiral of several turns. The transverse flagellum, which bears a unilateral row of mastigonemes, causes both rotation and forward movement. The longitudinal flagellum drives water posteriorly and contributes to forward motion. The dinoflagellate contractile vacuole, called a **pusule,** opens to the exterior near the bases of the flagella. The pusule is surrounded by contractile myonemes.

Dinoflagellates have a complex skeleton, or **theca,** which often contains deposits of skeletal cellulose in alveoli. Where the theca is thin and flexible, as in the common freshwater and marine genus *Gymnodinium,* the dinoflagellate is said to be unarmored, or naked (Fig. 3-11A). Armored dinoflagellates have a thick theca composed of a few to several plates (Fig. 3-11B) formed by cellulose-filled alveoli. Frequently the armor is sculptured, and often long projections or winglike extensions protrude from the body, creating bizarre shapes (Fig. 3-11C). The large, colorless, and aberrant *Noctiluca* (Fig. 3-11D) and many smaller species are the principal contributors to planktonic bioluminescence. At night on a quiet sea, their greenish light sparkles in the wake of a boat or as startled fish streak away like shooting stars.

Dinoflagellates are either pigmented photoautotrophs or colorless heterotrophs, but some pigmented species exhibit both modes of nutrition. The prey is usually captured with pseudopodia and ingested through an oral opening associated with the longitudinal flagellar groove. *Noctiluca* is a predator that uses a single contractile tentacle, containing myonemes, to catch prey and convey it to its cell mouth (Fig. 3-11D). Among the symbiotic dinoflagellates, the mutualistic zooxanthellae of corals, without which the coral-reef ecosystem probably would not exist, are primarily one dinoflagellate species, *Symbiodinium microadriaticum.*

Myriad dinoflagellates occur in marine plankton as important contributors to oceanic primary production, especially in the tropics. Marine species of the genera *Gymnodinium, Gonyaulax,* and others are responsible for outbreaks of the so-called red tides (Fig. 3-11E). Under ideal environmental conditions and perhaps with the presence of a growth-promoting substance, populations of certain species increase astronomically. Red tides, however, are not always red. The water may be yellow, green, or brown, depending on the predominant pigments of the blooming organisms. Concentrations of toxic alkaloids produced by the dinoflagellates can reach such high levels that other marine life may be killed. The 1972 red tides off the coasts of New England and Florida killed thousands of birds, fish, and other animals and wreaked havoc on the shellfish industry by infecting clams and oysters that fed on the dinoflagellates.

*Pfiesteria piscicida,* the cell from Hell, is the dinoflagellate responsible for fish kills in estuaries along the middle Atlantic and southeastern coasts of the United States. Under conditions of organic enrichment, either from human pollution or the feces of schooling fish, the normally nontoxic cells release a waterborne toxin that causes skin lesions in fish. The dinoflagellates then attack the sores and consume the fish. *Pfiesteria* is a colorless heterotroph that feeds by phagocytosis on a variety of organisms. When feeding on unicellular algae, it can digest the prey-cell but retain its chloroplasts intact and then use them to provide itself with photosynthate. The *Pfiesteria* life cycle includes several stages besides the typical biflagellated planktonic cell. These include a benthic ameba and encysted stages, as well as a planktonic form that superficially resembles a heliozoan (see Heliozoa later in this chapter).

Ciguatera food poisoning in humans is caused by a marine dinoflagellate that lives attached to multicellular algae. Ciguatoxin is acquired by grazing herbivorous fish that concentrate the toxin in their tissues and pass it up the food chain. The toxin can reach such high levels in the tissues of carnivorous fish that, when eaten by humans, it produces serious poisoning and even death. In addition to gastrointestinal symptoms such as diarrhea and nausea, there may be respiratory problems, muscle weakness, and long-lasting, strange skin sensations.

Dinoflagellates undergo longitudinal binary fission. Cysts are formed in many flagellate groups, including dinoflagellates. In addition to the ameboid form of *Pfiesteria* already noted, some dinoflagellates can adopt the form of a naked, nonflagellated ball called a **palmella.** Fission often transforms the unicellular palmella into a cluster of cells. The dinoflagellates that inhabit corals as zooxanthellae do so in the palmella stage.

## Ciliophora[sP]

Ciliophora is a monophyletic taxon of animated and engaging cell-organisms. Most seem like diminutive animals because of their sophisticated cellular organelles and the complexity of their behavior. Many animal tissues and organs, such as muscle and gut, have analogs in the cellular anatomy of ciliates. The 8000+ described species are widely distributed in fresh water, the sea, and in the water film around soil particles. All ciliates are heterotrophs, but about one-third of them are ecto- or endocommensals or parasites.

### FORM AND FUNCTION

Diverse body forms occur among the ciliates and, despite their motility and fixed anterior-posterior polarity, most are asymmetric. A few, however, are radially symmetric with an anterior

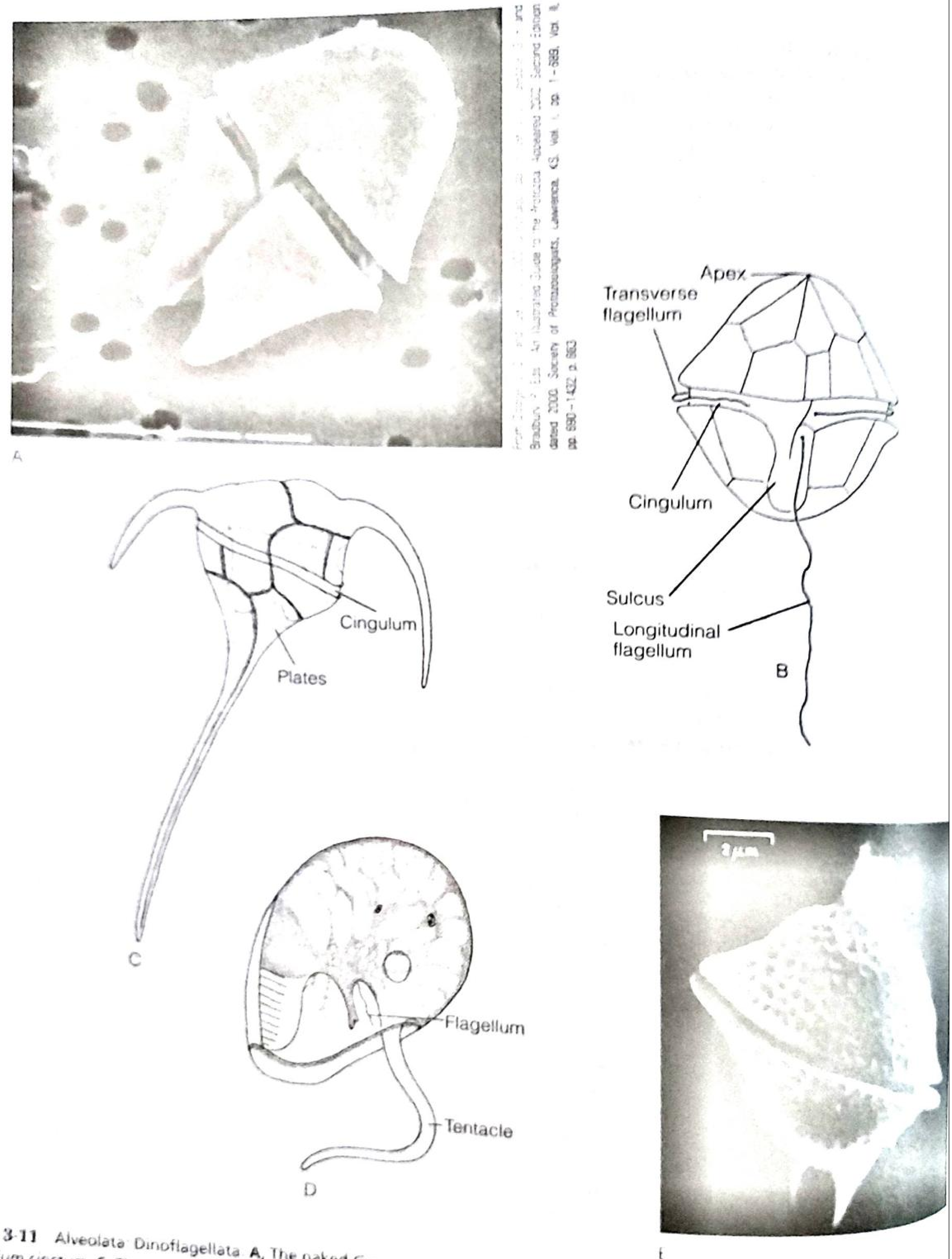



**FIGURE 3-11** Alveolata: Dinoflagellata. **A,** The naked *Gymnodinium*. **B,** A freshwater armored species, *Glenodinium cinctum*. **C,** The armored, *Ceratium*. **D,** *Noctiluca*, a bioluminescent carnivore with a prehensile tentacle. Only one small flagellum occurs in an "oral" depression. **E,** *Gonyaulax digitale*, a marine species that causes red tides. *(B, After Pennak, R. W. 1978. Freshwater Invertebrates of the United States. 2nd Edition. John Wiley and Sons, New York; C, After Jorgensen; D, After Robin)*

mouth (Fig. 3-12). Most ciliates are solitary and motile, but some species form colonies and are sedentary. Most ciliates are "naked," but tintinnids, some heterotrichs, peritrichs, and suctorians are housed in a test of secreted organic material or of cemented foreign matter (Fig. 3-13). Ciliate cell si[ze ranges] from 10 μm to 4.5 mm.

The surface cilia are specialized into a **somatic ci[liature]** ass[ociated with] the general body surface and an **oral ciliature** ass[ociated]

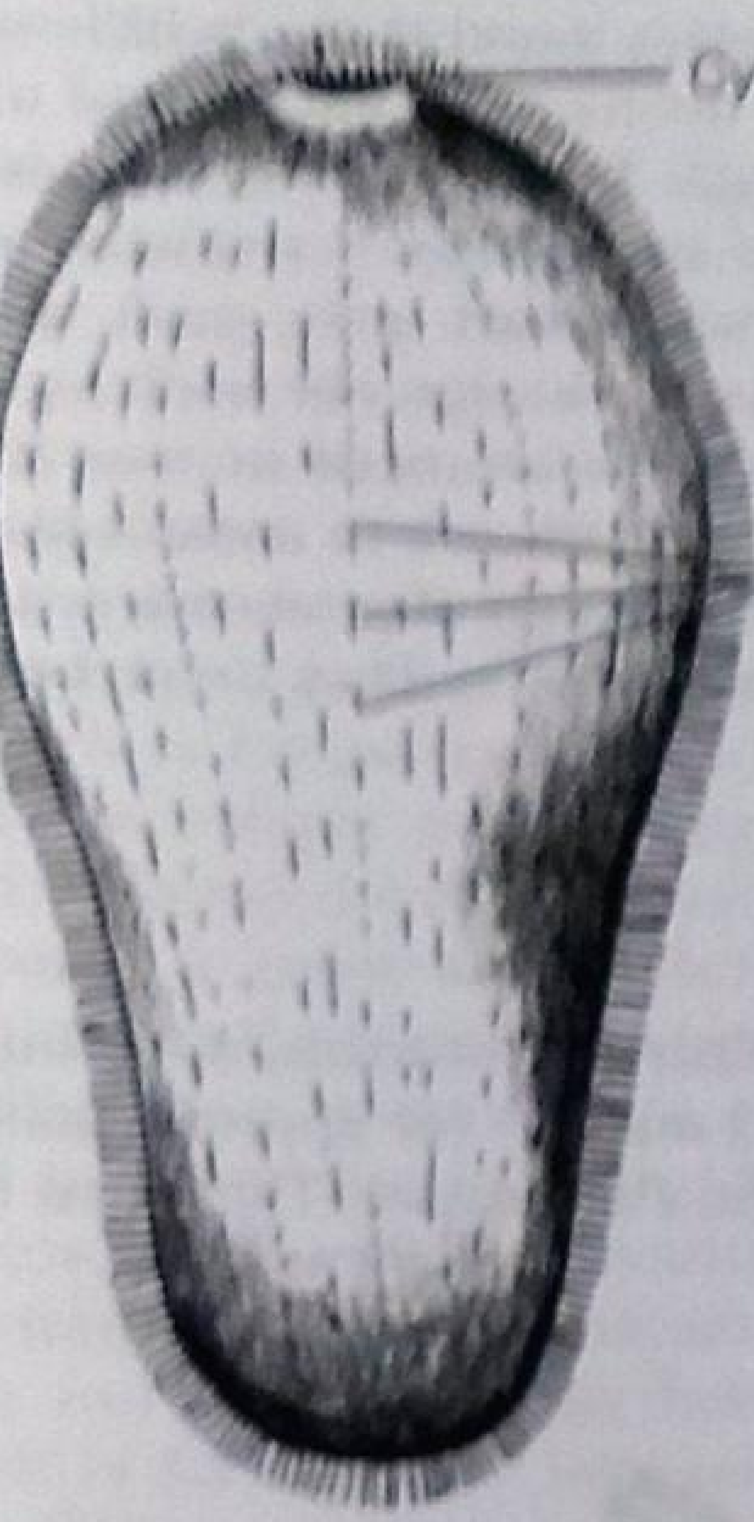



FIGURE 3-12 Alveolata: Ciliophora. *Prorodon*, a radially symmetrical ciliate. *(After Fauré-Fremiet from Corliss, 1979)*

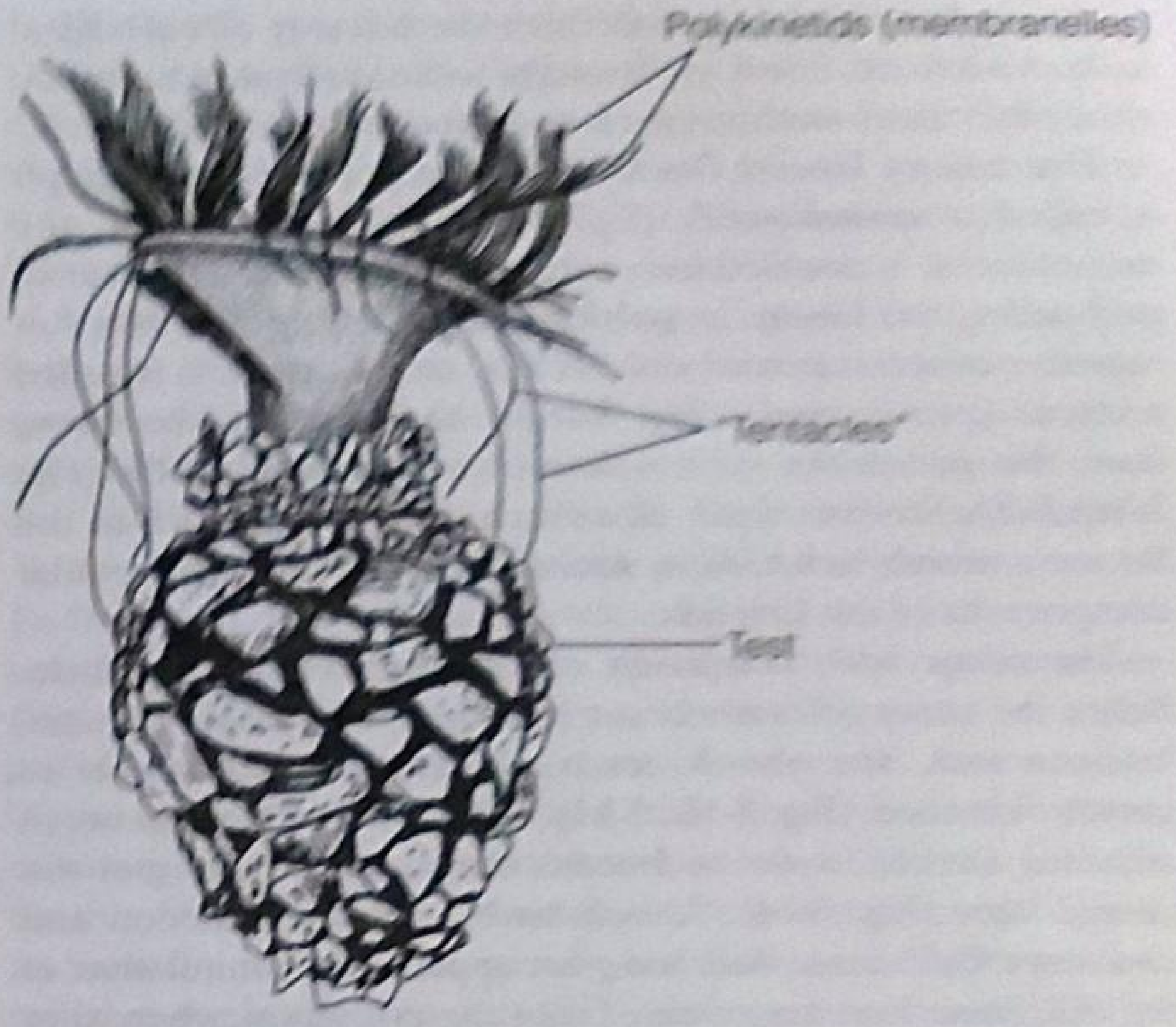



FIGURE 3-13 Alveolata: Ciliophora. *Tintinnopsis*, a marine ciliate (tintinnid) with a test composed of foreign particles. Note conspicuous polykinetids (membranelles) and tentacle-like organelles interspersed between them. *(After Fauré-Fremiet from Corliss, 1979)*

the mouth region. Distribution of body cilia varies between species. In some, cilia cover the entire cell and are arranged in longitudinal rows, each called a **kinety** (Fig. 3-12), but in more specialized taxa the cilia are restricted to regions of the body (Fig. 3-13, 3-18).

A kinety is a row of repeating **kinetids,** each comprising a cilium, basal body, and associated fibers (Fig. 3-14). One of the fibers attached to the basal body is a striated rootlet, which is oriented anteriorly. The rootlet fibers from all basal bodies in a row may combine, like wires in a cable, to form a single **kinetodesma,** which runs the length of the row (Fig. 3-14). The other fibers associated with each basal body are ribbons of microtubules. A postciliary microtubular ribbon extends posteriorly from each basal body. A transverse

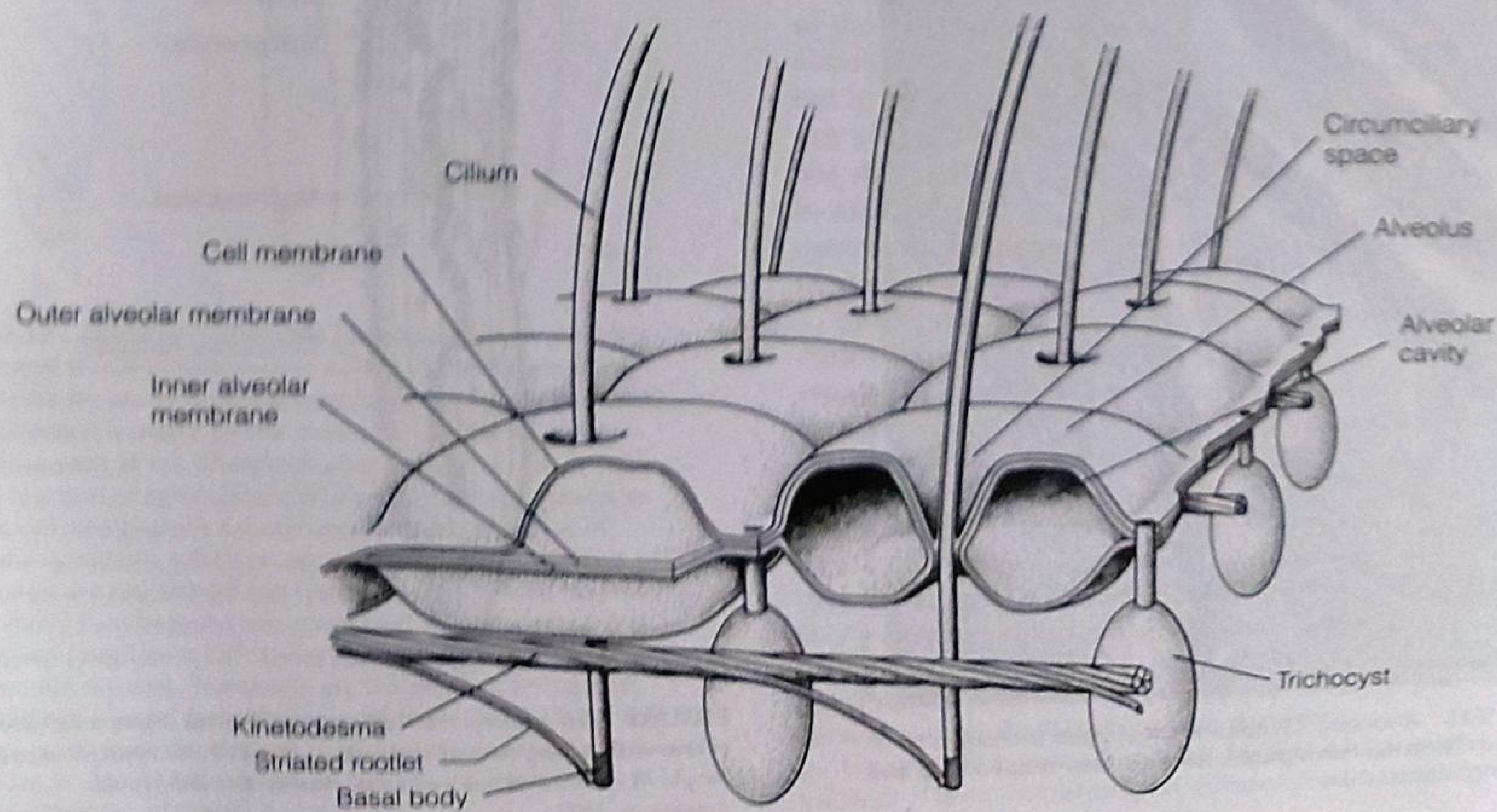



FIGURE 3-14 Alveolata: Ciliophora. The pellicle of *Paramecium*. *(After Ehret and Powers from Corliss, 1979)*

microtubular ribbon extends from the left side of each basal body. All kinetid fibers are thought to be skeletal in function, either for ciliary anchorage or maintenance of cell shape.

The unitary kinetid described in the preceding paragraph is called a **monokinetid** (Fig. 3-14). In some ciliates, the monokinetid is doubled into a **dikinetid** and the cilia occur in pairs along the kinety. In **polykinetids,** multiple cilia function together in a compound unit. If that unit is a tuft, it is called a **cirrus** (plural, **cirri**) (Fig. 3-18B), and if it is a short row, then the paddlelike unit is known as a **membranelle** (Fig. 3-18A,B,F). Kinetids typify all ciliates, even groups such as the Suctoria, which lack cilia as adults but retain the intracellular components of the kinetids.

The ciliate body is typically covered by a complex pellicle. Below the outer cell membrane is a single layer of small membranous sacs, the alveoli, each of which is moderately to greatly flattened (Fig. 3-1E, 3-14). Cilia emerge from between adjacent alveoli, as do trichocysts and other extrusomes discussed later (Fig. 3-14). Alveoli have a skeletal function and also store $Ca^{2+}$ ions. Following an appropriate stimulation of the cell, these ions are released into the cytoplasm, where they can initiate changes in ciliary beat or discharge of extrusomes.

**Extrusomes** are secretory bodies specialized for rapid release at the surface of the cell. In *Paramecium* and other ciliates, bottle-shaped extrusomes, **trichocysts,** alternate with the alveoli (Fig. 3-14). In the undischarged state, a trichocyst is perpendicular to the body surface. At discharge, the trichocyst rapidly ejects a long, striated, threadlike shaft surmounted by a barb (Fig. 3-15). The shaft is not evident in the undischarged state and probably polymerizes during discharge. Trichocysts appear to function in defense against pre[dators]. **Toxicysts** are extrusomes found in the pellicle of *Dilep[tus]* [and] *Didinium.* A toxicyst discharges a long thread with a b[ulbous] base containing a toxin. Toxicysts are used for defense [and] capturing prey. They are commonly restricted to the p[arts of] the ciliate body that contact prey, such as around [the] cytostome in *Didinium* or the anterior body region of *L*[...] (Fig. 3-16). **Mucocysts** are arranged in rows like tric[hocysts] and discharge a spray or network of mucoid filaments [that] may function in the formation of protective cysts or pr[ovide a] sticky surface for prey capture. They occur in many c[iliates,] including *Didinium.*

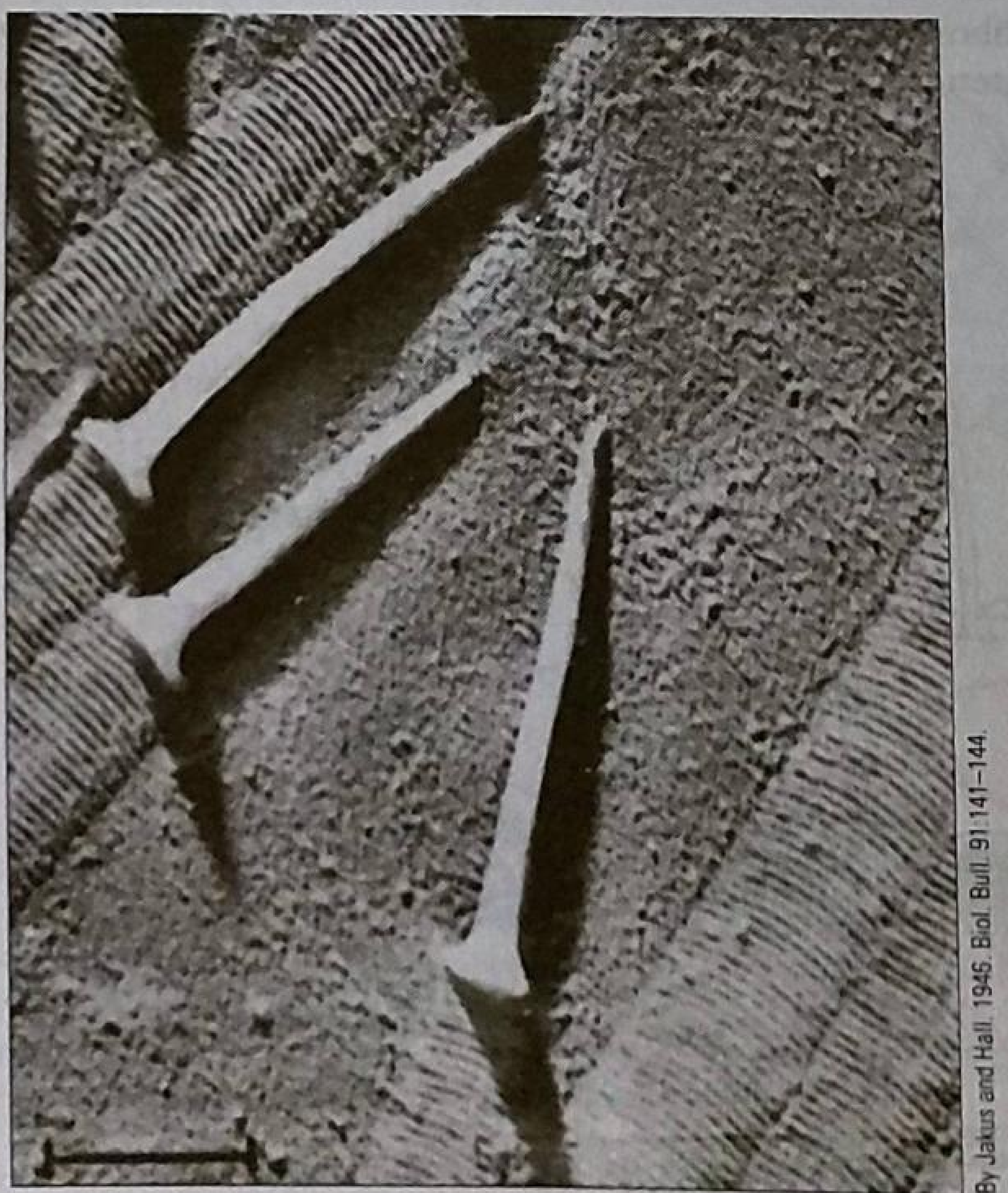



**FIGURE 3-15** Alveolata: Ciliophora. Discharged trichocysts of *Paramecium* (electron micrograph). Note golf-tee-shaped barb and part of long striated shaft.

## LOCOMOTION

The ciliates are the fastest protozoans, achieving velo[cities in] the range of 0.4 to 2 mm $s^{-1}$ (or approximately eigh[t body] lengths $s^{-1}$ for a typical *Paramecium*). The fastest flagell[ates]

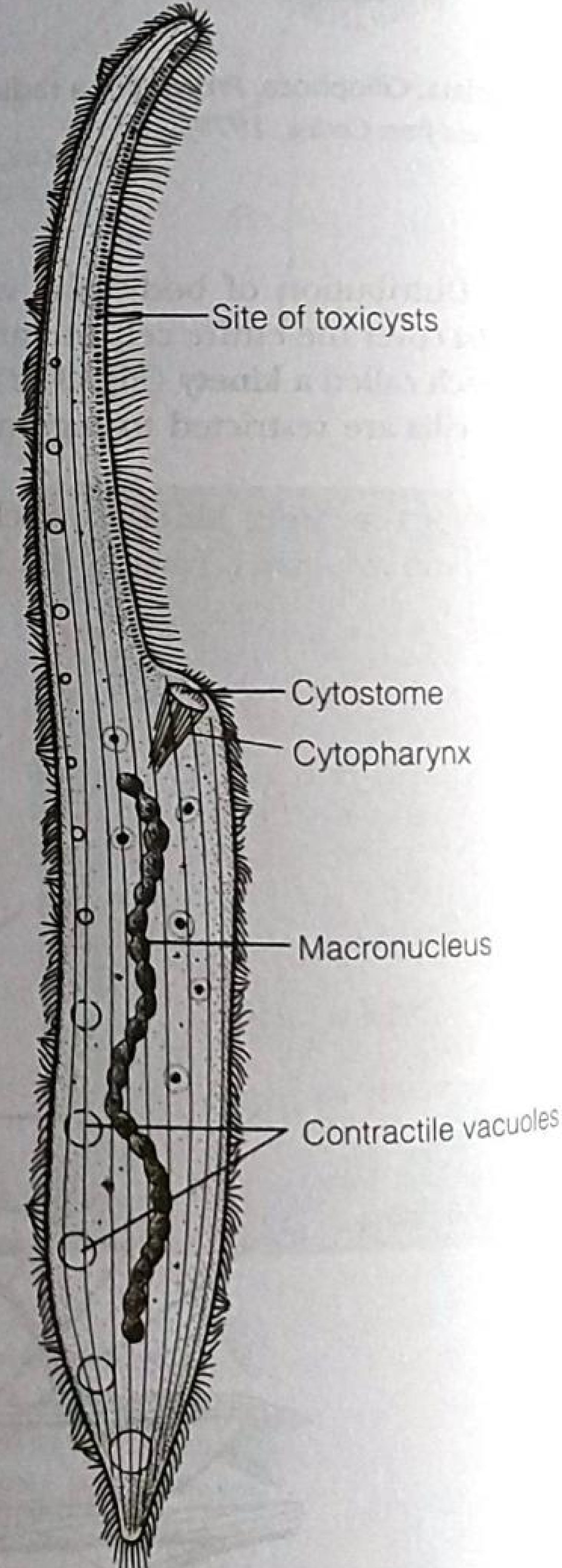



**FIGURE 3-16** Alveolata: Ciliophora. *Dileptus anser,* a carn[ivorous] ciliate with a long row of toxicysts in front of the cytostome. (*Sleigh, M. 1989. Protozoa and Other Protists. Edward Arnold, London. p. 198*)

the other hand, reach only 0.2 mm $s^{-1}$. On average, ciliates move faster than flagellates because of the numerous cilia on their surfaces.

Metachronal waves (Chapter 2 and Fig. 2-7A) pass over the surface of active ciliates, approximately 10 waves at any moment on the body of a *Paramecium*. The metachronal coordination of cilia is thought to be controlled by water motion. The water movement created by one cilium initiates movement in the next cilium, like a sequence of falling dominoes. The kinetodesmal fibers are not regarded as a conducting system in ciliary-beat coordination.

In genera such as *Paramecium*, the direction of the ciliary effective stroke is oblique to the long axis of the body (Fig. 3-17A). This causes the ciliate to swim in a spiral course and simultaneously to rotate around its longitudinal axis. To change direction, *Paramecium* instantaneously reverses the direction of ciliary beat, retreats, stops, turns, and then proceeds forward in a new direction (Fig. 3-17B). This turning sequence is known as an **avoidance reaction.** Mechanical stimuli may be detected by long, stiff, nonmotile (sensory) cilia. The direction and intensity of the beat are controlled by changing levels of $Ca^{2+}$ and $K^{+}$ ions released from alveolar stores in the pellicle.

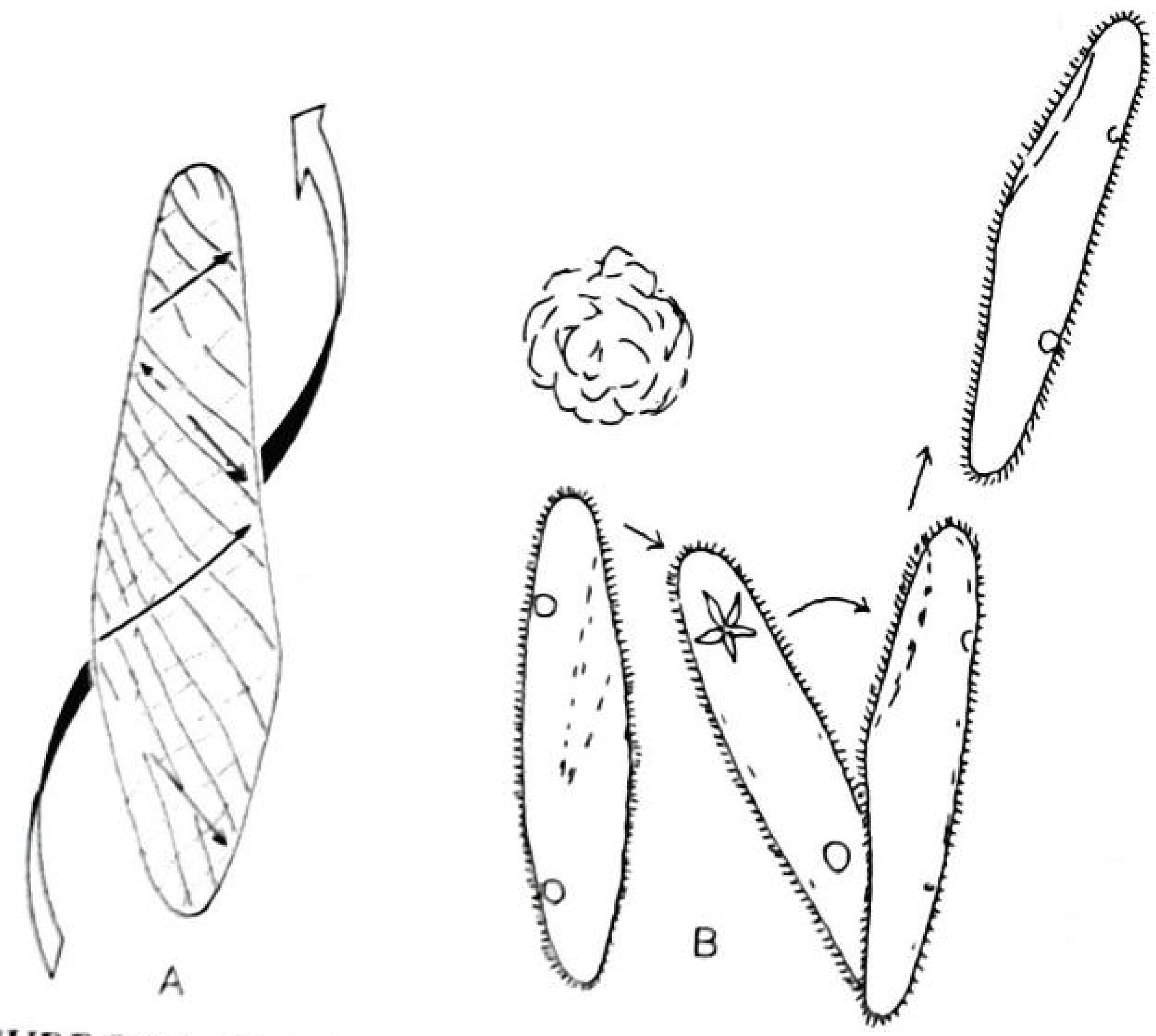



**FIGURE 3-17** Alveolata: Ciliophora. Locomotion in *Paramecium*. **A,** Metachronal waves in *Paramecium* during forward swimming. Wave crests are shown by diagonal lines (dotted on ventral surface), and their direction is shown by the small solid arrows. Rotational forward movement of the ciliate indicated by large arrow. **B,** The avoidance reaction of *Paramecium*. When *Paramecium* contacts an object, the cell membrane is depolarized, allowing an influx of $Ca^{2+}$ into the cytoplasm, which causes reversal of the ciliary beat. As $Ca^{2+}$ pumps are reactivated and cytoplasmic $Ca^{2+}$ levels begin to drop, the ciliary beat becomes uncoordinated and the cell turns as a result. When cytoplasmic $Ca^{2+}$ levels reach their normal level, forward motion resumes. The alveoli are the sites of $Ca^{2+}$ uptake, storage, and release. *(A, From Machemer, H. 1974. Ciliary activity and metachronism in Protozoa. In Sleigh, M. A. (Ed.): Cilia and Flagella. Academic Press, London. p. 224. B, After Hyman, L. H. 1940. The Invertebrates, Vol. 1. McGraw-Hill Book Co., New York)*

The highly specialized stichotrichs and hypotrichs, such *Urostyla, Stylonychia,* and *Euplotes* (Fig. 3-18A,B), have bodi differentiated into distinct dorsal and ventral sides. Cilia ha largely disappeared except on localized ventral areas that be cirri. The cilia of each cirrus are synchronized and the cirr beats functionally as a single large, forceful unit.

Some ciliates, such as the elongate karyorelictids that li between sand grains on marine beaches or common sessi species of *Vorticella* or *Stentor,* are highly contractile and wit draw rapidly from potential predators. Contraction results fro the shortening of striated protein fibers called **myoneme** *Stentor* shortens its entire body with pellicular myonemes, but *Vorticella* and the colonial *Carchesium,* the myonemes exter into the stalk as a single large, spiral fiber, the **spasmonem** (Fig. 3-18C,D). This spasmoneme contracts rapidly, in a fe milliseconds, presumably as an escape response. Re-extensio of the spasmoneme is slow and may result from the elast recoiling of the extracellular sheath around the stalk and th beating of the oral cilia. Myonemes are not composed of acti and myosin, as in animal muscle, but rather of another protei called **spasmin** that requires $Ca^{2+}$, but apparently not ATP, fo contraction.

## NUTRITION

Free-living ciliates may be detritivores, bacteriovores, herb vores, or predators. Predators may be raptorial, actively pursu ing their prey, or ambush predators that lie in wait for thei quarry. The predators feed on other protozoans, includin other ciliates, and even small animals such as rotifers. Man small ciliates move in search of food—bacteria, diatoms detritus—and ingest it after making contact. Others, usuall larger-bodied species, may use their body cilia to suspensior feed on similar foods. The preoral cilia of suspension feeder is usually complex, whereas ciliates that feed by direct inter ception have less complex oral regions.

Most ciliates have a cytostome, a dedicated endocytic area of the cell membrane that is free of cilia, infraciliature, and alveoli. In some groups the cytostome is anterior (Fig. 3-12), but in most ciliates it has been displaced more or less posteriorly (Fig. 3-16, 3-19). In its least complex form, the cytostome lies directly over a cytopharynx, a cylinder of microtubules located in the cytoplasm (Fig. 3-16). Food is ingested at the cytostome by phagocytosis and the cytopharynx conveys the food vacuole inward.

The oral structures may consist solely of the cytostome and cytopharynx (Fig. 3-16, 3-18F), but in most ciliates the cytostome is preceded by a preoral chamber that aids in food capture and manipulation. The preoral chamber, called a **vestibule,** may be lined only with simple cilia derived from somatic cilia. In other, more complex ciliates, the preoral chamber differs from a vestibule by containing compound ciliary organelles (polykinetids) instead of simple cilia and is then designated a **buccal cavity** (or peristome; Fig. 3-18A,D). In *Paramecium*, the preoral chamber is divided into an outer vestibule and an inner buccal cavity (Fig. 3-19). The polykinetids of its buccal cavity create a current that transports bacteria or small protozoans into the cavity.

Among predators, species of *Didinium* have been carefully studied. These barrel-shaped ciliates feed on other ciliates.

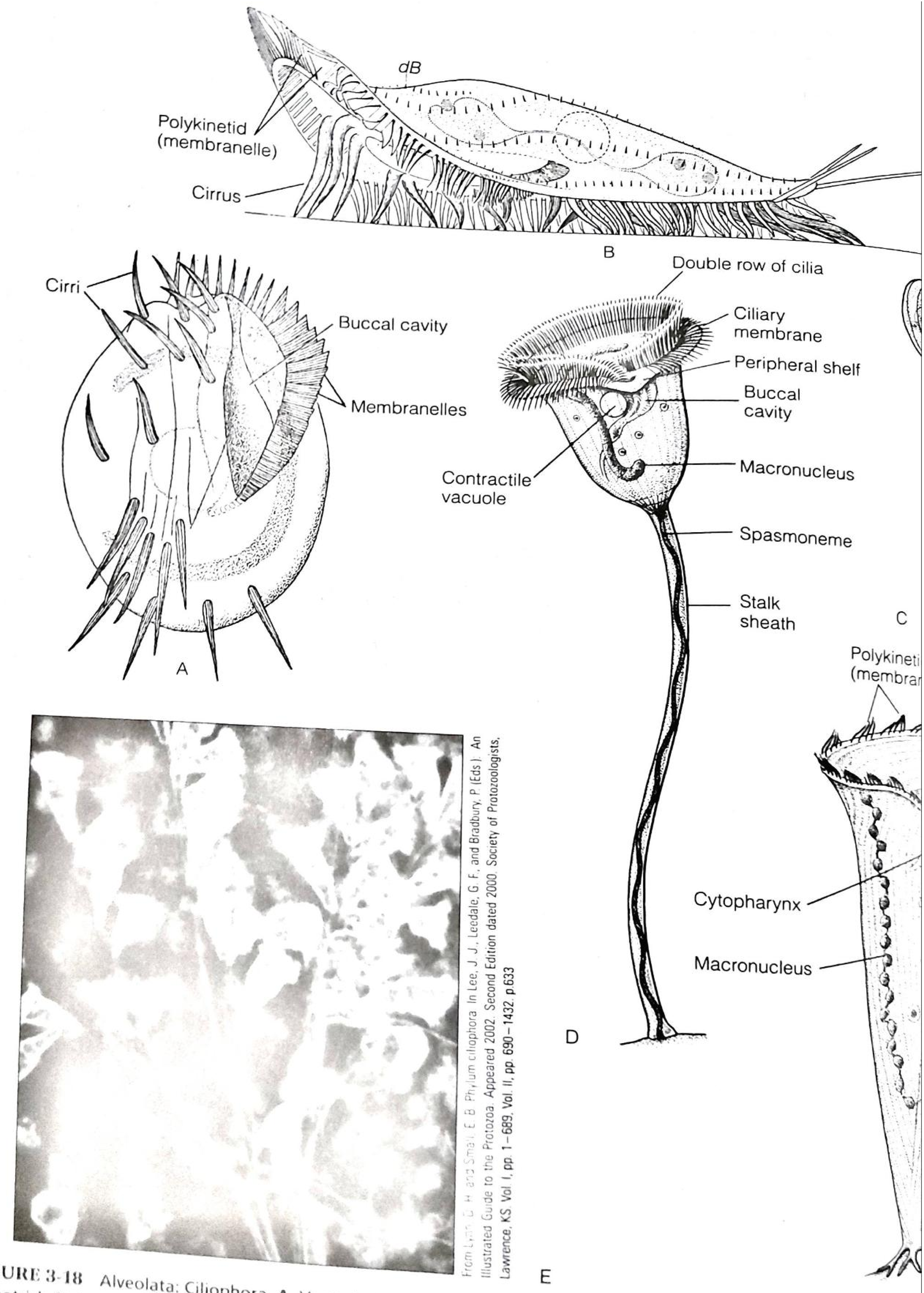



**FIGURE 3-18** Alveolata: Ciliophora. **A,** Ventral view of the hypotrich *Euplotes.* **B,** Lateral view of the
tichotrich *Stylonychia mytilus.* The arrangement of organelles on the ventral side is similar to that of *Euplotes.*
and **D,** *Vorticella convallaria* (Peritrichia) in contracted state (**C**) and extended state (**D**). **E,** *Carchesium*
olypinum, a colonial peritrich similar to *Vorticella.* **F,** *Stentor coeruleus* (Heterotrichia). Note the large
nacronucleus in *Vorticella* and *Stentor*, both of which are large cells (up to 2 mm). *(A, After Pierson from Kudo.*
*3. By Machemer, H. In Grell, K. G. 1973. Protozoology. Springer-Verlag, New York, p. 304. C, D, and F, from Sleigh, M.*
*989. Protozoa and Other Protists. Edward Arnold, London. pp. 211 and 213.)*

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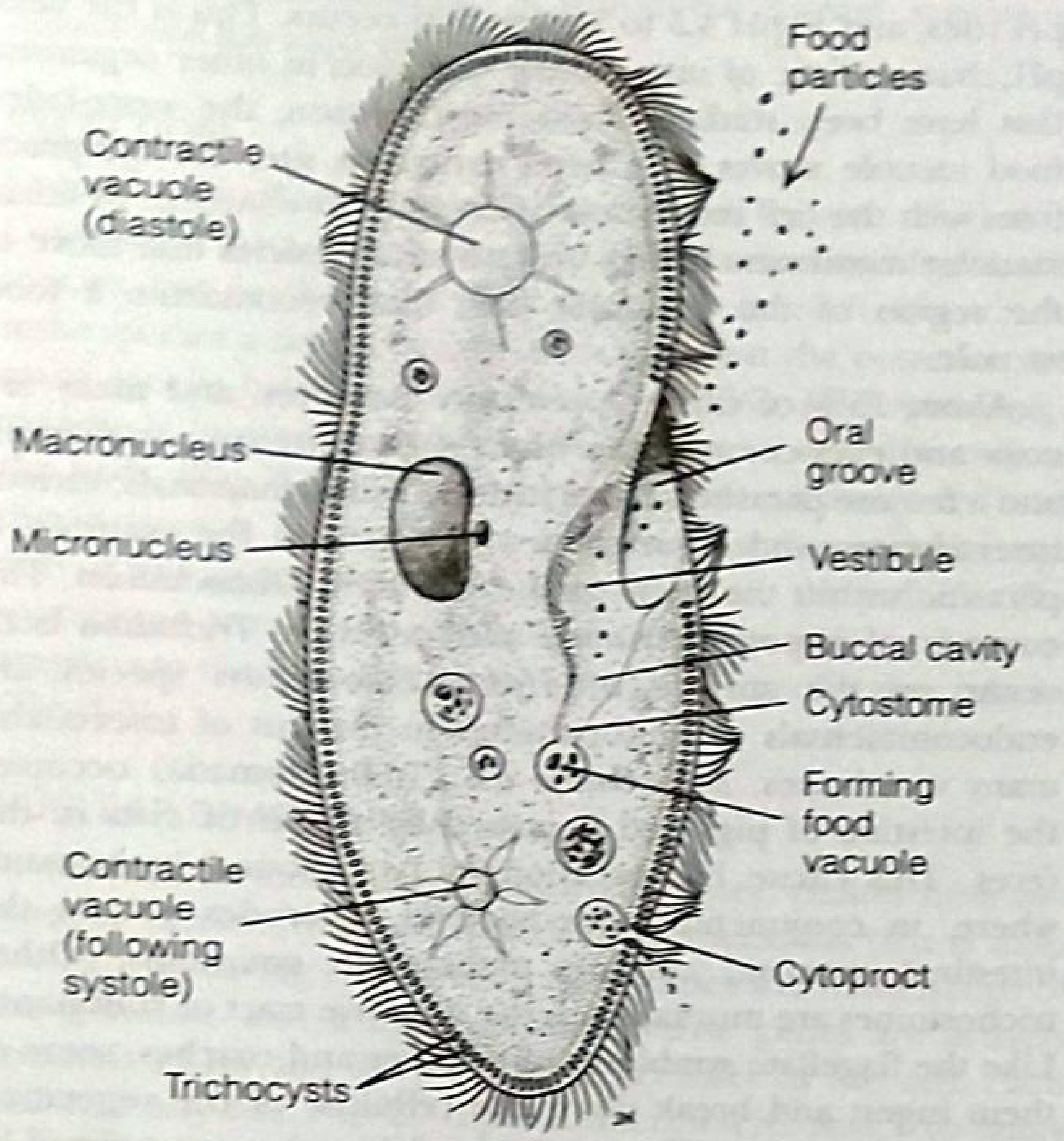



**FIGURE 3-19** Alveolata: Ciliophora. Structure of *Paramecium*. *(After Mast from Dogiel; B, After Clakins from Hyman; C and D, from Sleigh, M. A. 1973. The Biology of Protozoa. Edward Arnold Publishers, London. p. 64. Based on micrographs of Rudzinska, Bardele, and Grell.)*

particularly *Paramecium* (Fig. 3-20A). When *Didinium* attacks a *Paramecium*, it discharges toxicysts into the *Paramecium* and the proboscis-like anterior end attaches to the prey through the terminal cytostome, which can open almost as wide as the diameter of the body. Once seized, the *Paramecium* is ingested by phagocytosis.

The free-living members of the Suctoria are ambush predators that resemble tiny, carnivorous sundew plants (Fig. 3-20B). Unlike other ciliates, suctorians lack cilia, except in immature stages. Suctorians are sessile and most are attached by a stalk to the surface of marine and freshwater invertebrates. Stiff tentacles radiate outward from the body and may be knobbed at their tips or shaped like long, pointed spines (Fig. 3-20B). Each tentacle is supported internally by a cylinder of microtubules and bears special attachment extrusomes called **haptocysts** at the tentacle tips (Fig. 3-20C,D). When prey organisms, including other ciliates, strike the tentacles, the haptocysts are discharged into the prey, anchoring it to the tentacles. The contents of the prey are then "sucked" into the tentacle, entering a long food vacuole that eventually extends into the body of the suctorian. "Suction" is actually a rapid phagocytosis, accelerated by the microtubular cylinder, which functions as a cytopharynx in the axis of each tentacle.

Suspension feeders typically have a buccal cavity. Food is brought to the body and into the buccal cavity by the compound ciliary organelles. From the buccal cavity the food particles are driven through the cytostome and into the cytopharynx. When the particles reach the cytopharynx, they are collected in a food vacuole.

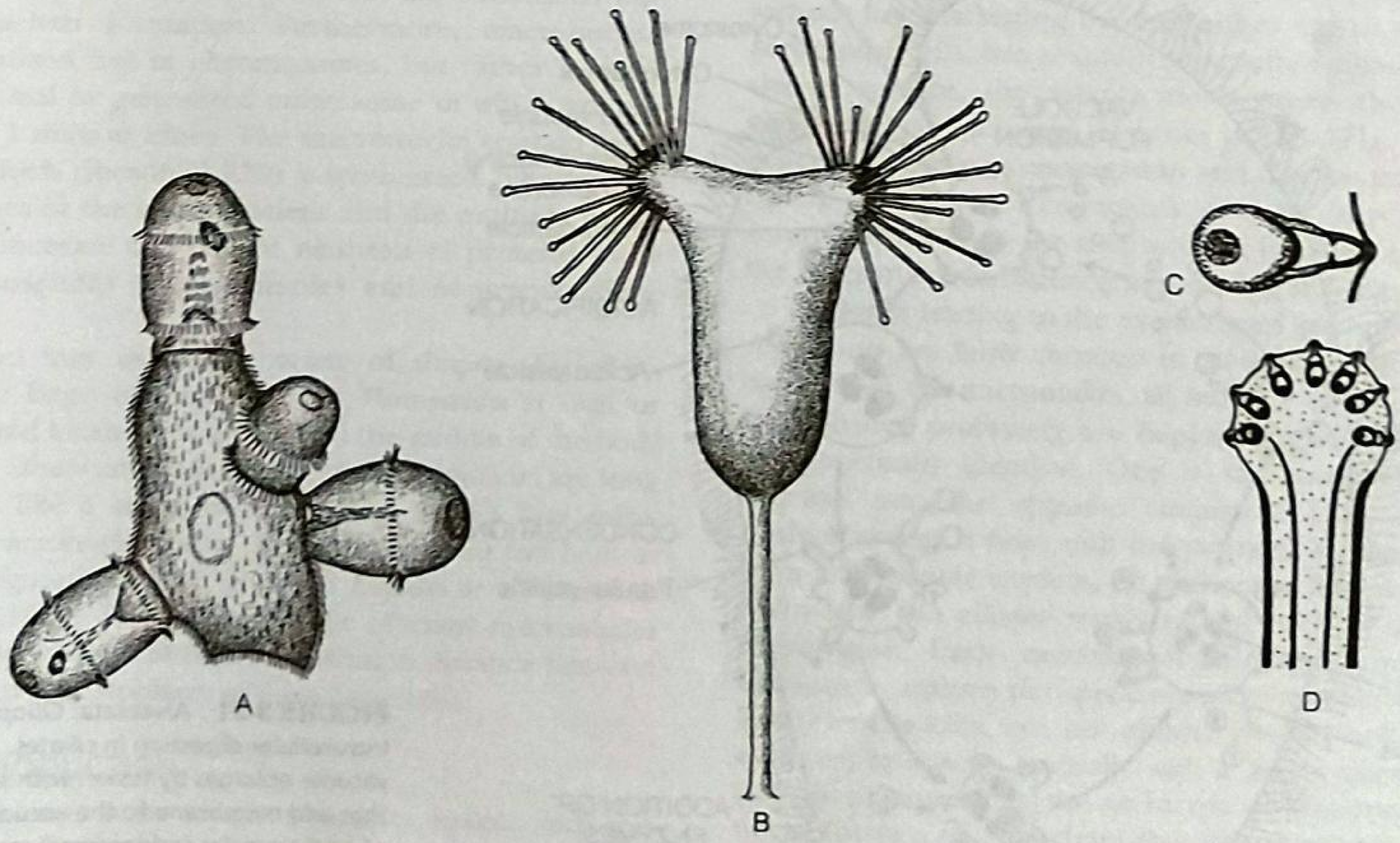



**FIGURE 3-20** Alveolata: Ciliophora. Predatory ciliates. **A,** Four *Didinium* attacking one *Paramecium*. **B,** *Acineta*, a suctorian. **C,** A single undischarged haptocyst below the surface of a tentacle cell membrane. **D,** Several haptocysts in a tentacle tip; the two lines below the haptocysts are a section through the microtubular cylinder in the tentacle. *(A, After Mast from Dogiel; B, After Clakins from Hyman, 1940; C and D, From Sleigh, 1973)*

In the filter-feeding Peritrichia, whose members possess little or no body cilia, the buccal ciliary structures are highly developed and are part of a disklike area at the oral end of the body. In *Vorticella*, a peripheral shelf (Fig. 3-18D) closes over the disk during retraction (Fig. 3-18C). The buccal cilia are in a groove between the edge of the disk and the peripheral shelf. These cilia form an outer membrane of fused cilia and an inner double row of unfused cilia. Both membrane and ciliary rows wind counterclockwise around the margin of the disk and then turn downward into the funnel-shaped buccal cavity (Fig. 3-18D). The inner ciliary rows generate the water current, and the outer membrane acts as the filter. The food, mostly bacteria, is transported between the membrane and ciliary rows into the buccal cavity.

Food is ingested by phagocytosis at the cytostome and the food vacuole is transported inward by the cytopharynx. When the food vacuole reaches a certain size, it breaks free from the cytopharynx and a new vacuole forms at the cytostome. Detached vacuoles then begin a more or less circulatory movement through the endoplasm.

Digestion follows the general pattern described in the Introduction to Protozoa, but is peculiar in that it develops a very low initial pH. In *Paramecium*, following the formation of the food vacuole (Fig. 3-21), acidic vesicles (acidosomes) fuse with the vacuole and some cell membrane is removed. As a result, the vacuole becomes smaller and the pH drops to 3. Lysosomes now join the vacuole, but the contents are too acid for effective enzymatic action. For reasons still unknown, the pH rises, and at pH 4.5 to 5, digestion occurs. This pH characteristic of intracellular digestion in other that have been studied. Following digestion, the food vacuole moves to a fixed exocytosis site, the fuses with the cell membrane and expels its contents vacuolar membrane breaks up into small vesicles the region of the cytostome and then reconstitute vacuole.

About 15% of ciliate species are parasites, and ecto- and endocommensals. Many suctorians are and a few are parasites. Hosts include fishes, invertebrates, and other ciliates. *Endosphaera*, for parasitic within the body of the peritrich *Telotrocha* commensal hypotrich *Kerona* and peritrich occur on the surface of *Hydra*. *Balantidium* endocommensals or endoparasites in the gut of many vertebrates. *Balantidium coli* (Trichostomatia) the intestine of pigs and is passed by means of feces. This ciliate has occasionally been found where, in conjunction with bacteria, it erodes intestinal mucosa, causing pathogenic trichostomes are mutualists in the digestive tract Like the flagellate symbionts of termites and them ingest and break down the cellulose of the eaten by their hosts. The products of digestion the host.

Some ciliates harbor symbiotic algae. The of these is *Paramecium bursaria*, in which the

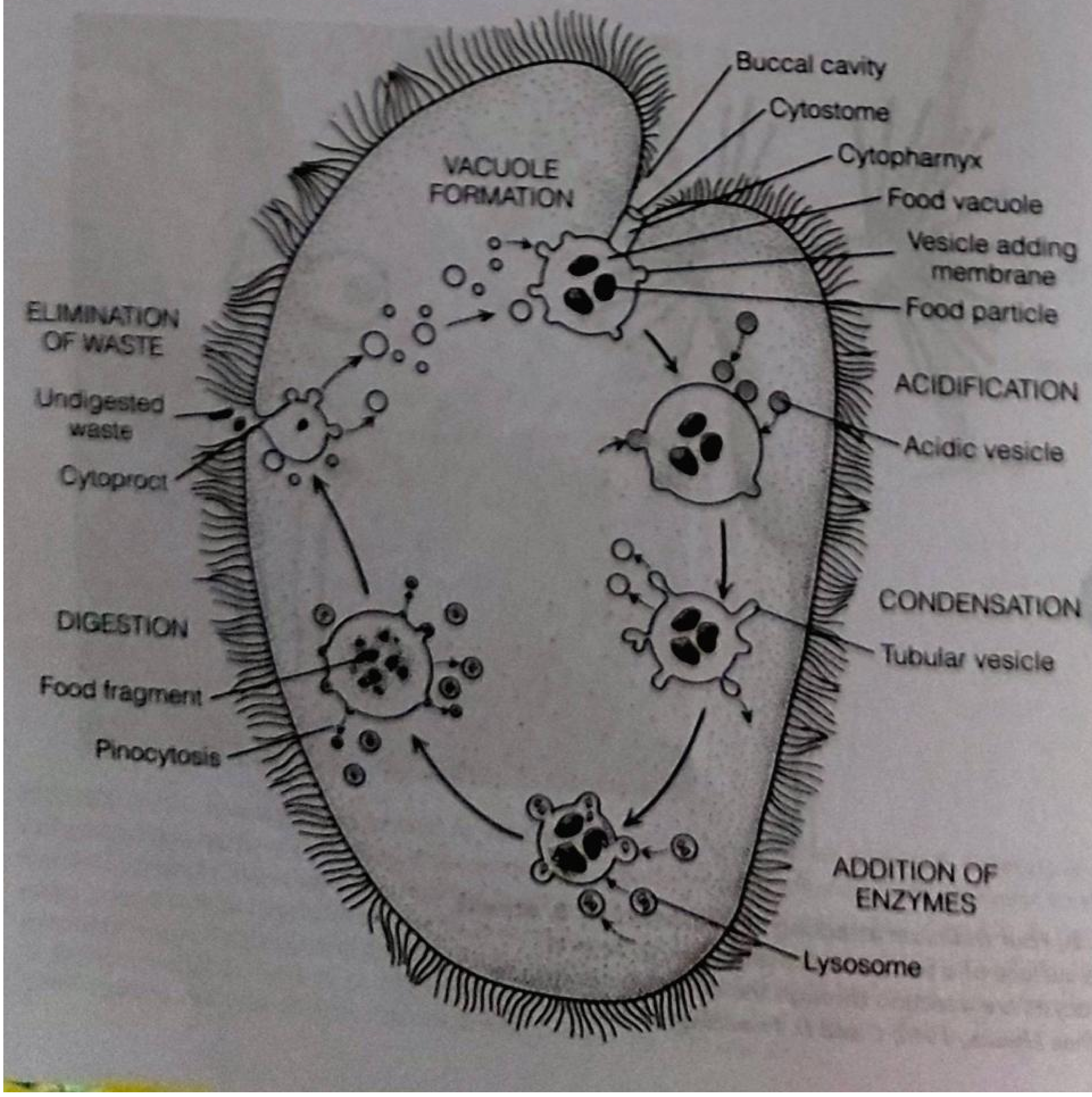



**FIGURE 3-21** Alveolata: Cilioph Intracellular digestion in ciliates. vacuole enlarges by fusion with that add membrane to the vacuole of acidic vesicles (acidosomes) ca pH. Fusion of lysosomes adds dige Eventually, the vacuole shrinks as small vesicles to be added to a new vacuole.

[illegible] genus [illegible]. A [illegible] marine species of [illegible] has algal symbionts.

## EXCRETION

Excretion in ciliates is largely a matter of volume regulation. Contractile vacuoles are found in both marine and freshwater species, but in the latter they discharge more frequently. In some species a single vacuole is located near the posterior, but many species have more than one (Fig. [illegible]). In *Paramecium*, a vacuole is located at both the posterior and anterior ends of the body (Fig. [illegible]). The vacuoles are always associated with the innermost region of the ectoplasm, and empty through one or two permanent pores that penetrate the pellicle. The spongiome contains a network of irregular tubules that may empty into the vacuole directly or by way of collecting tubules (Fig. 3-5).

## NUCLEAR DIMORPHISM

In contrast to most other protozoan classes, ciliates have two types of nuclei (heterokaryosis): a **micronucleus** that is inactive except during cell division and houses the master copy of the genome, and a **macronucleus** whose genes are actively transcribed for the daily synthetic activities of the cell. Each cell typically has 1 to 20 diploid micronuclei and 1 to many polyploid macronuclei; the numbers vary by species. The macronucleus is sometimes called the vegetative nucleus because it is not essential in sexual reproduction. Instead it is necessary for normal metabolism and the control of cell differentiation. The macronucleus contains hundreds to thousands of times more DNA than does the micronucleus because of duplications following the micronuclear origin of the macronucleus. But many of the DNA sequences of the micronucleus (up to 98% in *Stylonychia*) are eliminated during macronucleus formation. Furthermore, macronuclear DNA is organized not in chromosomes, but rather in small subchromosomal or gene-sized units, some of which are amplified up to 1 million times. The macronuclei contain many nucleoli in which ribosomal RNA is synthesized. The amplification of genes in the macronucleus and the multiple nucleoli probably increase the rate of synthesis of proteins to be used in the assembly of the complex and numerous ciliate organelles.

Macronuclei may assume a variety of shapes (Fig. 3-16, 3-18D,F). The large macronucleus of *Paramecium* is oval or bean-shaped and located just anterior to the middle of the body (Fig. 3-19). In *Stentor* and *Spirostomum*, the macronuclei are long and arranged like a string of beads (Fig. 3-18F). Not infrequently, the macronucleus is in the form of a long rod bent in different configurations, such as a **C** in *Euplotes* or a horseshoe in *Vorticella* (3-18D). The unusual shape of many macronuclei may be an adaptation to reduce the diffusion distance between the nucleus and the cytoplasm of these large cells.

## CLONAL REPRODUCTION

Clonal reproduction is by binary transverse fission, with the division plane cutting across the kineties (Fig. 3-22A) in contrast to the longitudinal fission of flagellates (Fig. 3-6). Many sessile ciliates, for example, *Vorticella*, reproduce asexually by budding (Fig. 3-22B).

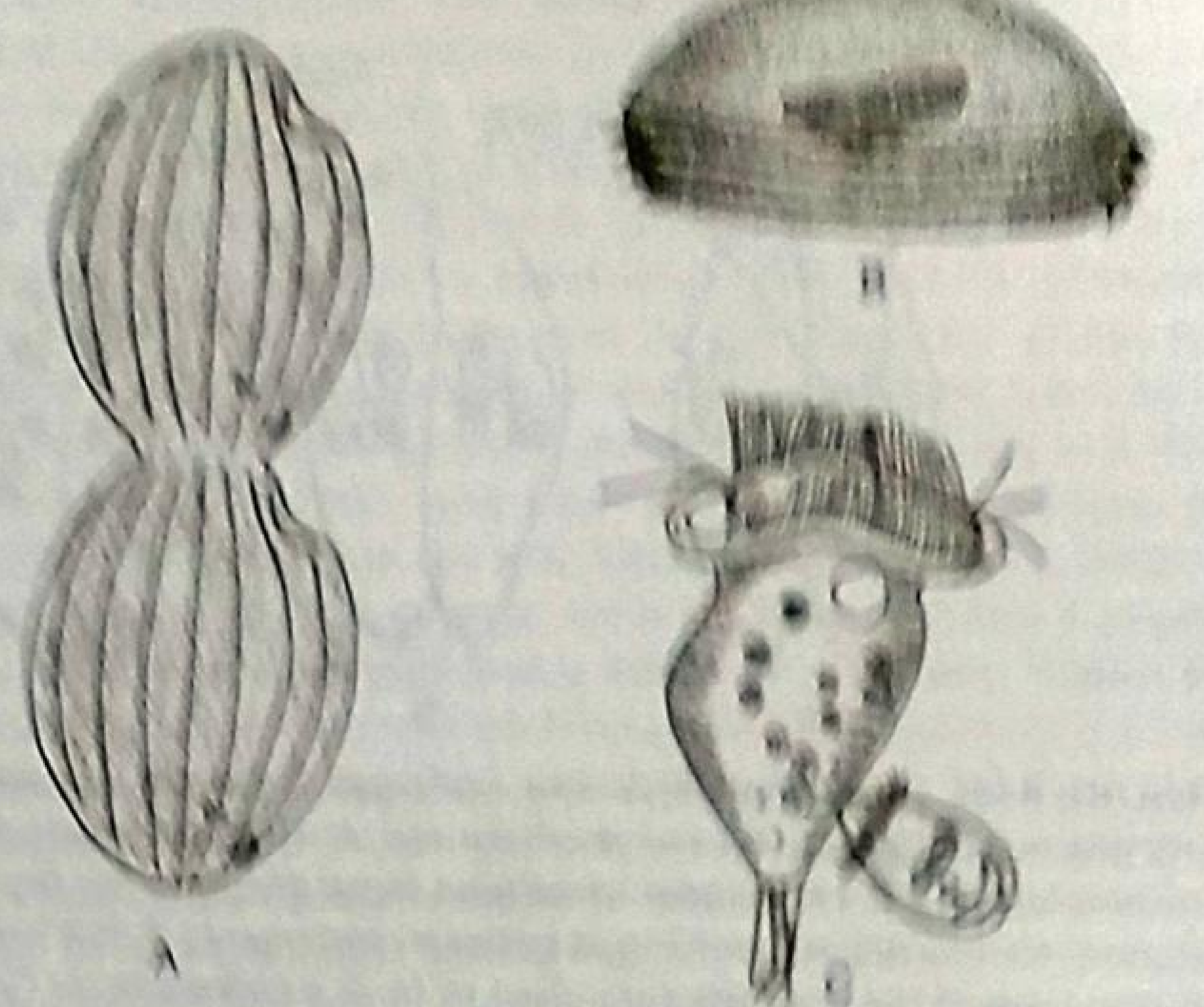



**FIGURE 3-22** Alveolata: Ciliophora. **A**, Transverse fission, in which the plane of division cuts across the kineties. **B**, Detached bud of *Dendrocometes*. **C**, Conjugation in *Vorticella*. Note the small, motile microconjugant. *(A, After Corliss, 1979; B, After Pestel from Hyman, 1940; C, After Kent from Hyman, 1940)*

The micronucleus divides by mitosis with a closed spindle. Division of the macronuclei is amitotic and is usually accomplished by constriction. When several macronuclei are present, they may first combine as a single body before dividing.

## SEXUAL REPRODUCTION

Sexual reproduction in ciliates is a direct exchange of genes without first packaging them in either egg or sperm cells. To accomplish this, two sexually compatible ciliates fuse along a shared surface, the membrane between them disappears, and a mutual exchange of genes occurs (Fig. 3-23A-F). This process is known as **conjugation** and the two fused ciliates are called **conjugants.** Conjugants may be blissfully fused for several hours. Only the micronuclei function in conjugation; the macronucleus disintegrates during the sexual process.

The steps leading to the exchange of genes between the two conjugants are fairly constant in all species. After two meiotic divisions of the micronuclei, all but one degenerate. This one then divides, producing two haploid gametic micronuclei that are genetically identical. One is stationary while the other migrates into the opposite conjugant. Once the migratory nucleus arrives, it fuses with the partner's stationary nucleus to form a 2N zygote nucleus, or **synkaryon.** Shortly after nuclear fusion the two ciliates separate, and each is then called an **exconjugant.** Each exconjugant undergoes mitotic nuclear divisions to restore the species-specific number of cell nuclei. This event usually, but not always, involves cell divisions. For example, in species normally with a single macronucleus and a single micronucleus, the synkaryon divides once. One of the nuclei forms a micronucleus; the other becomes the macronucleus. In this case, the normal nucleus number is restored without any cell divisions.

But in *Paramecium caudatum*, which also has a single nucleus of each type, the synkaryon divides three times, producing

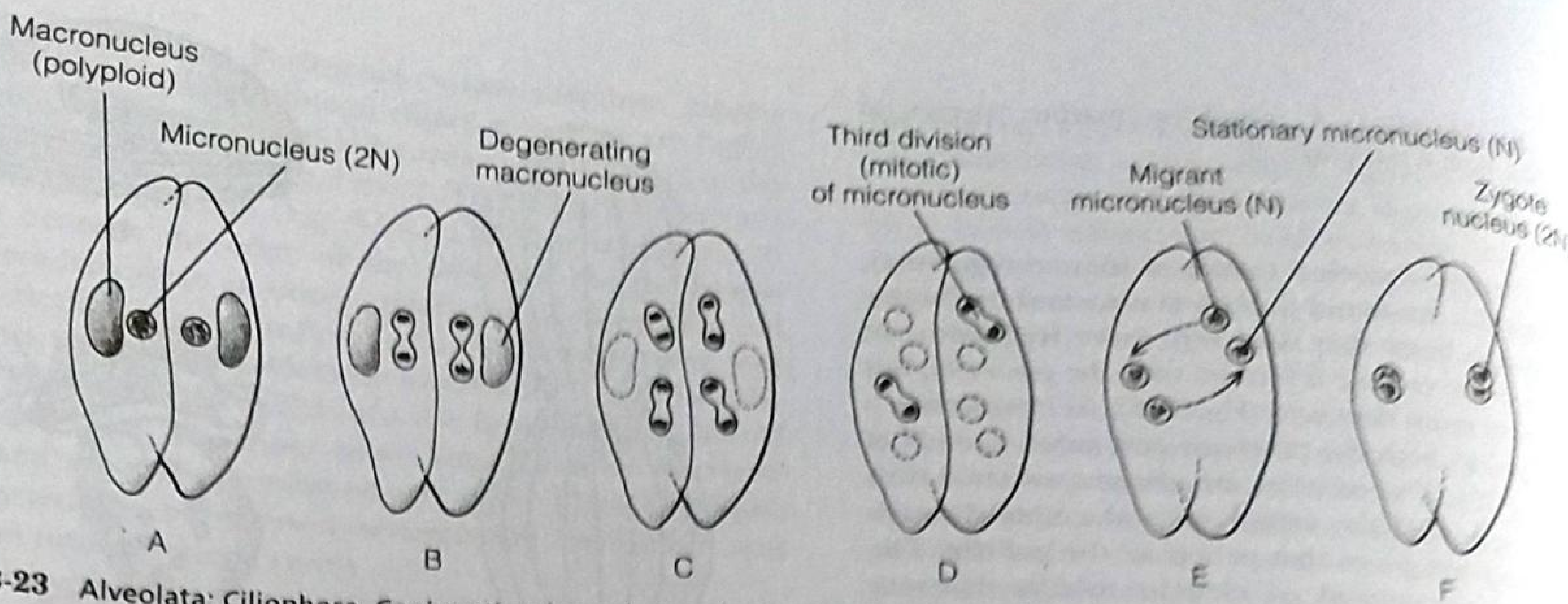



**FIGURE 3-23** Alveolata: Ciliophora. Conjugation (sexual reproduction) in *Paramecium caudatum*, a species with one macronucleus and one micronucleus. **A**, Two individuals are united in conjugation. **B–D**, The micronucleus of each conjugant undergoes three divisions, the first two of which (**B** and **C**) are meiotic. **E**, Migrant micronuclei are exchanged between conjugants. **F**, The migratory nucleus fuses with the stationary micronucleus of the opposite conjugant to form a synkaryon, or "zygote nucleus." Note that the micronuclear membrane does not break down during meiosis (or mitosis) in *Paramecium* (or other ciliates).

eight nuclei. Four become micronuclei and four become macronuclei. Three of the micronuclei degenerate. The remaining micronucleus divides during each of the two subsequent cell divisions and each of the four resulting offspring cells receives one macronucleus and one micronucleus. In those species that have numerous nuclei of both types, there is no cell division; the synkaryon merely divides a sufficient number of times to produce the appropriate number of macronuclei and micronuclei.

In some of the more specialized ciliates, the conjugants are a little smaller than nonconjugating individuals, or the two members of a conjugating pair are of strikingly different sizes. Such *gonochoric* macro- and microconjugants occur in *Vorticella* (Fig. 3-22C) and are an adaptation for conjugation in sessile species. The macroconjugant remains attached while the small bell of the microconjugant breaks free from its stalk and swims about. On contact with an attached macroconjugant the two bells adhere. A synkaryon forms only in the macroconjugant from one gametic N nucleus contributed by each conjugant. The conjugal bond is permanent and fatal to the microconjugant, which degenerates after contributing its gamete nucleus. In the sessile attached Suctoria, conjugation takes place between two adjacent individuals that lean together like lovers on a park bench.

The frequency of conjugation varies from once every few days to not at all (or not yet observed). In some species a period of "immaturity," in which only fission occurs, precedes a period during which individuals are capable of conjugation. Numerous factors, such as temperature, light, and food supply, are known to induce or influence conjugation.

In some ciliates, sex is rejuvenating and necessary for additional bouts of clonal fission. For example, some species of *Paramecium* are limited to only 350 clonal generations and die out in the absence of conjugation. Sex restores asexual capacity.

Most ciliates are capable of forming resistant cysts in response to unfavorable conditions, such as lack of food or desiccation. Encystment enables the species to ... or dry periods and provides a form for dispersal ... attachment to animals.

## DIVERSITY OF CILIOPHORA

**Karyorelictea[C]:** Freshwater *Loxodes* and marine *Geleia*, *Remanella*, and *Tracheloraphis*, all ... Macronuclei and micronuclei both ... dikinetids.

**Spirotrichea[C]:** Ciliates with oral membranelles ... that wind clockwise to the cytostome; somatic ... polykinetids. Includes Heterotrichia[sC], the ... *pharisma*, *Folliculina*, *Spirostomum*, *Stentor*; ... tintinnids, *Halteria* with somatic cirri; ... ventral cirri, such as the dorsoventrally flattened ... (Fig. 3-18B); Hypotrichia[sC], which are ... on the ventral surface and have ... (MT) ribbons, such as bacterivorous ... (Fig. 3-18B).

**Litostomatea[C]:** Somatic monokinetids; MTs ... tostomal dikinetids form basketlike cytopharynx ... transverse ribbon of MTs from ciliary basal bodies ... ally directed kinetodesmal fibers. Includes ... mostly predators with lateral, ventral, or posterior ... and toxicysts, *Didinium*, *Dileptus*, *Mesodinium* ... biotic dinoflagellates); and Trichostomatia[C], ... the gut of ruminants that assist in breakdown ... *Balantidium* and *Entodinium*.

**Prostomatea[C]:** Oral region similar to that of ... but some polykinetids are also present; ... monokinetids with radially arranged MT ribbons ... cytostome at the anterior end of the cell; toxicysts ... mon. Marine and freshwater *Coleps*, *Prorodon*.

**Phyllopharyngea[C]:** Leaflike ribbons of MTs ... longitudinal bundles of MTs that form a ... cytopharynx (cyrtos); somatic monokinetids ...

gia[sC], of which *Chilodonella* is flattened, ciliated ventrally, and found in sewage; Chonotrichia[sC], which are sessile, nonciliated filter feeders with a spiral oral end that attach to crustaceans; Suctoria[sC], which are sessile, cilia-free predators with prey-catching tentacles, resemble miniature sundews and include *Allantosoma* (in horse colon), *Ephelota, Heliophrya, Tokophrya.* Marine and fresh water.

**Nassophorea[C]:** Transverse MT ribbons tangential to the basal bodies; well-developed kinetodesma; MT bundles form a complex, basket-shaped cytopharynx (nasse); somatic mono- or dikinetids. Peniculida[O] has an oral apparatus that is an elastic slit and three oral membranelles (peniculus) on its left side and an undulating membrane on the right; a nasse is absent; includes the slipper ciliate, *Paramecium.*

**Oligohymenophorea[C]:** A few oral polykinetids, usually three, on left side of the cytostome; somatic monokinetids with MT ribbons that radiate from the basal bodies. Hymenostomatia[sC], oral apparatus like that of Nassophorea. The best-known ciliate is the free-living *Tetrahymena; Ichthyophthirius,* the cause of "ich" disease of freshwater fishes; *Pleuronema, Uronema.* Peritrichia[sC], a ciliary ring on its oral rim that winds helically counterclockwise to the cytostome and then splits into three membranelles; somatic cilia are reduced; often have contractile stalks (or bodies) and are mostly sessile and attached, but some can detach and swim: *Carchesium, Epistylis, Trichodina, Urceolaria, Vorticella.*

**Colpodea[C]:** Kidney-shaped cells with spiral kineties and somatic dikinetids: *Bursaria, Colpoda.*

## Apicomplexa[sP] (Sporozoa)

The some 5000 species of apicomplexans are widespread and common parasites of such animals as worms, echinoderms, insects, and vertebrates. Depending on the species, they may be extra- or intracellular parasites or both at different stages of the life cycle. Apicomplexans also are responsible for malaria, the number-one parasitic disease of humankind, as well as similar debilitating diseases of livestock.

Apicomplexans are so named because motile infective stages (sporozoites, merozoites) bear an anterior **apical complex** that attaches to or penetrates into host cells. A fully developed apical complex consists of an anterior conoid, one or two polar rings, 2 to 20 flask-shaped glandular structures (rhoptries), and numerous membranous Golgi-derived tubules (micronemes) (Fig. 3-24). The conoid is open at both ends and encircled by the polar rings, which link to subpellicular microtubules. The micronemes contain enzymes presumably used for host-cell penetration, but the functions of the other components are unclear. Apicomplexans lack cilia, but flagella occur on their microgametes. Pseudopodia also are absent. Infective stages move by gliding, which may result from microscopic undulations of the pellicle. One or more feeding pores, called **micropores,** are located on the side of the body (Fig. 3-24). The apicomplexan pellicle consists of the outer cell membrane and two additional membranes below it. The two inner membranes are actually the outer and inner walls of a flattened alveolus, which completely encloses the subpellicular cytoplasm except for breaks anteriorly (apical complex), laterally (micropores), and posteriorly (site of exocytosis).

The extraordinary life cycles of apicomplexans achieve mind-challenging complexity in species that infect more than one host. The basic life cycle, however, is reasonably straightforward. Its sexual and clonal stages are haploid, except for the zygote (haploid-dominant cycle; Fig. 3-4D). The motile infective stage is called a **sporozoite.** The haploid sporozoite enters the body of the host, takes up host nutrients, grows, and differentiates into a **gamont,** or gamete-producing cell. Generally, male and female gamonts pair, become enclosed in a common envelope (cyst), and each produces many gametes via multiple fission within the cyst. Once full grown, these gametes fuse to form diploid zygotes, each of which secretes a protective extracellular capsule and is then called a **spore.** Within the spore, the zygote nucleus undergoes meiosis to restore the haploid chromosome number and then mitosis to produce eight cells, which differentiate into sporozoites. The encapsulated sporozoites are liberated from the spore after it is ingested by a host. In this life cycle, **gamogony,** the production of gametes, refers to the period from the pairing of the gamonts to the fusion of gametes. **Sporogony,** the production of spores, refers to the period beginning with meiosis of the zygote to the differentiation of sporozoites within the spore.

The basic life cycle is illustrated by the gregarine (Gregarinea) *Monocystis lumbrici,* which parasitizes seminal vesicles of the earthworm, *Lumbricus terrestris* (Fig. 3-25). Worms become infected when they ingest soil containing spores. Within the earthworm's gizzard, the spores hatch and release

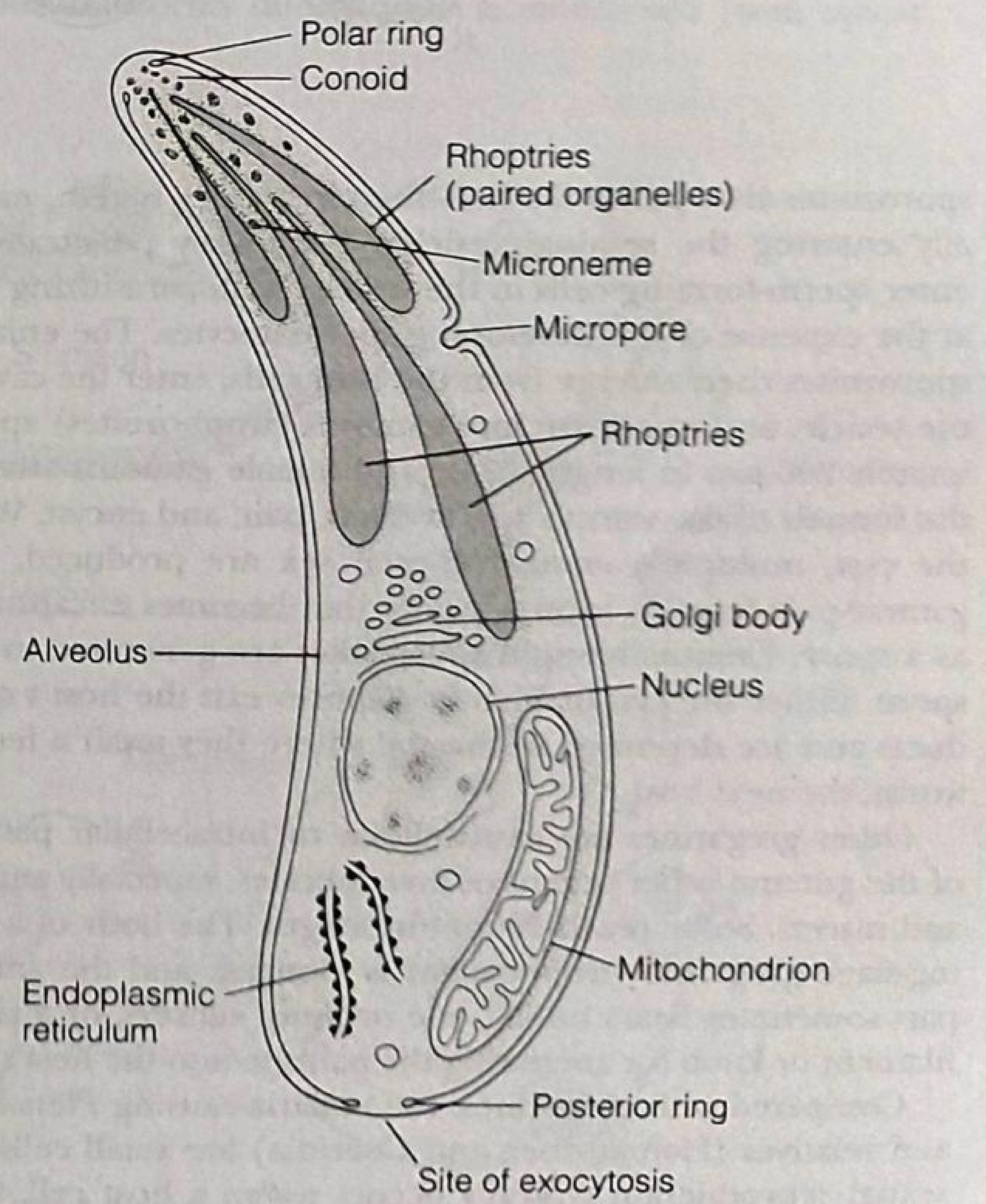



**FIGURE 3-24** Alveolata: Apicomplexa. Lateral view of a generalized sporozoan. The polar ring, conoid, micronemes, and rhoptries are parts of the apical complex. *(From Farmer, J. N. 1980. The Protozoa: Introduction to Protozoology. C. V. Mosby Co., St. Louis. p. 360)*

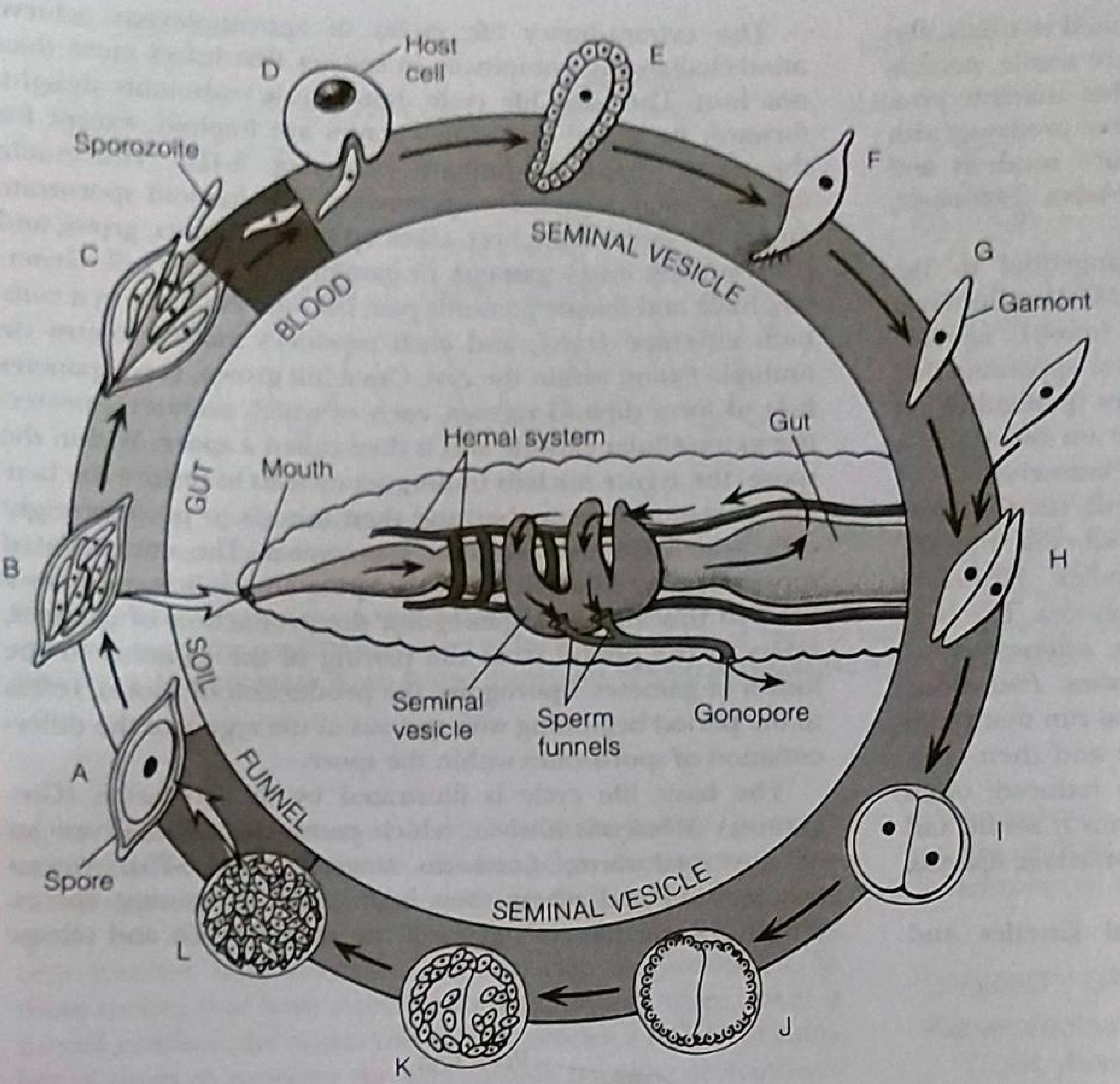



FIGURE 3-25 Alveolata: Apicomplexa. L cycle of the gregarine *Monocystis lumbric*, a parasite of earthworm seminal vesicles. A, Spore containing a 2N zygote, which undergoes meiosis and then mitosis to gene N sporozoites. B, Sporozoites in the spore. C, Sporozoites emerge from the spore in the gizzard. D, Sporozoite enters sperm-forming cell in the wall of the seminal vesicle. E, Sporozoite grows at the expense of the developing spermatocytes (small cells). F, Sporozoite enters the cavity of the semina vesicle bearing remnants (tails) of aborted sperm and transforms into a gamont. G, Gamonts pair. H, Paired gamonts. I–K Encysted gamonts mitotically produce micro and macrogametes. L, Gamete fusion produ zygotes, each one enclosed in a spore. *(Mo and redrawn from Janovy, J., and Roberts, L. Foundations of Parasitology. 6th Ed. McGraw-Hi Co., NY, 688 pp.)*

sporozoites that penetrate into the circulatory system, eventually entering the seminal vesicles. Here they penetrate and enter sperm-forming cells in the vesicle, wall, parasitizing them at the expense of the developing spermatocytes. The enlarged sporozoites then emerge from the host cells, enter the cavity of the vesicle, and transform into gamonts (trophozoites) approximately 200 μm in length. Male and female gamonts attach to the funnels of the worm's sperm ducts, pair, and encyst. Within the cyst, multiple gametes of each sex are produced. Each gamete-pair fuses to form a zygote that becomes encapsulated as a spore. Eventually, eight sporozoites are generated in each spore. Either the cyst or liberated spores exit the host's sperm ducts and are deposited in the soil where they await a feeding worm, the next host.

Other gregarines are extracellular or intracellular parasites of the gut and other organs of invertebrates, especially annelids and insects. Some reach 10 mm in length. The body of a feeding-stage gregarine (trophozoite) is elongate and the anterior part sometimes bears hooks, one or more suckers, or a simple filament or knob for anchoring the parasite into the host's cells.

Compared with gregarines, the malaria-causing *Plasmodium* and relatives (Hematozoea and Coccidia) are small cells, and sexual reproduction typically occurs *within* a host cell. For a given species, there may be only one host, as in gregarines, but many require two hosts to complete the life cycle.

These parasites add one or more rounds of multiple fission (schizogony) to the basic life cycle described above (Fig. 3-26).

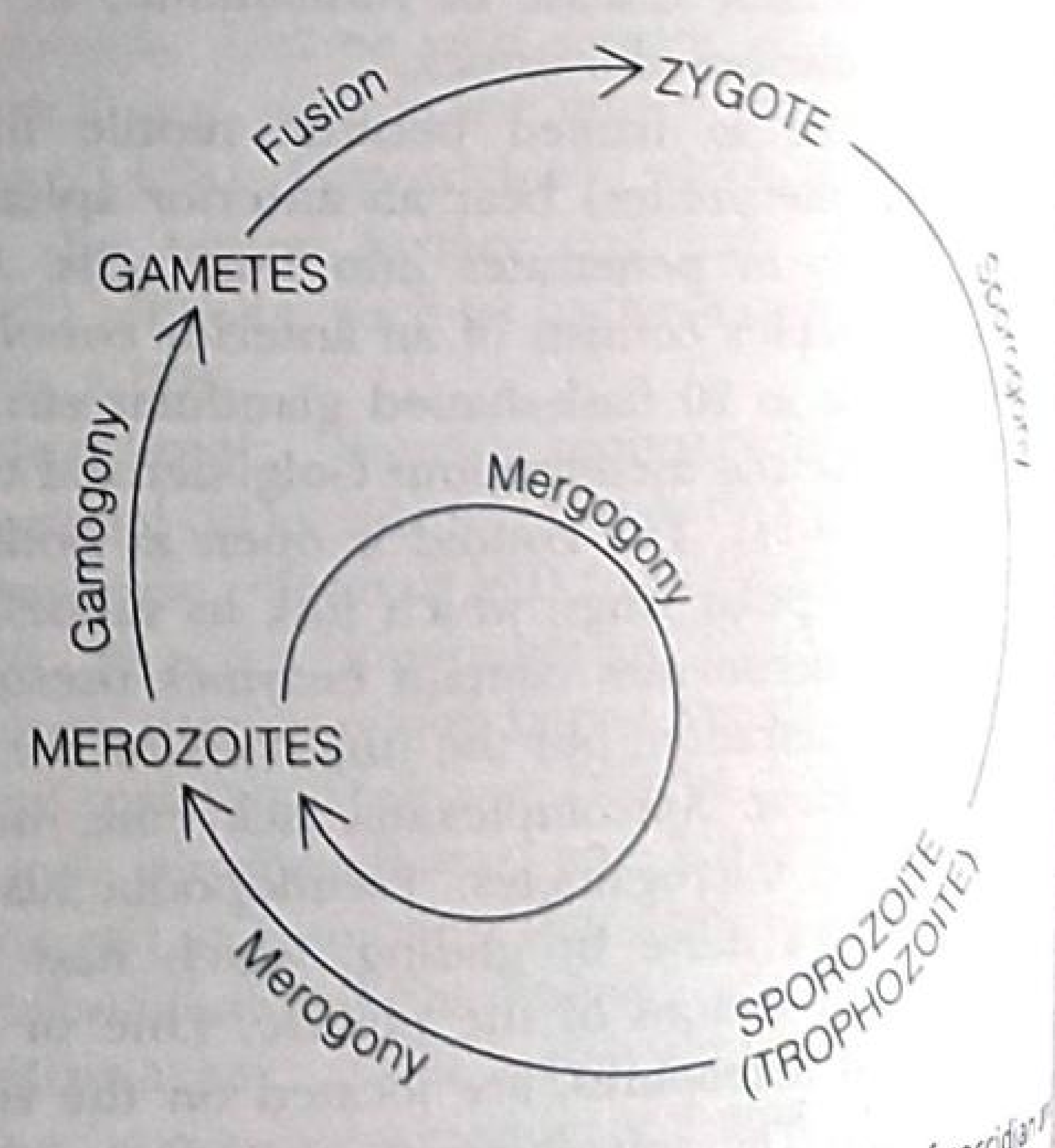



FIGURE 3-26 Alveolata: Apicomplexa. Life cycle of coccidian haematozoen sporozoans. All stages are haploid except the zyg which undergoes meiosis in the formation of spores (sporogony). The ability of merozoites to produce more merozoites (merogony) constitutes a clonal cycle within the sexual life cycle. *(From Le 1985. Phylum Apicomplexa. In Lee, J. J., et al. (Eds.): Illustrated Guide Protozoa. Society for Protozoology, Lawerence, KS. p. 325)*

Each of these additional rounds, called **merogony,** results in the production of motile, reinfective **merozoites.** The typical life cycle includes a sporozoite that infects a host cell, grows, and transforms into an ameboid trophozoite. The trophozoite undergoes merogony to form merozoites, each of which resembles a sporozoite. The merozoites infect other host cells in which they undergo another round of merogony or transform into gamonts, initiating gamogony. Each female gamont transforms into one macrogamete, but a male gamont, via multiple fission, produces many biflagellated microgametes. After fertilization, the zygote undergoes sporogony to produce sporozoites, which are encapsulated as an oocyst. This encysted zygote undergoes meiosis, then mitosis, to form several encapsulated spores. Later, sporozoites differentiate within each of the spores.

The most notorious hematozoeans are four species of *Plasmodium* that cause malaria, one of the worst scourges of humankind. Originally restricted to the Old World tropics, malaria was introduced into the New World by European colonists. Currently, about 300 million people (1 in 50) worldwide are believed to be infected each year, and the annual death rate is about 1% of those infected. Left untreated, the disease can be long-lasting, debilitating, and fatal.

Malaria has played a major but often unrecognized role in human history. The name means literally "bad air," because originally the disease was thought to be caused by the fetid air of swamps and marshes. Although malaria had been recognized since ancient times, the causative agent was not discovered until 1880, when Louis Laveran, a physician with the French army in North Africa, identified the parasite *Plasmodium* in the blood cells of a malarial patient. In 1887, Ronald Ross, a physician in the British army in India, determined that a mosquito was the vector.

The malarial parasite is introduced into a human host by the bite of *Anopheles* mosquitoes, which inject saliva and sporozoites into the capillaries of the skin (Fig. 3-27). The sporozoite is carried by the bloodstream to the liver, where it invades a liver cell and becomes a feeding trophozoite. After further development, the trophozoites reproduce clonally by merogony to form thousands of merozoites. These merozoites reinvade host liver cells and undergo another round of merogony. After a week or so, merozoites leave the liver cells and invade red blood cells. Within the red blood cell the merozoites transform into trophozoites, which increase in size and again undergo merogony to form yet more merozoites that reinvade other red cells. After a few days, merozoite release occurs in discrete pulses as their developmental cycles become synchronized. The periodic release of the merozoites, along with cell fragments and metabolic byproducts, causes chills and fever—the typical symptoms of malaria. Serious damage results from the blocking of capillaries by infected and less pliable red blood cells. While in the host's red cells, the trophozoites phagocytose protein (hemoglobin) at their micropores.

Eventually, some of the merozoites transform into gamonts (gametocytes) within the red blood cell, but these do not unite in pairs. Instead, each separately produces gametes only after being ingested by the mosquito. Once the mosquito imbibes infected blood, the gamonts are released from the red blood cells and produce gametes in the gut lumen. After fertilization, the zygote transforms directly into a motile cell (with apical

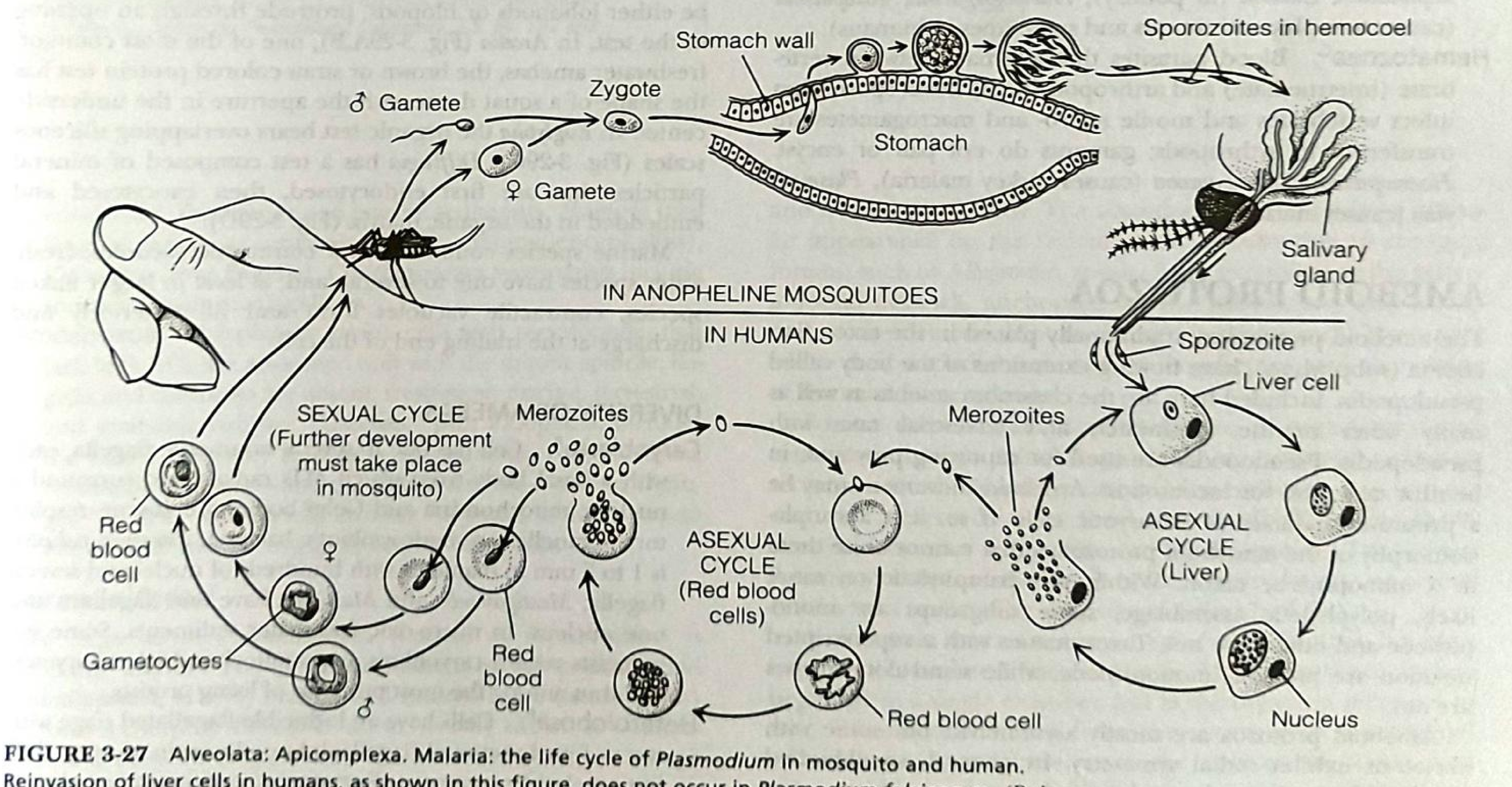



**FIGURE 3-27** Alveolata: Apicomplexa. Malaria: the life cycle of *Plasmodium* in mosquito and human. Reinvasion of liver cells in humans, as shown in this figure, does not occur in *Plasmodium falciparum*. *(Redrawn and modified from Blacklock and Southwell)*

complex) that penetrates and encysts in the gut wall. Sporogony within the cyst eventually results in the release of thousands of sporozoites into the mosquito's hemocoel. The sporozoites migrate into the insect's salivary glands, from which they will be injected into the next victim of the mosquito's bite.

Related parasites (Coccidia) cause diseases in domesticated animals. Species of the genus *Eimeria*, for example, affect chickens, turkeys, pigs, sheep, and cattle.

Two other taxa of spore-forming parasites, the Microsporidia and the Myxosporidia, were formerly considered to be close relatives of the apicomplexans. Now, the microsporidians are classified either with the fungi or placed near the base of the eukaryotes because they lack, and presumably never had, flagella, mitochondria, and Golgi bodies. The myxosporidians, currently called myxozoans, are multicellular organisms with cnidae (stinging capsules) that are now classified with the metazoan taxon Cnidaria (corals, anemones, and jellyfishes) and are described in Chapter 7.

### DIVERSITY OF APICOMPLEXA (SPOROZOA)

**Gregarinea$^{C}$**: Life cycle with one host; multiple fission by both male and female gamonts; constriction separates gamont body into anterior protomerite and posterior deutomerite, with epimerite (such as hooks) at tip of protomerite; gamont cells unite (syzygy) before encystment and move by gliding; most stages are extracellular parasites of echinoderms, molluscs, annelids, and especially arthropods. Species identification based on epimerite structure. *Gregarina, Monocystis.*

**Coccidia$^{C}$**: Each macrogamont forms but one macrogamete; gamonts encyst; most species are intracellular parasites of invertebrates and vertebrates in one or two hosts. *Cryptosporidium, Eimeria* (in poultry), *Haemogregarina, Toxoplasma* (causes toxoplasmosis in cats and sometimes in humans).

**Hematozoea$^{C}$**: Blood parasites that alternate between vertebrate (intermediate) and arthropod (final) hosts; sporozoites infect vertebrates and motile micro- and macrogametes are transferred to arthropods; gamonts do not pair or encyst. *Haemoproteus, Leucocytozoon* (causes turkey malaria), *Plasmodium* (causes malaria).

## AMEBOID PROTOZOA

The ameboid protozoans, traditionally placed in the taxon Sarcodina (subphylum), have flowing extensions of the body called pseudopodia. Included here are the classroom amebas as well as many other marine, freshwater, and terrestrial taxa with pseudopodia. Pseudopodia are used for capturing prey and, in benthic taxa, also for locomotion. Ameboid movement may be a primitive character of eukaryotic cells. If so, it is a symplesiomorphy of the amoeboid protozoans that cannot unite them in a monophyletic taxon. Within this paraphyletic or, more likely, polyphyletic assemblage, some subgroups are monophyletic and others are not. Taxon names with a superscripted notation are probably monophyletic, while stand-alone names are not.

Ameboid protozoa are mostly asymmetric, but some with skeletons exhibit radial symmetry. In general, small-bodied species have one nucleus whereas large species have many and, in one taxon (forams), heterokaryotic nuclei ... ciliates. Ameboid protozoa have relatively few ... organelles and in this respect are among the simpl... zoa. The skeletal structures that occur in the ma... species, however, reach a complexity and beau... surpassed by few other organisms. The three princ... of ameboid protozoa are the amebas (Caryoblasta, H... bosa, and Amoebozoa), the forams (Foraminifera), ... actinopods (Radiolaria, Acantharea, and Heliozoa).

### Amebas

Amebas (or amebae) may be naked or enclosed in a ... naked amebas, which include *Amoeba*, live in the se... water, and in the water film around soil particles (Fig... The shape, although constantly changing, is charact... different species. Some giants, such as *Pelomyxa pa...* *Chaos carolinense*, can be 5 mm in length and are ... cleated cells. The cytoplasm in amebas is divided in... clear, external ectoplasm and a more fluid internal en... (Fig. 3-28A). The pseudopodia adopt one of two ... forms. **Lobopodia,** which are typical of many ame... wide and rounded with blunt tips (Fig. 3-28A,B). T... commonly tubular and composed of both ectopla... endoplasm. **Filopodia,** which occur in many small ame... slender, clear, and sometimes branched, but the bran... not interjoin extensively to form nets (Fig. 3-28C).

In shelled (testate) amebas, which are largely inhabit... fresh water, damp soil, and mosses, either a radial or ... extracellular test is secreted by the cytoplasm. The ... organic matrix to which secreted siliceous elements ... materials are attached. The ameba is attached by cy... strands to the inner wall of the test. Pseudopodia, wh... be either lobopods or filopods, protrude through an a... in the test. In *Arcella* (Fig. 3-29A,B), one of the most ... freshwater amebas, the brown or straw-colored prote... the shape of a squat dome with the aperture in the ... center. In *Euglypha* the organic test bears overlapping ... scales (Fig. 3-29C). *Difflugia* has a test composed of ... particles that are first endocytosed, then exocyt... embedded in the organic matrix (Fig. 3-29D).

Marine species commonly lack contractile vacuole... water species have one to several, and, at least in large ... species, contractile vacuoles form and fill anter... discharge at the trailing end of the cell.

### DIVERSITY OF AMEBAS

**Caryoblasta$^{P}$**: Cell has one to several nonmotile flag... with a basal body from which MTs radiate and su... nucleus; mitochondria and Golgi bodies are absent... tory organelles are endosymbiotic bacteria. *Pelomyx...* is 1 to 5 mm in diameter with hundreds of nuclei and ... flagella; *Mastigamoeba* and *Mastigella* have one flag... one nucleus. In micro-oxic freshwater sediments. S... tematists regard caryoblasts as premitochondrial c... and thus among the most primitive of living protis...

**Heterolobosa$^{P}$**: Cells have an inducible flagellate ... two to four functional flagella; lobopodia seem to ... ing ameboid movement. Encystment occurs unde...

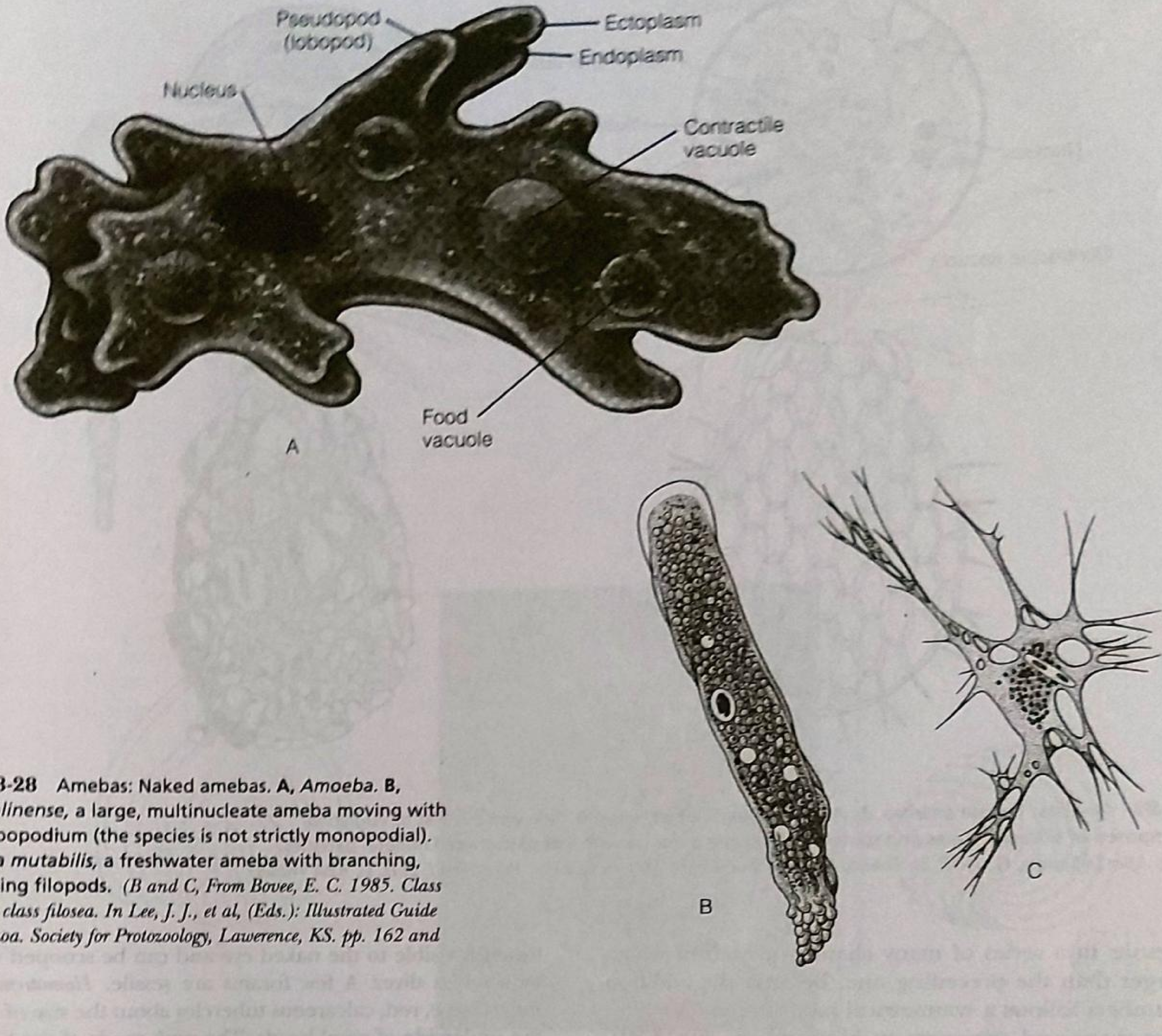



**FIGURE 3-28** Amebas: Naked amebas. **A,** *Amoeba.* **B,** *Chaos carolinense,* a large, multinucleate ameba moving with a single lobopodium (the species is not strictly monopodial). **C,** *Penardia mutabilis,* a freshwater ameba with branching, anastomosing filopods. *(B and C, From Bovee, E. C. 1985. Class lobosea and class filosea. In Lee, J. J., et al, (Eds.): Illustrated Guide to the Protozoa. Society for Protozoology, Lawerence, KS. pp. 162 and 230)*

conditions. Freshwater and marine sediments. *Naegleria* (two flagella; cause of primary amebic meningoencephalitis), *Tetramitus* (four flagella). Contemporary systematists include this taxon with the flagellates.

**Amoebozoa:** Polyphyletic taxon: cells with pseudopodia that lack MTs. MTs are associated only with the mitotic spindle; flagella and centrioles are absent; freshwater, marine, terrestrial, and symbiotic habitats. "Lobosea," with lobopodia, includes the naked (atestate) amebas—*Acanthamoeba, Amoeba, Chaos, Entamoeba, Vannella*—and the testate amebas—*Arcella, Difflugia.* "Filosea," with rapidly forming filopodia, includes testate and atestate species: *Euglypha, Gromia, Vampyrella.*

## Foraminiferea[P]

The large taxon Foraminiferea (forams or foraminifers) is primarily marine. The countless filiform pseudopodia, called **reticulopodia,** actively branch and interconnect (anastomose) to form a complex threadlike mesh, usually known as a **reticulopodial network** (Fig. 3-30B). Each reticulopodium has an axis of microtubules that shuttles vesicles bidirectionally to and from the cell body. The abundant vesicles confer a granular appearance on the reticulopods. Locomotion in creeping forams, such as *Allogromia,* results from extension of the reticulopodial network, anchorage on the substratum, and retraction of the net, which pulls the cell body forward. Movement of the reticulopodial net involves lengthening and shortening of the axial microtubules.

Forams construct an extracellular test of organic material, cemented foreign mineral particles, or calcium carbonate secreted onto the organic matrix. Calcareous tests are common and well preserved in the fossil record; 40,000 of the 45,000 described species of forams are fossil species. The largest forams, members of the deep-sea Xenophyophorea, are several centimeters in diameter (the size of a clenched fist).

A few foram species occupy a test of one chamber, but most have multichambered calcified tests. Multichambered forams begin life in a single chamber, but as the organism increases in size, reticulopods extend from the aperture of the original chamber, arrange themselves in the appropriate shape, and secrete the new chamber. This process continues throughout

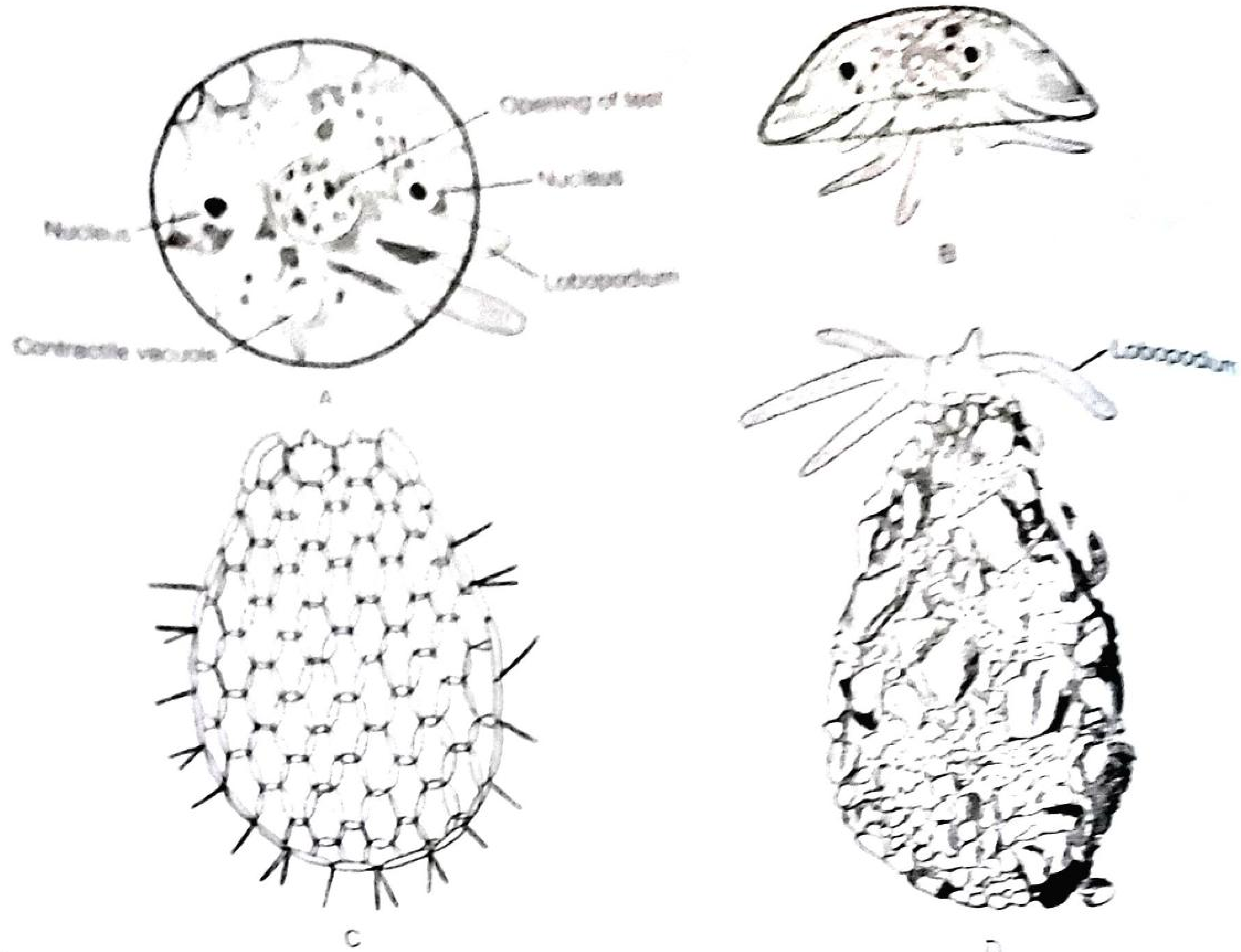



**FIGURE 3-29** Amebas. Testate amebas. **A,** *Arcella vulgaris*, apical view. **B,** Side view. **C,** Test of *Euglypha strigosa*, composed of siliceous scales and spines. **D,** *Difflugia oblonga* with test of gathered mineral particles. *(A, B, and D, After Deflandre, G. 1953. In Grassé, P. Traité de Zoologie, Masson and Co., Paris. Vol. I, pt II. C, After Wailes)*

life and results in a series of many chambers, each of which may be larger than the preceding one. Because the addition of new chambers follows a symmetrical pattern, the tests have a distinctive shape and arrangement of chambers (Fig. 3-30).

The entire test is filled by one cell that extends from one chamber to the next. An extension of the cell from the aperture also creates a thin layer outside the test. Reticulopodia may be restricted to the aperture or they may arise from the test layer (Fig. 3-30B). In some species they emerge through test pores, but others have blind pores that do not penetrate the test.

Forams cast their extensive reticulopodial nets widely over surfaces, into the water, or between grains of sand in search of food. The net is dynamic, with its shape and extent changing constantly as reticulopods shorten, lengthen, fuse, and arise or regress spontaneously anywhere in the net. No crevice is too small to be probed by the myriad tentacles of the net. Once a diatom, bacterium, or other small prey is contacted, it adheres to a reticulopod and is transported along it, as if on an escalator, to the cell body waiting like an orb spider at the net's hub. On reaching the cell body, food is ingested by phagocytosis.

Most forams are benthic, but species of *Globigerina* and related genera are common planktonic forms. The chambers of these species are spherical, but spirally arranged (Fig. 3-30B,D). Planktonic forams have more delicate tests than do benthic species and the tests commonly bear spines, which slow the rate of sinking. The spines are so long in some species that the foram is visible to the naked eye and can be ... by a scuba diver. A few forams are sessile. ... forms large, red, calcareous tubercles about ... the underside of coral heads. The pink sand ... Bermuda result from the accumulation of ...

Several forams harbor an unusual diver... tic photosynthetic protists—chlorophytes ... gellates, or unicellular red algae, depending ... One taxon harboring zooxanthellae, the ... includes mermaid's pennies), averages about ... and is common on coral reefs.

Forams first appeared in the Cambrian ... fossilized throughout geological history. ... tions of tests occurred during the Meso... zoic eras and contributed to the formation ... and chalk deposits in different parts of the ... Cliffs of Dover in England and the quarries ... stone for the Egyptian pyramids are composed ... of foram tests.

Their widespread fossil occurrence and their ... history make forams useful as index fossils. Because ... rock containing the same taxa of forams was ... same time, geologists use these index species ... containing strata. In some species of *Globigerina* ... direction of the test is influenced by water ... hand (sinistral) coiling is associated with ...

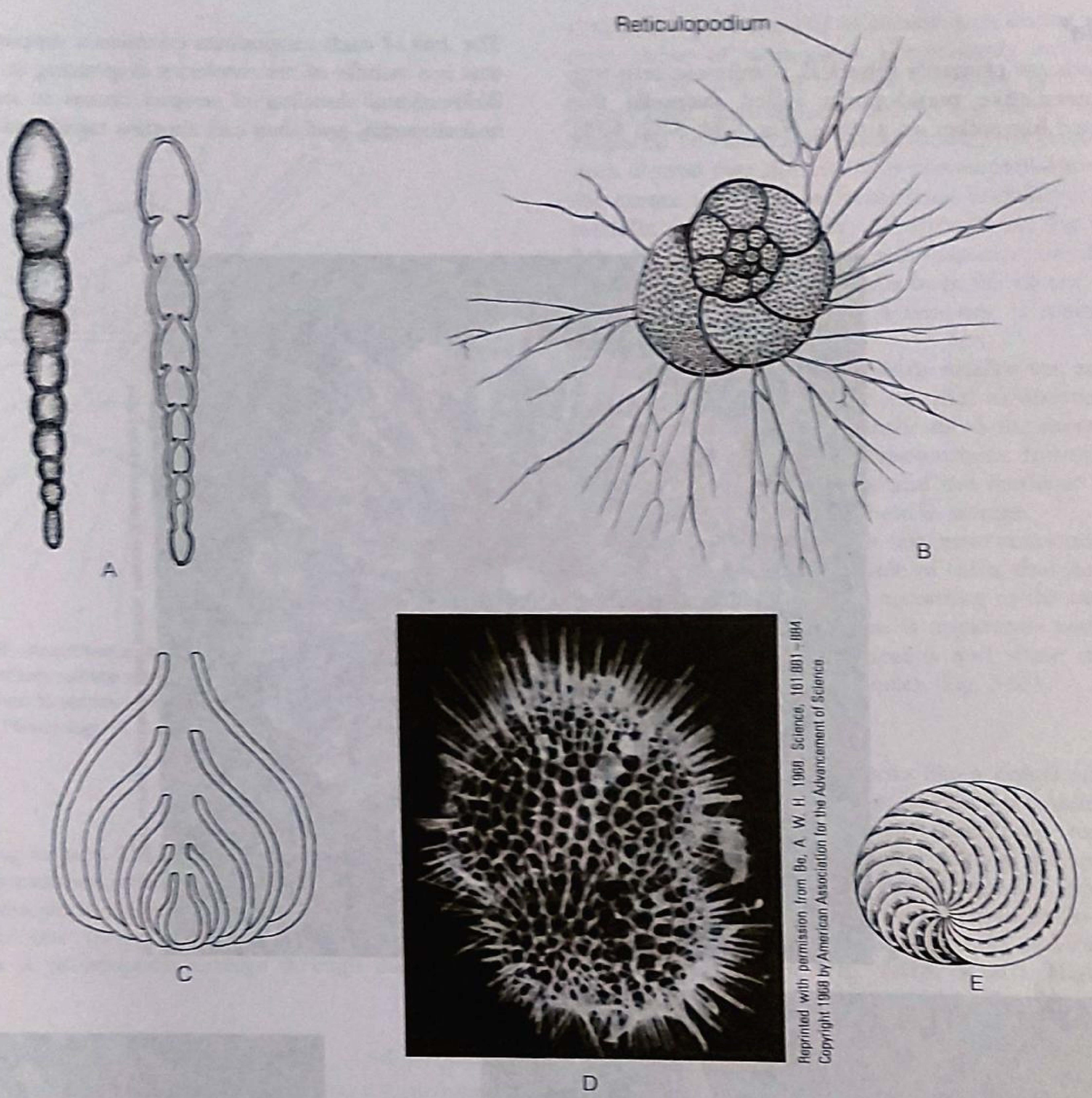



**FIGURE 3-30** Foraminiferea. **A,** Test of the foram *Rheophax nodulosa*, entire and in section. **B,** Living *Globigerina bulloides*. **C,** Test of an ellipsoidinid foram, in section. **D,** Cleaned test of *Globigerinoides sacculifer*, a tropical planktonic foram with spines. **E,** *Archaias* sp., a common benthic foram of shallow tropical seas.
*(A, After Brady. B, drawn form a photograph in Grell, K. G. 1973. Protozoology. Springer-Verlag, Berlin, p. 285)*

whereas right-hand (dextral) coiling is associated with high temperatures. Thus, the coiling direction of certain fossils provides a record of past cold and warm periods. The varying ratios of oxygen isotopes in foram tests from deep-sea sediments also provide clues about global temperature change and glacial ice accumulation.

## DIVERSITY OF FORAMINIFEREA

Until recently, Foraminiferea was included in Granuloreticulosa, a phylum-level taxon of three major subgroups—Athalamida, Monothalamida, and Foraminiferida—all sharing the character reticulopodia. In contrast to forams, however, the other two taxa lack an alternation of generations in their life cycle. Athalamids lack a test and occur in fresh water; monothalamids have an organic or calcareous test of one chamber and occur primarily in fresh water, although some species are marine. Recent molecular studies suggest that athalamids are forams modified for life in fresh water. Here we consider only taxa traditionally considered to be forams.

**Allogromiina**[C]: Organic test is flexible and sometimes has attached foreign matter. *Iridia, Myxotheca, Nemogullmia.*

**Textulariina**[C]: Organic test made rigid by adding foreign particles. *Allogromia, Ammodiscus, Astrorhiza, Clavulina, Textularia.*

**Miliolina**[C]: Calcareous test resembles porcelain. *Amphisorus* (mermaid's penny), *Pyrgo* (ooze former), *Quinqueloculina, Sorites.*

**Rotaliina**[C]: Calcareous test is glassy (hyaline) and has pores. *Bulimina, Discorbis, Globigerinoides* (planktonic), *Homotrema, Lagena, Marginulina, Rotaliella.*

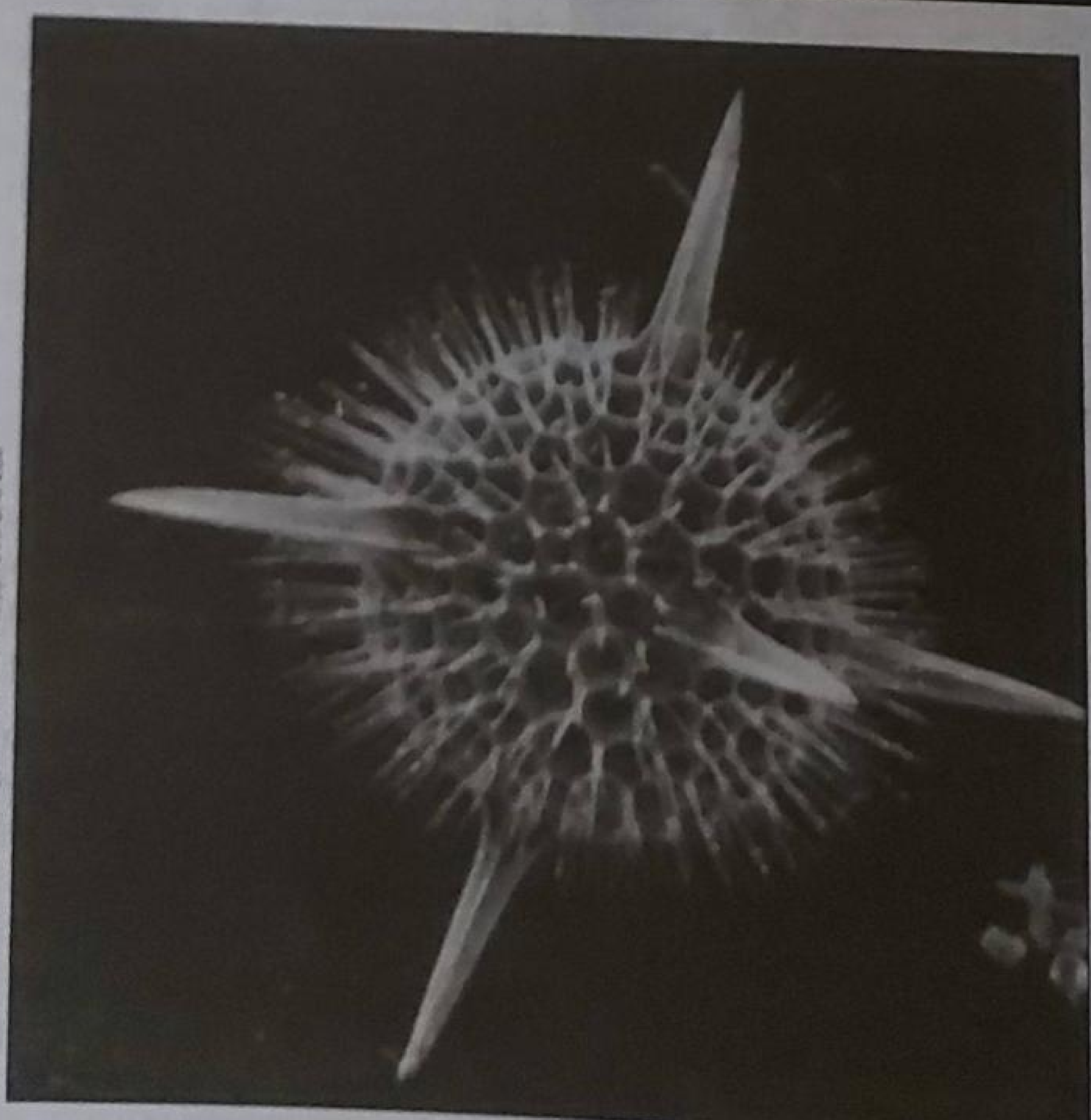
## Actinopoda[P]

The actinopods are primarily spherical, planktonic cells with long, stiff, needlelike pseudopodia called **axopodia** that radiate outward like spikes on a mace (Fig. 3-31, 3-32, 3-33).

The axis of each axopodium contains a supportive that is a bundle of microtubules originating in the Bidirectional shuttling of vesicles occurs in axopo reticulopodia, and they can shorten rapidly after c

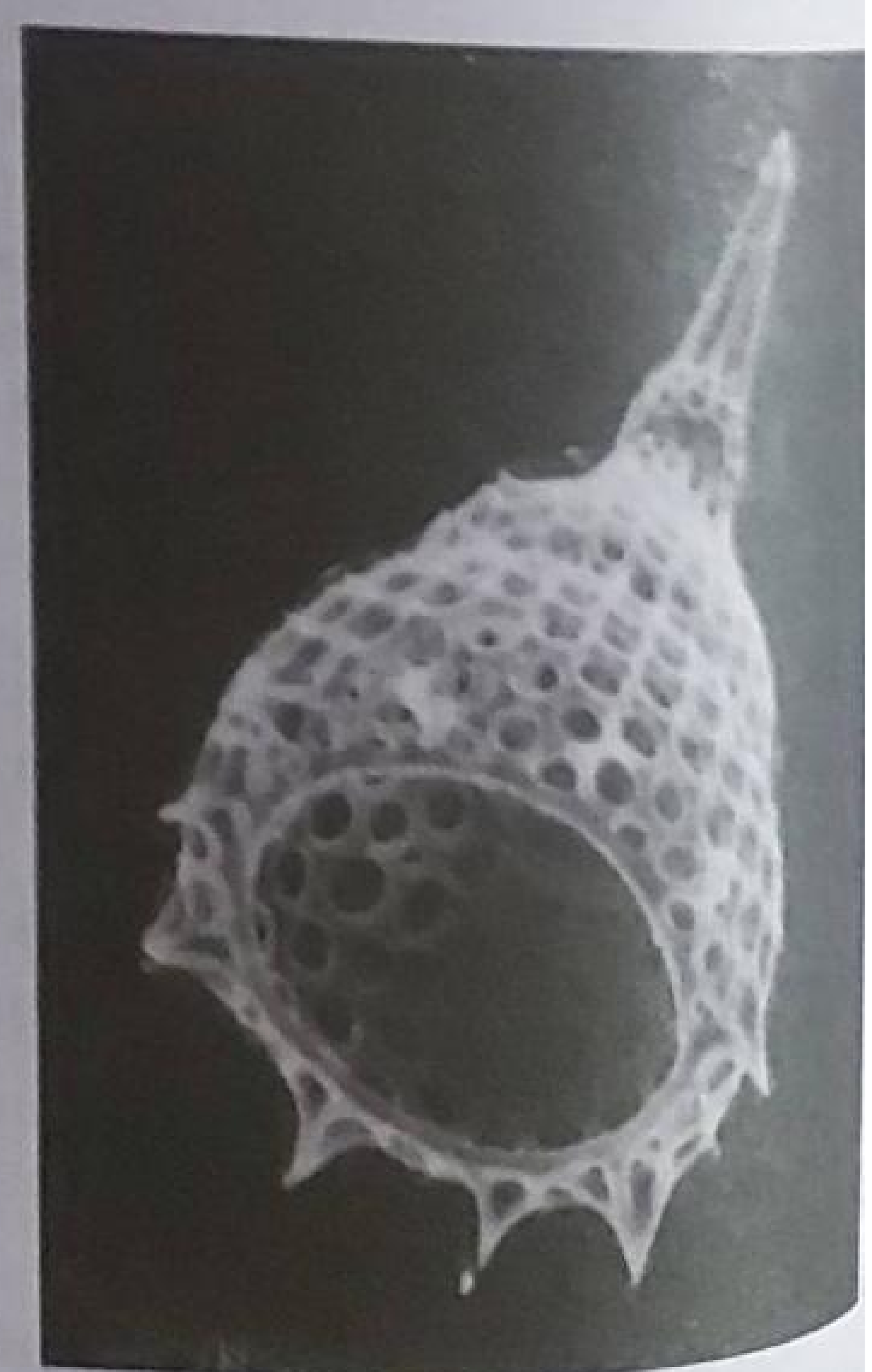
A

Neg./Trans. No. 318863. Courtesy Department of Library Services, American Museum of Natural History



B

From Cachon, J. and Cachon, M. 1985. Class Polycystinea. In Lee, J. J., et al. (Eds.) Illustrated Guide to the Protozoa. Society for Protozoology, Lawrence, KS, pp. 288 and 296



C

**FIGURE 3-31** Radiolaria. **A,** Glass model of a colonial radiolarian, *Trypanosphaera transformata.* Note the radiating axopodia, thick vacuolated cortex, and medulla overlaid by a skeletal grid. **B,** Spherical siliceous test of *Hexacontium.* **C,** Conical test of *Lamprocyclas.*

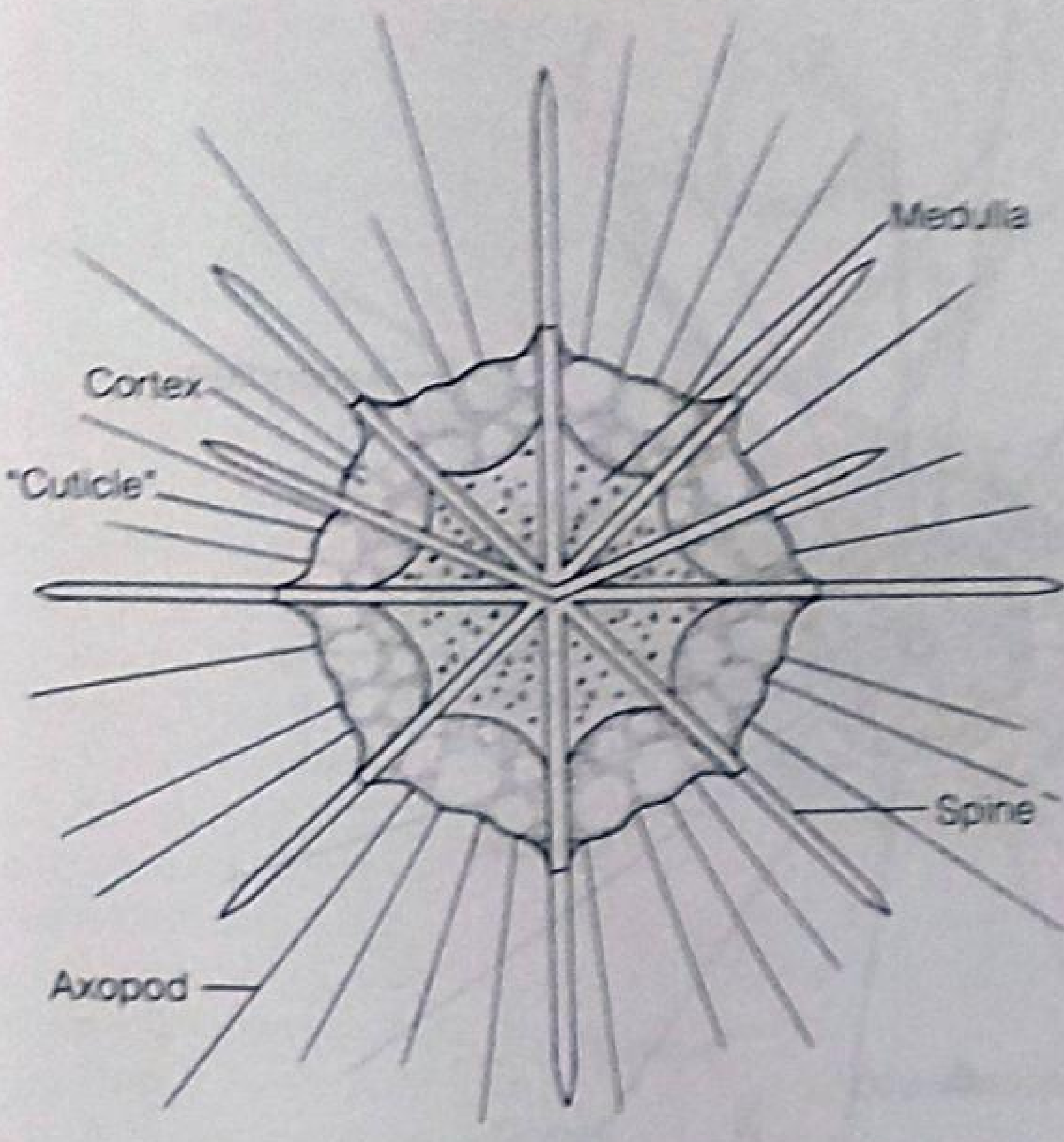



FIGURE 3-32 Acantharea. *Acanthometra*, with mineralized test of radiating strontium sulfate spines. Note extracellular cuticle enclosing cell and attached to spines. *(From Farmer, J. N. 1980. The Protozoa: Introduction to Protozoology. C. V. Mosby Co., St. Louis, p. 353)*

and adhering to prey. The axopods are used for prey capture, flotation, locomotion, and attachment to surfaces.

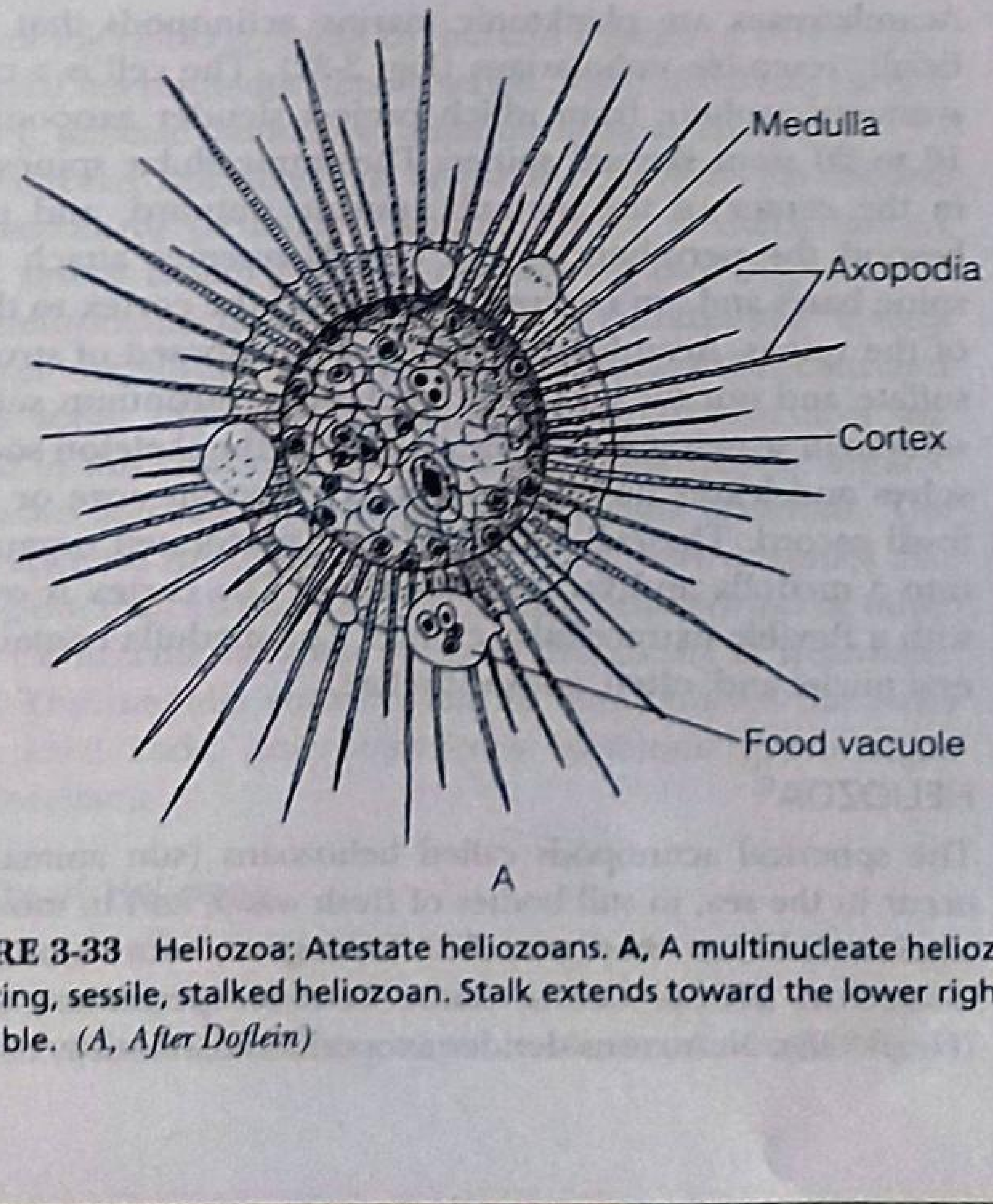
Most actinopods are enclosed in a perforated, organic, extracellular test (central capsule). The actinopodia and other types of pseudopodia emerge through the test pores. Unlike the pseudopodia of forams and testate amebas, however, those of actinopods permanently extend over and beyond the test and do not withdraw into it. The non-actinopodia pseudopods, which are often reticulopodia, filopodia, or vacuolated pseudopodia (for flotation), form a thick shroud over the test. This pseudopodial shroud is called the **cortex** (calymma, or ectoplasm) and the cell body is the **medulla** (central capsule, or endoplasm; Fig. 3-32, 3-33A, 3-34, 3-35). The perforated test (capsular membrane), when present, separates the medulla from the cortex. If the cortex is experimentally removed, a new one is regenerated from the medulla.

Medulla and cortex compartmentalize the actinopod cell. The cortex encounters the external environment, captures and digests prey, conveys nutrients to the medulla, provides flotation, and often bears photosynthetic endosymbionts. The medulla houses the nucleus and the synthetic machinery of the cell, as well as nutrients held in storage.

In addition to the organic test, most actinopods also have a mineral skeleton, usually made of silica, that may be intracellular, extracellular, or both, according to the taxon. In heliozoans, the siliceous skeleton is apparently restricted to the cortex, whereas in acanthareans and some radiolarians, it occurs in the medulla and cortex (Fig. 3-35).

## RADIOLARIA[C]

With a siliceous test that looks like a crystal starburst, radiolarians are among the most elegant protozoans (Fig. 3-31). Entirely marine and primarily planktonic, radiolarians are relatively large protozoa: A few solitary species are millimeters in diameter, and some colonial species attain a length of up to 20 cm (*Collozoum*). The radiolarian cell is usually spherical and divided distinctly into medulla and cortex by a perforated organic test (Fig. 3-31A, 3-35C). Highly specialized



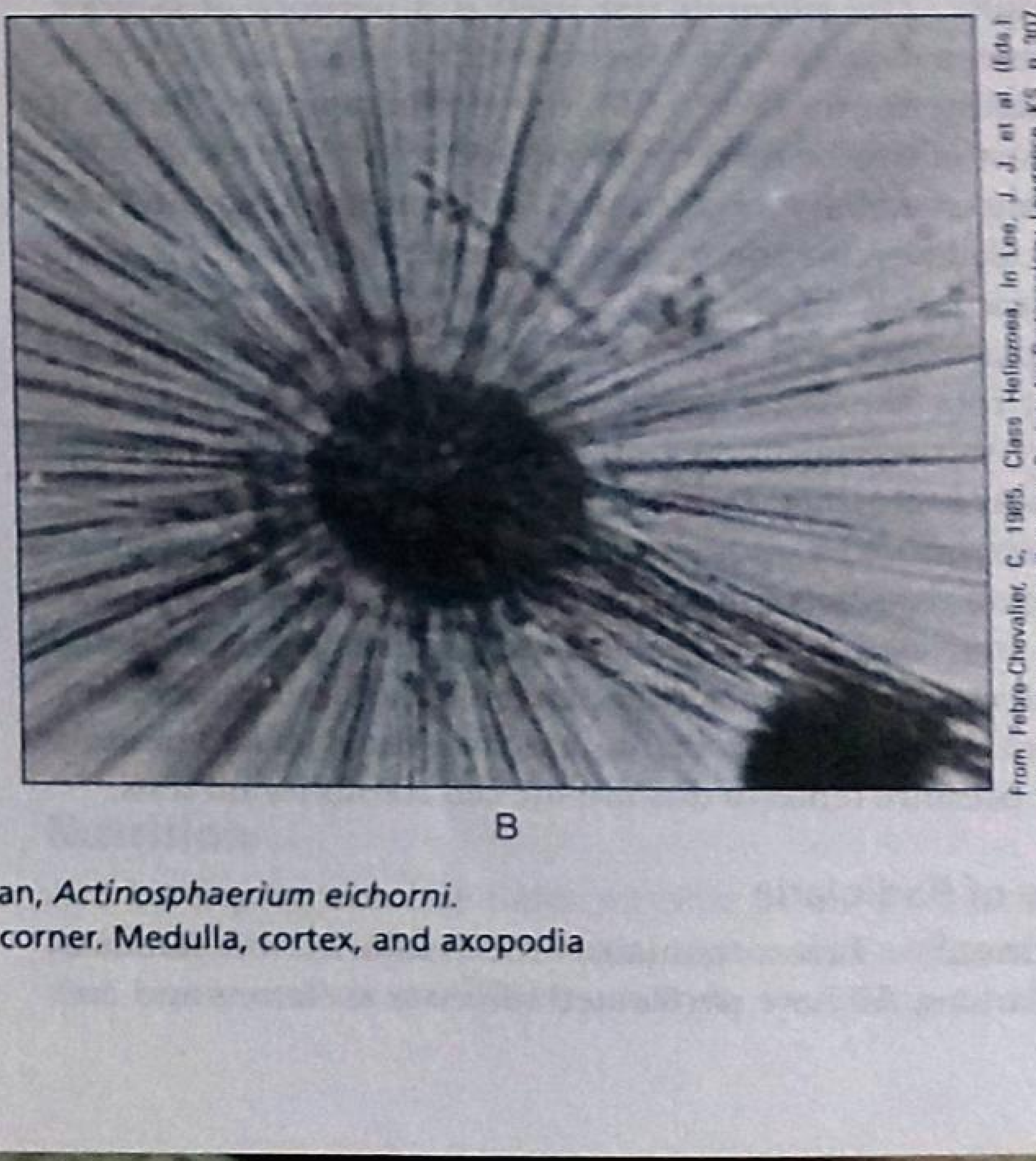




FIGURE 3-33 Heliozoa: Atestate heliozoans. A, A multinucleate heliozoan, *Actinosphaerium eichorni*. B, A living, sessile, stalked heliozoan. Stalk extends toward the lower right corner. Medulla, cortex, and axopodia are visible. *(A, After Doflein)*

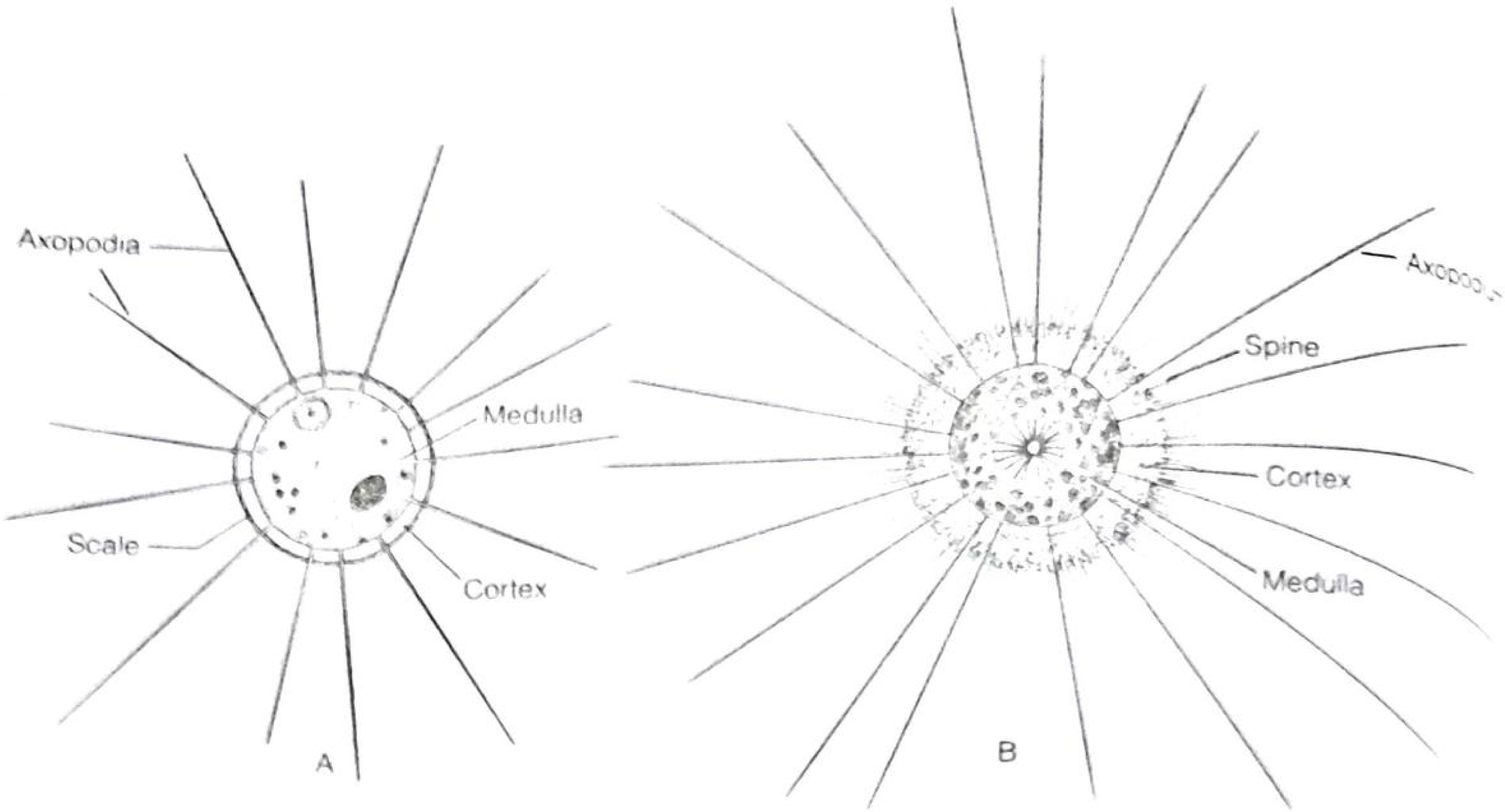



**FIGURE 3-34** Heliozoa: Testate heliozoans. **A,** *Pinaciophora fluviatilis* with a test of scales. **B,** *Heterophrys myriopoda* with cuticle-bearing spines. *(A and B, After Penard from Hall)*

perforations (fusules) in the test allow for the passage of the axopodia as well as vacuolated filopodia and reticulopodia that form the cortex. The cortex, sometimes highly vacoluated (Fig. 3-31A), functions in flotation, prey capture, and intracellular digestion as well as often bearing symbiotic dinoflagellates (zooxanthellae) or other photosynthetic protists. The medulla, which is often vacuolated peripherally, contains one to many nuclei and nutritional reserves, such as lipid drops (also used for buoyancy).

In addition to the organic test, radiolarians also have an intracellular mineral test of silica ($SiO_2$) synthesized in the reticulopodial network of the cortex and sometimes also in the medulla. The siliceous test itself is a network of slender, interconnected rods that resembles a geodesic dome, often with radiating spines (Fig. 3-31). In its more complex forms, it can consist of two or three interconnected concentric spheres of striking symmetry and beauty. In some radiolarians the siliceous skeleton is rudimentary or even absent, but if absent, the organic test is still present.

The planktonic radiolarians display a distinct vertical stratification from the ocean surface down to 5000 m depths. A testimony to the enormous population densities of planktonic radiolarians is provided by the thick accumulation of their tests, after death, on many parts of the ocean floor. In some of these areas, where tests account for 30% or more of sediment composition, the sediment is called **radiolarian ooze.** Similarly, **foraminiferan ooze,** from accumulated foram tests, characterizes other parts of the ocean floor. At depths below 4000 m, however, the great pressure tends to dissolve the calcareous foram tests.

### Diversity of Radiolaria

Polycystinea[O]: Taxon contains the majority of familiar radiolarians. All have perforated siliceous skeletons and are solitary and colonial species, 30 μm to 2 mm. *Collozoum, Eucoronis, Thallasicola.*

Phaeodarea[O]: Taxon of deep-sea radiolarians [illegible] siliceous test with hollow spines and incorporated [illegible] matter. Central capsule has three openings [illegible] and two for axopods. Yellow-brown pigment [illegible] odium) near the oral opening. *Astracantha, [illegible] Phaeodina.*

## ACANTHAREA[C]

Acanthareans are planktonic marine actinopods [illegible] ficially resemble radiolarians (Fig. 3-32). The cell [illegible] symmetric sphere from which project slender [illegible] 10 to 20 stout skeletal spines. The intracellular [illegible] in the center of the medulla, radiate outward [illegible] beyond the periphery of the cell. Myonemes [illegible] spine bases and, on contraction, expand the cortex [illegible] of the spines. Acantharean spines are composed [illegible] sulfate and not the silica of radiolarians. Strontium [illegible] soluble in seawater and, after cell death, the skeleton [illegible] solves and leaves no trace either as a bottom ooze [illegible] fossil record. The cell is divided by a perforated [illegible] into a medulla and vacuolated cortex. The cortex [illegible] with a flexible extracellular cuticle. The medulla [illegible] eral nuclei and, often, zooxanthellae.

## HELIOZOA[C]

The spherical actinopods called heliozoans (sun [illegible] occur in the sea, in still bodies of fresh water, and in [illegible] aquatic habitats, they may be floating or, more [illegible] located in bottom debris. Some benthic species [illegible] (Fig. 3-33B). Numerous slender axopodia radiate [illegible]

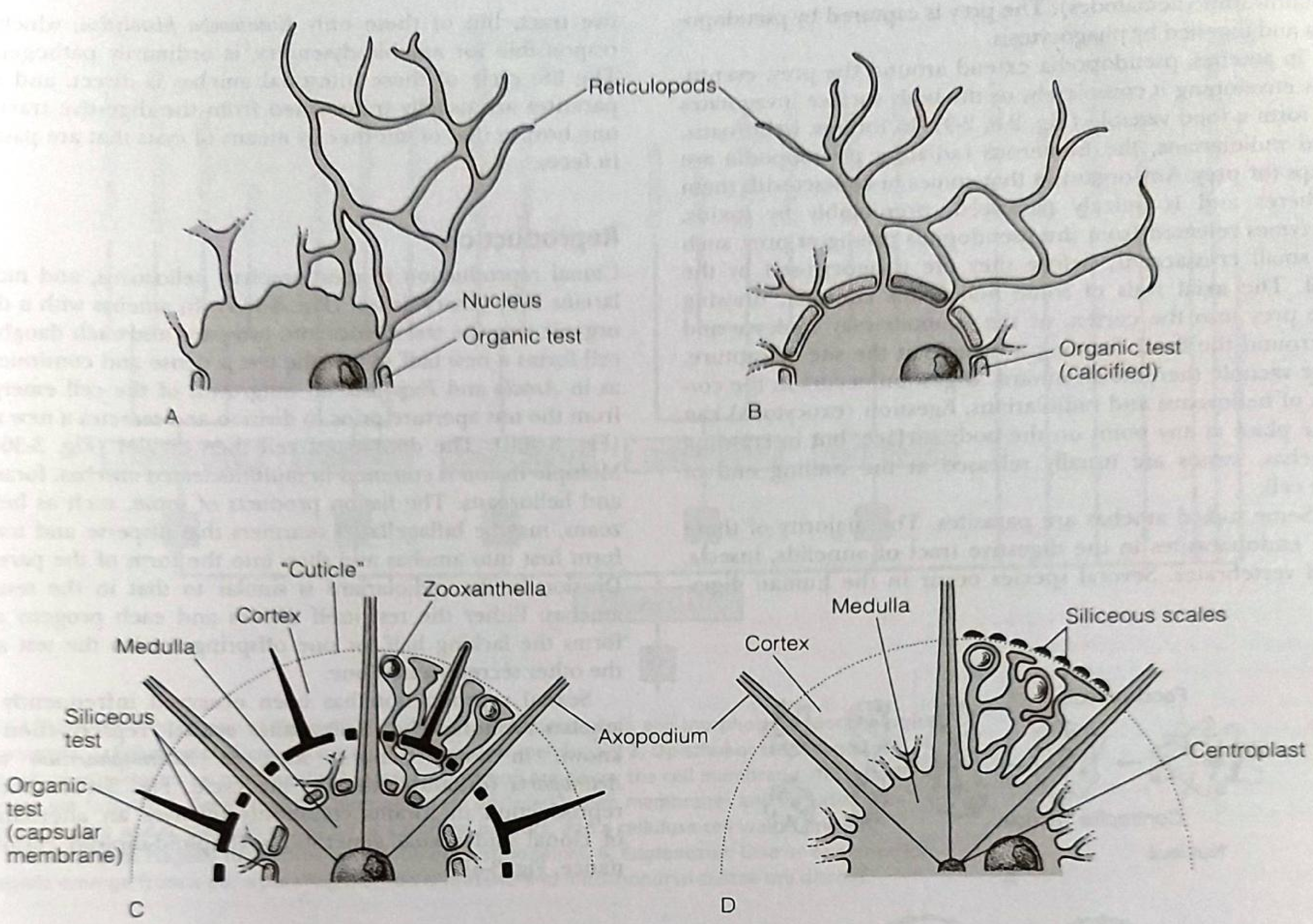



**FIGURE 3-35** Anatomy of forams, radiolarians, and heliozoans. **A**, A single-chambered foram; **B**, A multichambered foram with test pores; **C**, A radiolarian; **D**, A heliozoan. **B–D**, Partly hypothetical.

surface of the cell (Fig. 3-33A,B), but can shorten or even "melt" as the axial microtubules depolymerize. Some heliozoan species have long, delicate filopodia in addition to the axopodia.

A heliozoan cell, like that of other actinopods, is divided into a cortex of vacuolated filopods and a medulla, but an organic test is absent between the two regions (Fig. 3-33A). Some heliozoans, however, secrete an extracellular cuticle (gel) over the surface of the cortex, as do acanthareans and perhaps some radiolarians. Discrete skeletal structures are attached to this cuticle in some species. These may be organic or siliceous spicules or incorporated foreign materials. The diverse siliceous spicules may be scales (Fig. 3-34A), spines that radiate from the cell surface (Fig. 3-34B), or structures of other shapes. Contractile vacuoles occur in the cortex of freshwater species. The medulla contains one to many nuclei, the bases of the axial rods, and sometimes symbiotic green algae (zoochlorellae).

### Diversity of Heliozoa

Actinophryida$^{O}$: Axopodial MTs originate on the nuclear membrane and form two intertwined spirals; uni- and multinucleate species are capable of encystment; marine, freshwater, terrestrial (peat). *Actinophrys, Actinosphaerium, Camptonema.*

Desmothoracida$^{O}$: Sessile, mostly stalked species; irregularly arranged axopod MTs; filopodia are present. *Clathrulina, Hedriocystis, Orbulinella.*

Ciliophryida$^{O}$: Similar in form to actinophryids, but adult bears a single flagellum with pinnate mastigonemes; axopods with few MTs. *Actinomonas, Ciliophrys, Pteridomonas.*

Taxopodida$^{O}$: Bilaterally symmetric with stout siliceous spines in rosettes; axopodal MTs in a hexagonal pattern; marine. *Sticholonche.*

Centrohelida$^{O}$: Numerous slender and long axopods arise from a central point (centroplast); axopods bear extrusomes used in prey capture; often have surface covering of extracellular siliceous scales or spinelets; axopod MTs in hexagonal or triangular arrays. *Acanthocystis, Gymnosphaera, Hedraiophrys, Heterophrys.*

## Nutrition

Ameboid protozoa are heterotrophs. Their food consists of small organisms such as bacteria, algae, diatoms, protozoans, and even small multicellular animals, including rotifers and roundworms (nematodes). The prey is captured by pseudopodia and ingested by phagocytosis.

In amebas, pseudopodia extend around the prey, eventually enveloping it completely, or the body surface invaginates to form a food vacuole (Fig. 2-8, 2-9). In forams, heliozoans, and radiolarians, the numerous radiating pseudopodia are traps for prey. Any organism that comes in contact with them adheres and is quickly paralyzed, presumably by toxins. Enzymes released from the pseudopods predigest prey, such as small crustaceans, before they are phagocytosed by the cell. The axial rods of some heliozoans contract, drawing the prey into the cortex, or the axopods may coalesce and surround the food, forming a vacuole at the site of capture. The vacuole then moves inward. Digestion occurs in the cortex of heliozoans and radiolarians. Egestion (exocytosis) can take place at any point on the body surface, but in crawling amebas, wastes are usually released at the trailing end of the cell.

Some naked amebas are parasites. The majority of these are endoparasites in the digestive tract of annelids, insects, and vertebrates. Several species occur in the human digestive tract, but of these only *Entamoeba histolytica*, responsible for amebic dysentery, is ordinarily [...]. The life cycle of these intestinal amebas is dir[...] parasites are usually transmitted from the diges[...] one host to that of another by means of cysts that [...] in feces.

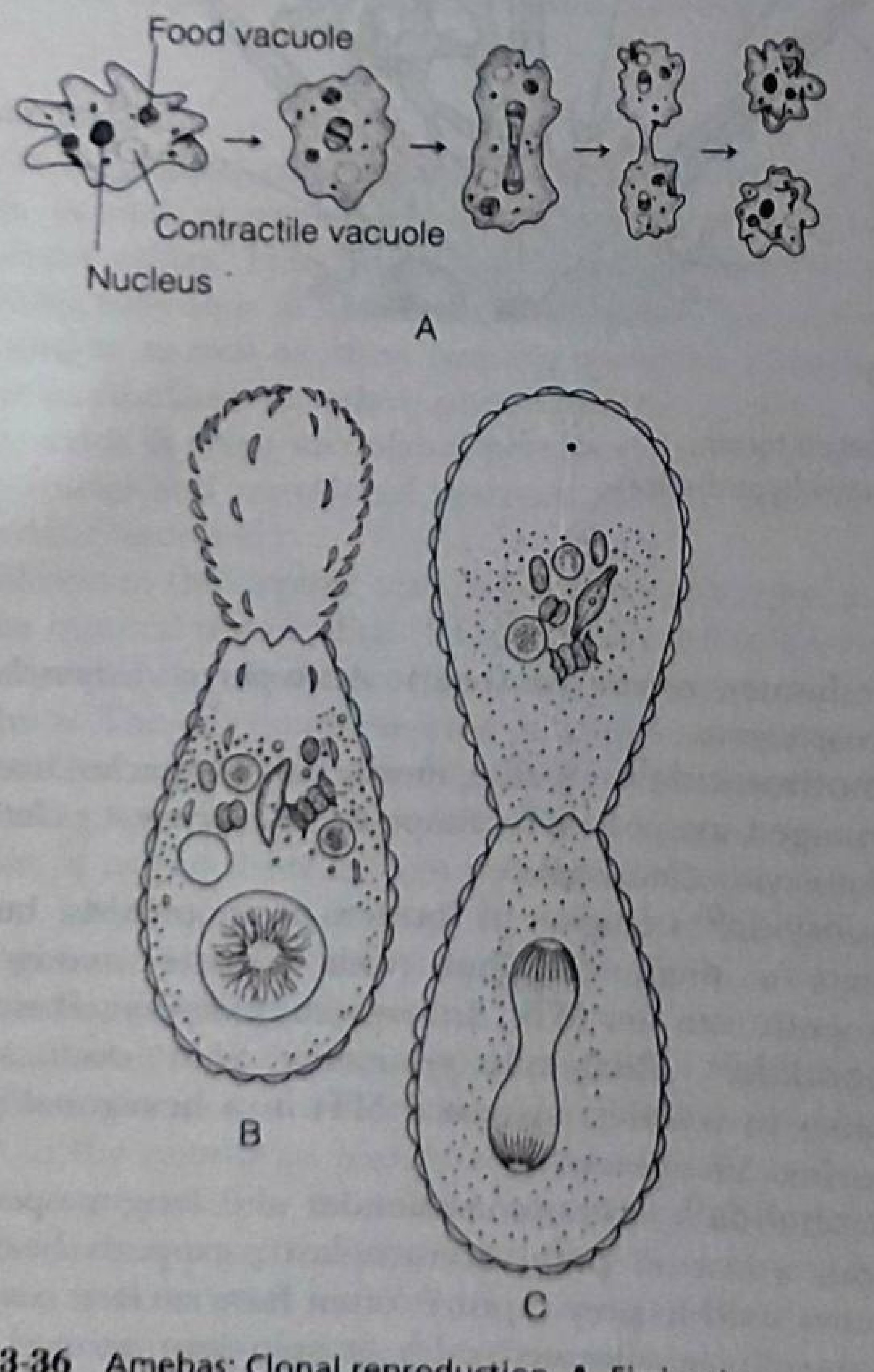



**FIGURE 3-36** Amebas: Clonal reproduction. **A**, Fission in a naked ameba. **B** and **C**, Two stages in the division of *Euglypha*, a testate ameba. B, Formation of test plates on a cellular mass protruding from the aperture. C, Division of the nucleus. One of the daughter nuclei will move into the new cell. Note that the nuclear membrane remains intact during mitosis. *(B and C, After Sevajakov from Dogiel)*

## Reproduction

Clonal reproduction in most amebas, heliozoans, [...]larians is by binary fission (Fig. 3-36A). In amebas [...] organic test, the test divides into two parts and each [...] cell forms a new half. When the test is dense and [...] as in *Arcella* and *Euglypha*, an outgrowth of the [...] from the test aperture prior to division and secretes [...] (Fig. 3-36B). The double-test cell then divides [...] Multiple fission is common in multinucleated amebas and heliozoans. The fission products of some, [...]zoans, may be biflagellated swarmers that disperse [...] form first into amebas and then into the form of [...] Division in the radiolarians is similar to that in [...] amebas: Either the test itself divides and each [...] forms the lacking half, or one offspring retains [...] the other secretes a new one.

Sexual reproduction has been observed infr[...] amebas. Among the heliozoans, sexual repr[...] known in some genera, such as *Actinosph*[...] *Actinophrys* (diploid-dominant life cycle, Fig. 3-4[...] reproduction in forams commonly involves an a[...] of clonal and sexual generations (haploid-dip[...]nance, Fig. 3-4D).

# PHYLOGENY OF PROTOZOA

The evolutionary origin of protozoa is discussed [...] Introduction to Protozoa. The phylogenetic [...] among the protozoan taxa have been notorious[...] unravel, but progress is ongoing thanks to the [...] of microanatomical and molecular techniques. [...] general, the ameboid taxa (and some flagellates [...] to represent primitive taxa, although their [...] ships are presently unclear. At least five monop[...] have been proposed. One of these is the Euglen[...] includes the euglenoids and kinetoplastids. An[...] Chlorophyta, which includes the Volvocida, [...] and multicellular green plants. Ciliates, dinoflag[...] apicomplexans form another monophyletic taxon [...] based on their common possession of alveoli and [...]dria with tubular cristae. From the perspective [...] evolution, the most interesting monophyletic ta[...] Opisthokonta, characterized by a posterior fla[...] motile cells as well as gene-sequence similarities [...] in this taxon are the sister taxa Choanoflagellata [...]zoa (multicellular animals) as well as Fungi an[...] Microsporidia. The only other opisthokont ta[...] former protozoan group Myxosporidia, which is now [...] among the metazoans as Myxozoa.

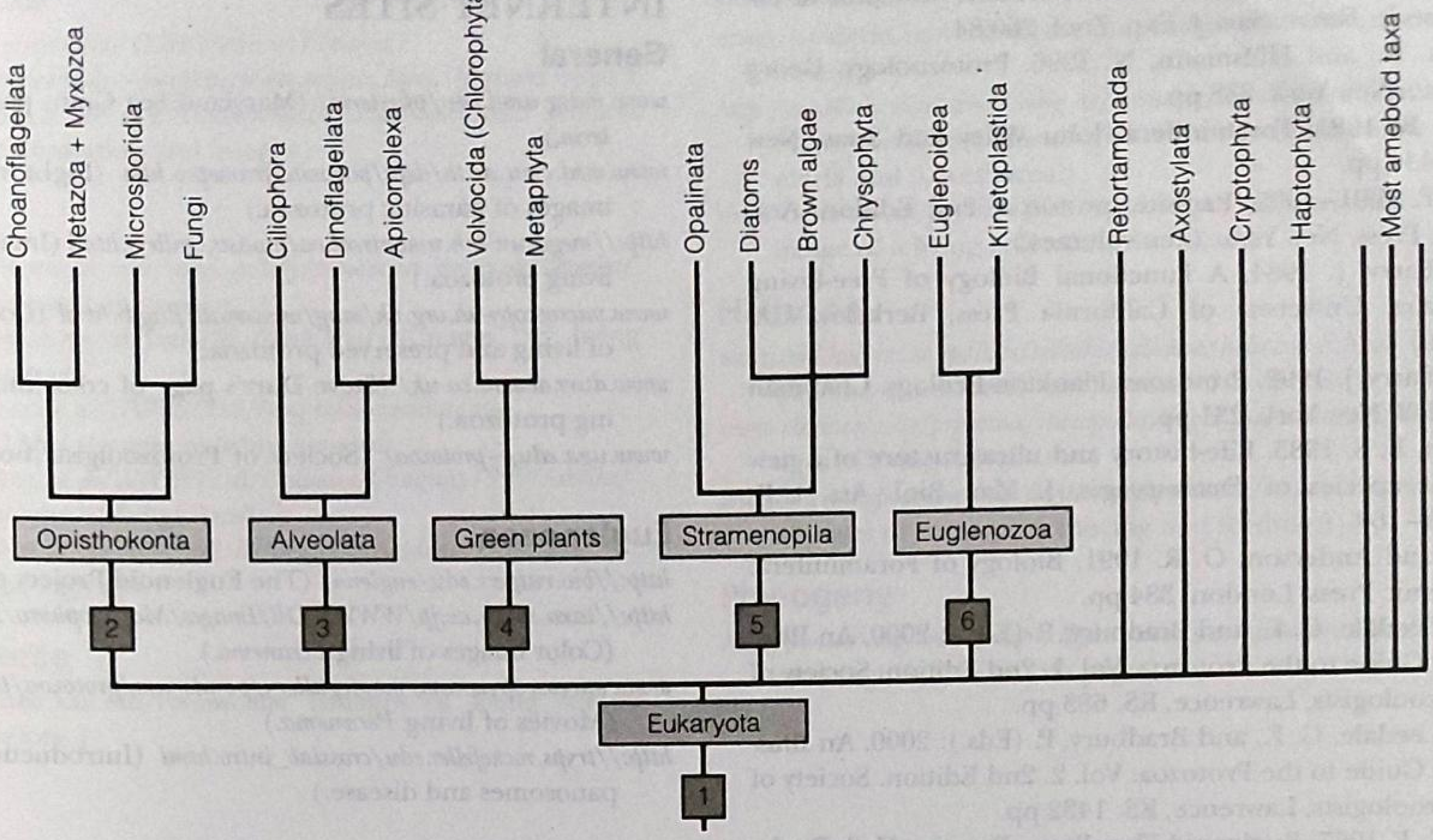



**FIGURE 3-37** Phylogeny of Protozoa based on gene-sequence data and morphology. Morphological characters: **1, Eukaryota:** Nucleus is enclosed in a nuclear membrane. **2, Opisthokonta:** Locomotory flagellum is posterior on motile cells. **3, Alveolata:** Alveoli are below the cell membrane, mitochondrial cristae are tubular. **4, Green plants:** Chloroplasts are enclosed in two membranes and include chlorophylls a and b, starch is produced as a storage product, and a cellulose cell wall is present. **5, Stramenopila:** Flagella have three-part, tubular mastigonemes. **6, Euglenozoa:** One or two anterior flagella emerge from a pit, a paraflagellar rod is present, and mitochondrial cristae are discoid.

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# INTERNET SITES

## General

*www.mdsg.umd.edu/pfiesteria/* (Maryland Sea Grant ... teria.)

*www.med.cmu.ac.th/dept/parasite/framepro.htm* (Lig... images of parasitic protozoa.)

*http://megasun.bch.umontreal.ca/protists/gallery.html* (... living protozoa.)

*www.microscopy-uk.org.uk/mag/wimsmall/flagdr.html* ... of living and preserved protozoa.)

*www.durr.demon.co.uk/* (Steve Durr's page of color... ing protozoa.)

*www.uga.edu/~protozoa/* (Society of Protozoologists

## Euglenozoa

*http://bio.rutgers.edu/euglena/* (The Euglenoid Proj...

*http://taxa.soken.ac.jp/WWW/PDB/Images/Mastigopho...* (Color images of living *Peranema*.)

*www.microscopyu.com/moviegallery/pondscum/protoz...* (Movies of living *Peranema*.)

*http://tryps.rockefeller.edu/crosslab_intro.html* (Introdu... panosomes and disease.)

## Retortamonada and Axostylata

*www.geocities.com/CollegePark/Lab/4551/* (*Giardia* pag...

*http://vm.cfsan.fda.gov/~mow/chap22.html* (U.S. Foo... Administration page on *Giardia*.)

*www.utoronto.ca/forest/termite/flagella.html* (List of flag... found in the gut of termites.)

*http://comenius.susqu.edu/bi/202/ProtistPix/parabasa...* *nympha.htm* (Images of *Trichonympha* from a term...

## Volvocida

*http://megasun.bch.umontreal.ca/protists/chlamy/appe...* (Image of living *Chlamydomonas* and other ...

*http://taxa.soken.ac.jp/WWW/PDB/Images/Chloropyta...* (Color images of living *Volvox*.)

## Choanoflagellata

*http://thalassa.gso.uri.edu/rines/ecology/choanofl.htm* (Ima... choanoflagellates.)

*http://protist.i.hosei.ac.jp/taxonomy/Zoomastigophora/...* *ida.html* (Color images of living choanoflagellates...

## Dinoflagellata

*www.geo.ucalgary.ca/~macrae/palynology/dinoflagellates...* *dinoflagellates.html* (Dinoflagellate images and ...

## Ciliophora

*www.uoguelph.ca/~ciliates/* (The Ciliate Resource Arch...

*www.micrographia.com/specbiol/protis/cili/peri0100.htm* ... ages of peritrichs.)

*http://members.magnet.at/p.eigner/* (Information on ... hypotrichs.)

*http://taxa.soken.ac.jp/WWW/PDB/images/Protista/Cili...* (Color images of living ciliates.)

## Apicomplexa

*www.saxonet.de/coccidia/* (Life cycle of *Eimeria.*)

*www.biosci.ohio-state.edu/~parasite/plasmodium.html* (Malaria page.)

*www-micro.msb.le.ac.uk/224/Bradley/Biology.html* (Another malaria page with animation and images.)

## Amebas

*http://micro.magnet.fsu.edu/moviegallery/pondscum/protozoa/amoeba/* (Movies of ameboid motion.)

*www.microscopy-uk.org.uk/intro/illu/dark.html* (Images of living *Amoeba proteus.*)

*http://taxa.soken.ac.jp/WWW/PDB/Images/Sarcodina/ap/intactcell2.html* (Images of living *Amoeba.*)

*http://taxa.soken.ac.jp/WWW/PDB/Galleries/Uruguay1999/Arcella/* (Color images of living *Arcella.*)

*http://taxa.soken.ac.jp/WWW/PDB/Images/Sarcodina/Difflugia/* (Images of *Difflugia.*)

## Foraminiferea

*http://cushforams.niu.edu/Forams.htm* (Images of living forams and skeletons.)

## Radiolaria and Acantharea

*www.radiolaria.org/* (Images and information on fossil radiolarians.)

*http://caliban.mpiz-koeln.mpg.de/~stueber/haeckel/radiolarien/index.html* (Ernst Haeckel's 1862 color illustrations of Radiolaria and Acantharea.)

*www.cladocera.de/protozoa/rhizopoda/imgal_radiolaria.html* (Color image of a living colonial radiolarian.)

## Heliozoa

*www.biol.kobe-u.ac.jp/labs/suzaki/heliozoa/heliozoa-E.html* (Research page on contraction mechanism of axopodia.)

*www.cladocera.de/protozoa/rhizopoda/imgal_heliozoa.html* (Color images of living heliozoans.)

*www.microscopyu.com/moviegallery/pondscum/protozoa/actinophrys/* (Movies of *Actinophrys* moving and feeding.)

## Phylogeny

*http://tolweb.org/tree?group=Eukaryotes&contgroup=Life* (Patterson and Sogin's Tree of Life page.)