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CONTENTS

Excretion and Excretory Systems

Every organism, from the smallest protist to the largest mammal, must rid itself of the potentially harmful by-products of its own vital activities. This process in living things is called elimination, which may be considered to encompass all of the various mechanisms and processes by which life forms dispose of or throw off waste products, toxic substances, and dead portions of the organism. The nature of the process and of the specialized structures developed for waste disposal vary greatly with the size and complexity of the organism.

Four terms are commonly associated with waste-disposal processes and are often used interchangeably, though not always correctly: excretion, secretion, egestion, and elimination.

Excretion. Excretion is a general term referring to the separation and throwing off of waste materials or toxic substances from the cells and tissues of a plant or animal.

Secretion. The separation, elaboration, and elimination of certain products arising from cellular functions in multicellular organisms is called secretion. Though these substances may be a waste product of the cell producing them, they are frequently useful to other cells of the organism. Examples of secretions are the digestive enzymes produced by intestinal and pancreatic tissue cells of vertebrate animals, the hormones synthesized by specialized glandular cells of plants and animals, and sweat secreted by glandular cells in the skins of some mammals. Secretion implies that the chemical compounds being secreted were synthesized by specialized cells and that they are of functional value to the organism. The disposal of common waste products should not, therefore, be considered to be of a secretory nature.

Egestion. Egestion is the act of excreting unusable or undigested material from a cell, as in the case of single-celled organisms, or from the digestive tract of multi-cellular animals. The elimination of digestive wastes is treated in the article DIGESTION AND DIGESTIVE SYSTEMS.

Elimination. As defined above, elimination broadly defines the mechanisms of waste disposal by living systems at all levels of complexity. The term may be used interchangeably with excretion.

This article discusses the eliminatory processes and mechanisms of various organisms, from the egestion of the simplest single-celled organism to the highly developed excretory process of vertebrates and of human beings. Human excretion, along with the diseases and disorders that disrupt healthy function, is explained in detail.

For coverage of related topics in the *Macropædia* and *Micropædia,* see the *Propædia,* sections 421 and 423.

The article is divided into the following sections:

Elimination

BIOLOGICAL SIGNIFICANCE OF ELIMINATION

Waste disposal by unicellular and multicellular organisms is vital to their health and to the continuance of life. Animals must take in (ingest) energy-containing chemical compounds, extract a portion of the energy to power their life processes, and dispose of the unusable material or by-products formed during the energy-extraction process. An analogous series of events occurs in an internal-combustion engine. Fuel, containing energy, is taken into the engine, where it is burned, and a portion of the energy released is used to move the pistons. As in living cells, a portion of the energy-containing material (fuel) not utilized in the engine is exhausted in the form of carbon monoxide, carbon dioxide, and other by-products of combustion. Blockage of the exhaust system in an engine results in loss of efficiency and eventual total breakdown. Similarly, the rate of waste disposal in biological systems can and does provide a means of controlling the metabolic rate. Complete blockage of waste-disposal mechanisms in living systems is as effective in destroying vital functions as the cutting off of food, oxygen, or water from the system. In addition, some substances produced as metabolic by-products are toxic in themselves and must be removed from living cells at a rate equal to that at which they are produced by those cells. Thus, the excretion of waste products from living cells must occur continually in order to ensure the normal progression of vital chemical events.

Importance of elimination in living systems

Waste and poisonous substances produced by the metabolic activities of plant and animal communities must, in a similar manner, be removed or detoxified if community health is to be preserved. Collective wastes of individual organisms constituting a community, if allowed to accumulate to any marked degree, will eventually destroy the lives of all the community members.

The biosphere, composed of all individuals and communities of life forms and their environments on the Earth, is equally sensitive to the effects of waste and poison accumulation. A continual buildup of substances harmful to life forms can only result in the eventual destruction of most or all of the presently existing species of plants and animals. Humans are unique among living things in that their activities result in the production of waste materials (pollutants) that, by virtue of their chemical structure, are poisonous to all living things, including themselves. (For information about waste disposal in the biosphere, see BIOSPHERE and CONSERVATION OF NATURAL RESOURCES.)

TYPES OF WASTE: METABOLIC AND NONMETABOLIC

Waste products may be categorized as metabolic or nonmetabolic. The difference lies in whether the substances in question are produced by the chemical processes of a living cell or are merely passed through the digestive tract of an organism without actually entering into its life processes.

Nonmetabolic wastes. The nonmetabolic wastes are mainly materials that, by virtue of their chemical makeup, are indigestible or unusable by an organism. In addition, nonmetabolic wastes include any substances that are absorbed, ingested, or otherwise taken into a living system in excess of the needs and storage capabilities of the organism. These substances include digestible (metabolizable) as well as indigestible materials, and they may be excreted almost immediately, even though they are often usable as food.

Heat as a waste product

Metabolic wastes. Metabolic wastes may be separated into gases, liquids, solids, and heat. Heat, though usually not classified as a waste product, should be classified as such because it is a by-product of metabolic activity and must be eliminated to avoid harmful elevation of body temperatures in warm-blooded animals.

Gaseous wastes. Oxygen produced during photosynthetic reactions in green plants and certain bacteria may be considered to be a waste product, or at least a by-product, requiring removal. Carbon dioxide is produced by all animals and by green plants in darkness. Nitrogen gas is produced by denitrifying sulfur bacteria (*Thiobacillus*), and ammonia is excreted by decay-causing bacteria and by most invertebrate and vertebrate animals.

Liquid wastes. The sole liquid waste produced as a metabolic by-product by all animals and photosynthetic plants in darkness is water.

Solid wastes. Several important kinds of materials may be classified as solid wastes. Among them are nitrogenous wastes, by-products of protein and amino-acid metabolism by animals; nitrite and nitrate compounds produced by nitrifying bacteria; and sulfur and sulfates resulting from the metabolic activities of sulfur bacteria. Many other substances also enter into solid wastes to be disposed of by organisms. Iron compounds in an insoluble form are secreted by iron bacteria that have used soluble iron compounds. Various resins, fats, waxes, and complex organic chemicals are exuded from certain plants—as in the latex from rubber trees and milkweeds. Organic pigments from the breakdown of biological pigments, such as hemoglobin in vertebrates, become components of solid waste. Inorganic salts, including molecules and ions such as carbonates, bicarbonates, and phosphates resulting from life-sustaining chemical reactions, eventually may become solid waste products.

METHODS OF WASTE DISPOSAL

Disposal of metabolic and nonmetabolic wastes involves both active and passive mechanisms. In general, gaseous wastes are eliminated through passive mechanisms without the direct expenditure of energy on the part of the living system. The solid and liquid waste-disposal mechanisms used by higher animals are active (energy consuming) systems that separate waste materials from vital substances prior to excretion. Methods of disposal may be classified into specific and nonspecific systems.

Specific elimination mechanisms. Three pathways exist in this context: (1) the alimentary canal, (2) the respiratory system, and (3) the kidneys.

Alimentary canal. The alimentary canal is a pathway used almost exclusively for the elimination of solid wastes of an indigestible nature, and the act of elimination by this means is termed egestion. Materials disposed of in this manner have not entered the tissues of the animal but rather are the residues of enzymatic and absorptive activities occurring in the digestive tract. True metabolic wastes are excreted by means of the flow of bile from the liver into the intestine. The destruction of cells in animals produces bile pigments—residues of hemoglobin and other pigments—which may be considered to be the principal metabolic wastes eliminated via the alimentary canal. Waste disposal in this manner requires little energy expenditure other than that employed in the peristaltic contractions of muscle in the walls of the tract that act to push material along the length of the tube (see DIGESTION AND DIGESTIVE SYSTEMS).

Respiratory system. The respiratory pathway is concerned principally with the gaseous waste products of metabolism (carbon dioxide and ammonia), which move to the external environment by diffusing from the cells of origin. In invertebrate and vertebrate members of the animal kingdom, transport is by means of the circulatory system when present or simply by diffusion through the cell membranes of lower animals. A few multicellular aquatic animals lose carbon dioxide to the surrounding water by way of diffusion through the thin vascular membranes of their general body surface. In most higher animals, however, the skin is too hard or thick and nonvascular to function effectively in gas disposal. In these animals, gills and lungs—aggregations of thin, moist, vascular membranes—have evolved. Membranes of the gills of aquatic animals and the lungs of terrestrial forms are provided with large surface areas for the diffusion of waste gases from the circulatory system to the outside environment. Because carbon dioxide is soluble in the body water, it can easily diffuse into the circulatory system, in solution, from the cells of origin. Transport and excretion of carbon dioxide requires little energy as it diffuses along concentration gradients from cells to the circulation and finally to the outside environment.

Carbon dioxide elimination

Because more carbon dioxide (CO_2) is produced by metabolic activity than can be carried in the circulatory system in the form of dissolved carbon dioxide, the major portion of carbon dioxide is transported to the gills and lungs as bicarbonate (HCO_3^-), via two chemical reactions:

$$CO_2 + H_2O \leftrightarrows H_2CO_3 \rightleftarrows H^+ + HCO_3^-.$$

Thus, carbon dioxide reacts with water, producing carbonic acid (H_2CO_3), which in turn dissociates to produce a hydrogen ion (H^+) and a bicarbonate ion (HCO_3^-). In the lungs or gills, these reactions occur in the opposite direction, and carbon dioxide diffuses from the body into the outside environment. Certain aquatic animals are capable of eliminating gaseous ammonia—derived from protein breakdown—by way of specialized cells in their gill tissues.

Salt secretion via specialized gill cells occurs in marine vertebrates that constantly absorb salt through thin membranes of their oral, respiratory, and body surfaces (see RESPIRATION AND RESPIRATORY SYSTEMS).

The kidneys. Kidneys have evolved in multicellular animals as a highly sophisticated channel for waste disposal, and they function to regulate the levels of water, salts, and organic materials in the bodies of higher animals. Materials eliminated via the kidney include nitrogenous waste products (ammonia, uric acid, urea, creatine, creatinine, and amino acids), excess quantities of salts and water that may be taken into the body, and various other organic materials produced by life-sustaining chemical reactions. Functionally, the kidney is a microfilter that initially removes dissolved as well as some suspended materials from the circulatory system, along with large quantities of water. These substances are differentially reabsorbed into the blood by various kidney structures during urine formation to a degree that varies considerably throughout the animal kingdom. For example, animals that absorb large quantities of water into their bodies (such as freshwater fishes) excrete copious quantities of water in their urine. The reverse is true of many desert animals, who must conserve water and therefore produce a thick, semisolid urine. The kidney, in its various stages of evolution, functions at the expense of considerable metabolic energy and cannot be considered to be a passive system. (For a specific account of kidney structure and function, see below *Human excretion.*)

Nonspecific mechanisms of waste disposal. A multitude of disposal mechanisms exist throughout the plant and animal kingdoms for the elimination of excess plant and animal material. Among plants, the shedding and dropping of bark, leaves, and twigs might, in a broad sense, be said to represent disposal mechanisms. Certain plants, in addition, secrete or exude resins, sap, and other substances that accumulate in excessive quantities within the plant.

Elimination of particulate wastes

Specialized, mobile, amoeba-like cells exist in the blood and tissues of animals and engulf particulate wastes resulting from the disintegration of dead cells or the intake of foreign particles into the bodies of animals. Waste matter thus stored inside these small cells is removed from contact with the organism or its metabolism and may be considered to be eliminated whether or not the material is ever actually eliminated from the body of the organism during its normal life cycle.

Toxic substances are produced by normal metabolic activities. Though some of these poisons are eliminated in their original chemical form, others, such as some nitrogenous compounds, are altered biochemically to less toxic compounds. In this manner, more of the original waste may be safely stored, or permitted to accumulate without harmful effects to the organism, until it can be eliminated. In addition, toxic chemicals that are inadvertently ingested or produced by bacterial action (infection) are frequently converted to nontoxic forms by enzymatic and antibody (immune) reactions. Such materials can then be eliminated safely with other wastes along normal pathways of excretion.

Heat is eliminated from the bodies of animals by conduction to the external surface of the organism. In animals possessing a circulatory system, heat travels in its fluid from the deeper portions of the body to the surface. At the body surface, heat is lost by physical processes of convection, radiation, conduction, and evaporation of sweat.

COMPARATIVE OVERVIEW OF ELIMINATORY MECHANISMS FROM PROTISTS TO VERTEBRATES

Protista. No specialized elimination mechanisms are present in algae, fungi, protozoans, and slime molds, the main groups of protists. Metabolic wastes (carbon dioxide, water, oxygen, and nitrogenous compounds) diffuse through the cell membranes of these unicellular organisms into the outside environment. Particulate wastes pass from the bodies of certain protozoans to the exterior by way of small openings in the body surface—anal pores and other cell openings. Elimination in protists is carried out passively and therefore requires little or no expenditure of metabolic energy on the part of the organism.

Plants. Plants are not generally considered to possess special mechanisms of elimination. Photosynthetic activities of green plants, in the presence of light, produce oxygen, which diffuses out through openings in the leaves (stomata) or through the cell walls of roots and other plant structures. Excess water passes to the exterior via similar routes and is eliminated by processes of guttation (droplet exudation) and transpiration (evaporation of water from plant surfaces).

Green plants in darkness or plants that do not contain chlorophyll produce carbon dioxide and water as respiratory waste products. Carbon dioxide is secreted in the same manner as oxygen via diffusion through stomata and cell walls. Materials that are exuded by some plants—resins, saps, latexes, etc.—are forced from the interior of the plant by hydrostatic pressures inside the plant and by absorptive forces of plant cells. These forces are passive in nature, and exudation requires no energy expenditure on the part of the plant.

Animals. Diverse mechanisms have evolved that enable the various animal species to inhabit a wide range of environments. In animals whose bodies consist of a single layer of cells, waste disposal is accomplished principally by diffusion from the site of waste production to the outside environment. This method is efficient when the distances over which wastes diffuse are relatively short, when there is a high surface area to volume relationship, and when the rate of waste production is relatively low. In more complex animals, however, waste elimination by diffusion through the body wall to the exterior is less efficient because individual cells are farther removed from the exterior surface of the organism. The presence of specialized mechanisms of elimination in higher animals enables wastes to be rapidly transported to the exterior surface of the body (see below *Vertebrate excretory systems*).

Efficiency of the diffusion mechanism of waste disposal

Sponges. Phylogenetically, the sponges (phylum Porifera) are the simplest of animals. They are multicellular and composed of specialized cells, arranged in a single layer, for the maintenance of life processes. Elimination in these aquatic animals proceeds by diffusion of gaseous wastes into the surrounding water and by the ejection of solid wastes and indigestible material from the digestive cells into the streams of water that constantly flow through the animal.

Cnidarians. The jellyfishes, coral animals, ctenophores, and comb jellies have a rudimentary canallike cavity in their two-layered bodies for the ingestion, digestion, and egestion of food and wastes. Gaseous wastes are eliminated by diffusion, and solid wastes in dissolved or undissolved form pass out through an opening in the body wall that serves the dual purposes of food intake and waste elimination.

Flatworms. Flatworm bodies consist of three layers of cells, and in this aquatic group elimination is similar to that of the less complex animals. Food and solid wastes enter and leave through a common opening in the well-developed digestive tract, which consists of a mouth, pharynx, and gastrovascular cavity.

Nemertine worms. The digestive and excretory system of the aquatic proboscis worms is more efficient than that of lower animals in that a well-defined mouth, intestine, and excretory opening (anus) permit the one-way flow of food and waste through the animal. Egested food and nitrogenous wastes, which are secreted into the intestine, are passed along it to the anus by peristaltic waves of the smooth muscle lining the intestinal walls. The efficiency of waste elimination is increased by the presence of a well-defined circulatory system, which enhances the carriage of wastes to the intestine.

Nematodes. An additional excretory structure has evolved in the roundworms. Excretory canals located on both sides of the intestine facilitate waste disposal by carriage of material to an excretory pore in the body wall.

Other invertebrates. In invertebrates, increasing structural complexity is accompanied by more efficient waste-disposal mechanisms. In the phylum Mollusca (clams, snails, oysters, mollusks, octopuses, and squids), gills add another more efficient channel for waste disposal. A heart increases the rate of flow in the circulatory system and speeds the transport of wastes to the gills. An excretory, kidneylike organ removes metabolic wastes from the circulation and body fluid prior to excretion. All basic mechanisms of excretion are thus present in relatively simple animals. As invertebrates become more specialized and complex, as in the arthropods (insects, crabs, and other joint-legged animals) and annelids (segmented worms), adaptations in excretion methods allow survival in non-aquatic environments.

Vertebrates. Though the wastes produced by vertebrates differ little qualitatively from those of higher invertebrates, increased structural complexity and body size, in combination with environmental adaptations, require more specific waste-disposal mechanisms in order to maintain a constant internal environment. The presence of highly efficient, water-retaining kidneys, for example, permits vertebrates to inhabit arid, hot regions of the earth. It seems proper, within the vertebrate group, to consider elimination schemes as variations of mechanisms common to all higher animals but which enable animals to inhabit widely diversified environments. (F.C.Ke./Ed.)

General features of excretory structures and functions

The physiological process by which an organism disposes of its nitrogenous by-products is called excretion. The mechanisms for that process constitute the excretory systems, particularly such organs of vertebrate animals as elaborate and complicated as the kidney and its associated urinary ducts.

Definitions and distinctions

The meaning of excretion is most easily understood in the context of vertebrate physiology. The animal swallows food (ingestion). In the stomach and intestine some of the food is broken down into soluble products (digestion) that are absorbed into the body (assimilation). In the body these soluble products undergo further chemical change (metabolism); some are used by the body for growth, but most provide energy for the various activities of the body. Metabolism involves the uptake of oxygen and the elimination of carbon dioxide in the lungs (respiration).

Besides carbon dioxide, compounds of nitrogen arise from metabolism and are eliminated, chiefly by the kidney, in the urine (excretion). Food not digested is eliminated through the anus (defecation).

These processes are characteristic of animals in general, but not of plants. A green plant takes in carbon dioxide from the atmosphere and nitrogen (as nitrate) from the soil. It uses the energy of sunlight to build these nutrients into the materials required for growth and in the process gives out oxygen (see PHOTOSYNTHESIS).

In a broad sense animals live on plants, and the by-products of animals are the raw materials on which plants grow. These mutually supporting activities of plants and animals are kept precisely in balance by the activities of bacteria. Bacteria convert the urine and feces of animals (and also the dead bodies of both plants and animals) to carbon dioxide and nitrate. In the living world as a whole, carbon and nitrogen are in continuous circulation, driven by the energy of sunlight (see BIOSPHERE). Over most of the earth, for most of time, no by-products accumulate. Occasionally the cycles get out of balance, as they must have done during the prehistoric period when coal was being formed in the earth as a consequence of the failure of bacteria to decompose all the remains of plants.

PRODUCTS OF EXCRETION

Although every type of organism takes in some materials and eliminates others, excretion in the strict sense is a process found only in animals. For the purposes of this article excretion will be taken to mean the elimination of nitrogenous by-products and the regulation of the composition of the body fluids.

The primary excretory product arising naturally in the animal body is ammonia, derived almost entirely from the proteins of the ingested food. In the process of digestion proteins are broken down into their constituent amino acids. Some of the amino-acid pool is then used by the animal to build up its own proteins, but a great deal is used as a source of energy to drive other vital processes. The first step in the mobilization of amino acids for energy production is deamination, the splitting off of ammonia from the amino-acid molecule. The remainder is oxidized to carbon dioxide and water, with the concomitant production of the energy-rich molecules of adenosine triphosphate (ATP; see METABOLISM).

Since excessive levels of ammonia are highly toxic to most animals, they must be effectively eliminated. This is no problem in small aquatic animals because ammonia rapidly diffuses, is highly soluble in water, and escapes easily into the external medium before its concentration in the body fluids can reach a dangerous level. But in terrestrial animals, and in some of the larger aquatic animals, ammonia is converted into some less harmful compounds (detoxication). In mammals, including humans, it is detoxified to urea, which may be considered as being formed by the condensation of one molecule of carbon dioxide with two molecules of ammonia (though the biochemistry of the process is more complex than that). Urea is highly soluble in water but cannot be excreted in a highly concentrated solution because of the osmotic pressure (see below) it would exert. Because the conservation of water is important for most terrestrial animals, it is not surprising that many of them have evolved more economical methods for disposing of nitrogenous by-products. Birds, reptiles, and terrestrial insects excrete nitrogen in the form of uric acid, which is highly insoluble in water and can be removed from the body as a thick suspension or even as a dry powder.

EXCRETORY MECHANISMS

Osmotic pressure. In order to understand the advantages of the excretion of uric acid over urea it is necessary to know something about the behaviour of molecules in solution. Molecules of a solute (*e.g.*, salt, sugar) in water tend to move by diffusion from a region where they are in high concentration to one where they are in low concentration, and molecules of water tend to move in the opposite direction. If a porous membrane is placed between these regions, the movements of molecules may be variously restricted depending upon their size in relation to the size of the submicroscopic pores in the membrane. The passage of water molecules from pure water through such a membrane into a solution containing molecules that are too large to pass is called osmosis, a process that takes place spontaneously and does not require energy. This process can be reversed by applying hydrostatic pressure to the solution, a process that does require energy. The level of hydrostatic pressure at which there is no net movement of water in either direction across the membrane is called the osmotic pressure of that particular solution; the greater the concentration of dissolved molecules in the solution the greater is its osmotic pressure and the greater the force needed to remove water from it.

The osmotic process

These principles explain why more energy is required to remove water from urine containing urea than from urine containing the same weight of uric acid. The molecule of urea is smaller than that of uric acid, so that with the same weight, there are more molecules of urea to exert osmotic pressure. But an even more important difference is that whereas urea is highly soluble in water, uric acid is not. As water is progressively removed from a solution of urea, the osmotic pressure opposing further removal progressively increases. For the uric acid solution, however, as water is removed, the uric acid comes out of solution, or precipitates, when the solution is at a lower concentration, and, therefore, at a lower osmotic pressure, which does not increase further.

Regulation of water and salt balance. The mechanisms of detoxication that animals use are related to their modes of life. This is true, with greater force, of the mechanisms of homeostasis, the ability of organisms to maintain internal stability. A desert-living mammal constantly faces the problem of water conservation; but a freshwater fish faces the problem of getting rid of the water that enters its body by osmosis through the skin. At the level of the individual cell, whether it is the cell that constitutes a unicellular organism or a cell in the body of a multicellular organism, the problems of homeostasis present themselves in similar ways.

To continue its intracellular processes a cell must maintain an intracellular chemical environment in which the concentrations of various ions (see below) are kept constant in the face of changing concentrations in the medium surrounding the cell. This is the task of the cell membrane. In the higher animals the task is easier since cells in the interior of their bodies are bathed in an internal medium—the blood—whose composition is regulated so as to minimize the effects of changes in the external medium. This regulatory function is undertaken by specialized cells or organs such as the kidney, thereby lessening the regulatory burden of the other cells of the body.

The biological necessity for homeostatic mechanisms is particularly urgent for controlling the inorganic components of cells and body fluids. Inorganic salts can exert even greater osmotic pressure against membranes impermeable to them than urea. This is so because, under the conditions in the body, they are almost completely dissociated into their component ions. For example, a molecule of common salt (sodium chloride) is dissociated into two inorganic ions—a positively charged sodium ion and a negatively charged chloride ion—both of which can exert osmotic pressure.

Aside from their osmotic effects, inorganic ions have profound effects upon metabolic processes, which in general will take place only in the presence of appropriate concentrations of these ions. The most important inorganic ions in organisms are the positively charged hydrogen, sodium, potassium, calcium, and magnesium ions, and the negatively charged chloride, phosphate, and bicarbonate ions. The membranes of cells are not completely impermeable to these ions and are in fact endowed with the ability to transport ions between the inside and outside of the cell, whereby they control the concentrations of ions within the cells; when such transport is in the direction that requires a supply of energy, it is called active transport (see CELLS: *The plasma membrane*).

Active transport of ions

Osmotic regulation is the maintenance of the normal concentration of the body fluids; *i.e.*, the total concentration of all dissolved substances (solutes) that would exert osmotic pressure against a membrane impermeable to them. Osmotic regulation controls the amount of water in the body fluids relative to the amount of osmotically active solutes. Ionic regulation is the maintenance of the concentrations of the various ions in the body fluids relative to one another. There is no consistent distinction between the two processes; organs that participate in one process at the same time participate in the other.

Principal excretory structures. Whereas the kidney is the principal organ subserving both nitrogenous excretion and osmotic and ionic regulation in the mammalian body, these functions are not always performed by a single organ in other animals. As indicated earlier, primitive aquatic animals do not require any special provision for nitrogenous excretion. But by reason of their permeable skins they may have serious problems of osmotic and ionic regulation, especially in fresh water, where cells covering the surface of the body have the ability to actively transport salts into or out of the animal. In some cases these nonkidney regulatory activities are performed by certain specialized cells; *e.g.*, in the gills of fishes (see below). In other cases, specialized cells are assembled into organs of salt uptake or salt elimination; *e.g.*, the salt glands of birds (see below).

This dispersal of the regulatory function may be the primitive condition, for it is only in the more highly evolved terrestrial animals that the regulatory function is restricted to an excretory system proper. This is readily understandable in view of the need of terrestrial animals to conserve water. This evolutionary development toward one system reaches its climax in the birds, reptiles, and terrestrial insects, in which all the processes of elimination that might involve loss of water—defecation, nitrogenous excretion, and ionic regulation—converge upon the same final channel.

For the excretory organs of a wide variety of vertebrate and invertebrate animals, there is evidence that the primary process of urine production is nonselective, in that in those animals all substances dissolved in their body fluids, with the possible exception of proteins, are found in the primary urine. In many animals the primary urine is produced by filtration from the blood. At a later stage, substances in the primary urine that are useful to the body are selectively reabsorbed. In addition, a few substances are known to be actively transported (secreted) into the urine.

The nonselective formation of primary urine serves another aspect of excretion: the elimination of foreign substances. Mechanisms of active transport are highly specific to the substances transported. All dissolved constituents of the body fluids pass freely into the primary urine, and then specific reabsorptive mechanisms gather up the "wanted" substances. In this way a natural economy automatically eliminates "unwanted" substances simply by not providing mechanisms for their reabsorption.

INVERTEBRATE EXCRETORY SYSTEMS

Regulation of body fluids

In their detoxication mechanisms, so far as they have been investigated, the invertebrates in general conform to the principles applying to all animals, namely, that aquatic forms get rid of ammonia by diffusion through the surface of the body; terrestrial forms convert ammonia to uric acid. This implies that in aquatic forms the excretory organ is principally of importance for the composition of their body fluids. Normally, the body fluids of marine invertebrates have the same concentration as seawater; they usually differ, however, in the proportions of ions, with relatively more potassium and less magnesium than seawater. Furthermore, their urine normally has the same concentration as seawater, but correspondingly it contains less potassium and more magnesium. In freshwater invertebrates the urine is commonly, though not invariably, more dilute than the body fluids. By producing dilute urine a freshwater invertebrate conserves the salt content of its body while eliminating the water that enters its body by osmosis through its water-permeable surface.

Some invertebrates, notably echinoderms, cnidarians, and sponges, have no organs to which an excretory function can be confidently ascribed. Since all of these animals are aquatic, it is reasonable to suppose that they excrete nitrogen (as ammonia) by simple diffusion. Their body fluids (where present) are closely similar to seawater in composition, and it may be presumed that regulation operates only at the cellular level.

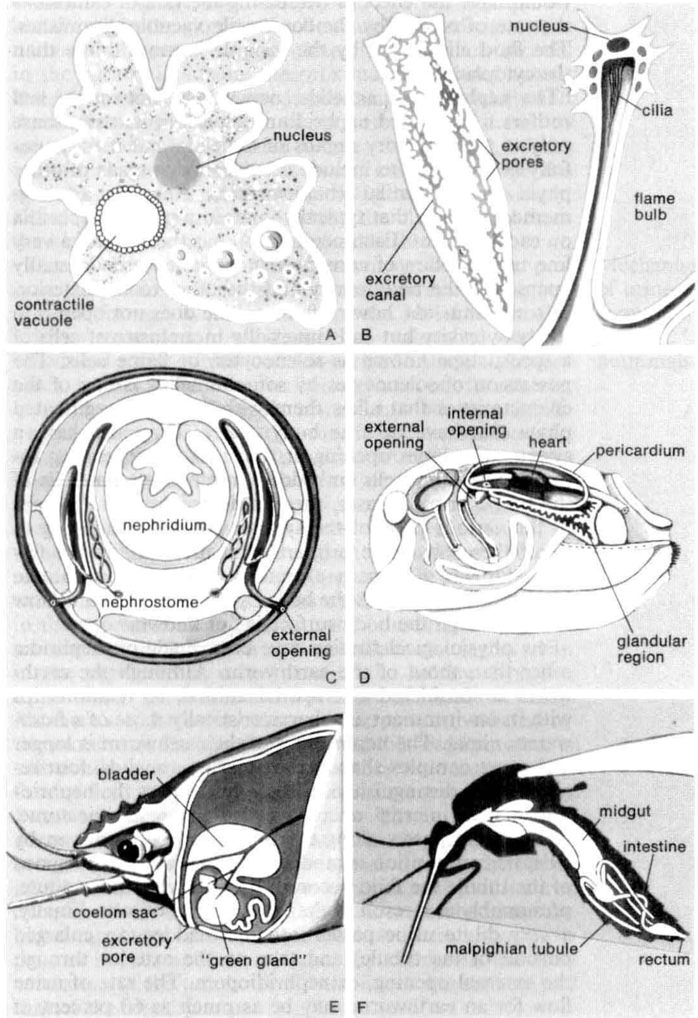

Figure 1: *Invertebrate excretory systems.*
(A) Contractile vacuole of an amoeboid protozoan. (B) Protonephridial system of a flatworm, with enlargement of a single-celled flame bulb that terminates the tubules of excretory canals. (C) Metanephridial system of an earthworm, with paired nephridia in one segment. (D) Renal organ of a clam, cut away to show glandular region. (E) Renal system of a crayfish, exposed through cut-away shell. (F) Excretory system of a mosquito.

The excretory organs of other invertebrates are of diverse evolutionary origin. This is not to say, however, that each invertebrate phylum has evolved its own particular type of excretory organ; rather, there appear to be five main types of invertebrate excretory organ: contractile vacuole, nephridium, renal gland, coxal gland, and malpighian tubule.

The contractile vacuoles of protozoans. Some protozoan animals possess an organelle having the form of an internal sac, or vacuole, which enlarges by the accumulation of a clear fluid and then discharges its contents to the exterior. The cycle of filling and emptying may be repeated as frequently as every half minute. The chief role of the contractile vacuole appears to be in osmotic regulation, not in nitrogen excretion.

Contractile vacuoles occur more frequently and are more active in freshwater species than in closely related marine species. In fresh water, the concentration of dissolved substances in the cell is greater than in the external medium, and the cell takes in water by osmosis. If the contractile vacuole is put out of action, the cell increases in volume. If the concentration of salts in the medium increases—which would have the effect of decreasing the rate of osmosis—the rate of output by the contractile vacuole diminishes. The fluid eliminated by the vacuole is more dilute than the cytoplasm.

The nephridia of annelids, nemertines, flatworms, and rotifers. The word nephridium applies in its strict sense only to the excretory organs of annelids, but it may usefully be extended to include the excretory organs of other phyla having similar characteristics. Annelids are segmented animals that typically contain a pair of nephridia on each segment. Each nephridium has the form of a very fine tubule, often of considerable length; one end usually opens into the body cavity and the other to the exterior. In some annelids, however, the tubule does not open into the body cavity but ends internally in a cluster of cells of a special type known as solenocytes, or flame cells. The possession of solenocytes by some annelids is one of the characteristics that allies them with other nonsegmented phyla that have no true body cavity. They also have a system of tubules opening at the surface and ending internally in flame cells embedded among the other cells of the body. In most cases, there is no regular arrangement of the various parts of the system. Animals belonging to all of these phyla are primarily aquatic, and, in the few cases known, the main excretory product is ammonia. How much of it leaves the body by the nephridia and how much through the body surface is not known.

Few physiological studies have been made on nephridia other than those of the earthworm. Although the earthworm is considered a terrestrial animal, its relationships with its environment are characteristically those of a freshwater animal. The nephridium of the earthworm is longer and more complex than that of marine annelids, four regions being distinguishable. Body fluid enters the nephridium via an internal opening called the nephridiostome. As the fluid passes along the tubule, probably driven by cilia, its composition is modified. In the two lower regions of the tubule the fluid becomes progressively more dilute, presumably as a result of the reabsorption of salts. Finally, a very dilute urine passes into the bladder (an enlarged portion of the tubule) and then to the exterior through the external opening, or nephridiopore. The rate of urine flow for an earthworm may be as much as 60 percent of its body weight in a period of 24 hours.

The renal glands of mollusks. The anatomical form of the renal gland varies from one class of mollusks to another, but a common plan is clearly evident. The renal gland is a relatively wide tube opening from a sac (the pericardium) surrounding the heart, at one end, and to the mantle cavity (effectively to the exterior) at the other. There is a single pair of renal glands; in some forms one member of the pair may be reduced or absent. Clams have the simplest arrangement; the region nearest to the pericardium has glandular walls and gives way to a nonglandular, wider tube that extends to the urinary opening.

The common plan of the renal gland

The vast majority of mollusks are aquatic and excrete nitrogen in the form of ammonia. In octopuses, however, nitrogen is excreted as ammonium chloride, which is quite strongly concentrated in the urine. Terrestrial snails and slugs excrete uric acid but may also excrete ammonia when living in moist surroundings.

In all mollusks so far investigated the primary process in urine production appears to be filtration of the blood. This may take place through the wall of the heart into the pericardium, or from blood vessels that supply the glandular part of the renal gland. The composition of the primary urine may be altered by reabsorption or secretion, or both. In freshwater mollusks salts are reabsorbed in the glandular tube and in the wide tubule, and the final urine is more dilute than the blood. The rate of urine flow is high, up to 45 percent of the body weight per day in the freshwater mussel. In marine mollusks the urine has the same concentration as the blood, but (in the few cases examined) its ionic composition is different.

The coxal glands of aquatic arthropods. Coxal glands are tubular organs, each opening on the basal region (coxa) of a limb. Since arthropods are segmented animals, it is reasonable to suppose that the ancestral arthropod had a pair of such glands in every segment of the body. In modern crustaceans there is, as a rule, only a single pair of glands, and in higher crustaceans these open at the bases of the antennae. Each antennal gland is a compact organ formed of a single tubule folded upon itself. When unraveled the tubule is seen to comprise three or four easily recognizable regions. The tubule arises internally as a small sac, the coelomic sac, which opens into a wider region, the labyrinth, having complex infoldings of its walls. The labyrinth opens either directly into the bladder, as in marine lobsters and crabs, or into a narrow part of the tubule, the canal, which in turn opens into the bladder, as in freshwater crayfishes.

Ion concentration in urine

The coelomic sac, well supplied with blood vessels, gives evidence that the primary process in urine production is filtration of the blood through the wall of the coelomic sac in a manner analogous to filtration in the glomerulus and Bowman's capsule of the vertebrate kidney (see below). In lobsters and marine crabs the urine in all parts of the organ has the same ion concentration as the blood. In freshwater crayfishes the urine has the same concentration as far as the end of the labyrinth; from that point on reabsorption takes place in the canal and the urine leaves the body as a very dilute solution. The addition of the canal to the system demonstrates one way crustaceans have adapted to life in fresh water. But this is not the only way in which the regulatory problem is solved in freshwater crustaceans. In freshwater crabs, for example, there is a great decrease in the water permeability of the surface (principally the gills) so that water enters by osmosis quite slowly. In contrast to the rate of urine flow in a freshwater crayfish (about 5 percent of the body weight per day), that of the freshwater crab is 100 times less (about 0.05 percent). In the crab the urine has the same concentration as the blood, but because the flow is so small the salt loss via the urine is negligible. A few semiterrestrial crabs are known to produce urine more concentrated than the blood.

In all crustaceans for which analyses are available the concentrations of ions in blood and urine differ. At a urine flow of 5 percent of the body weight per day the activities of the antennal glands are certainly capable of effecting changes in the composition of the blood. These activities are somehow coordinated with salt uptake by the cells of the body surface so as to subserve homeostasis. The role of the antennal glands in nitrogenous excretion seems to be unimportant.

The malpighian tubules of insects. Although some terrestrial arthropods (*e.g.*, land crabs, ticks) retain the coxal glands of their aquatic ancestors, others, the insects, have evolved an entirely different type of excretory system. The malpighian tubules, which vary in number from two in some species to more than 100 in others, end blindly in the body cavity (which is a blood space) and open not directly to the exterior but to the alimentary canal at the junction between midgut and hindgut. The primary urine issuing from the malpighian tubules has to pass through the rectum before it leaves the insect's body, and in the rectum its composition is markedly changed. The insect excretory system therefore comprises the malpighian tubules and the rectum acting together.

Primary urine formation in insects

The malpighian tubules are bathed in the insect's blood, but since they are not rigid it is impossible for any hydrostatic pressure to be developed across their walls, such as could bring about filtration. The primary urine is formed by a process of secretion in the following way: Potassium ions are actively transported from the blood into the cavity of the tubule and are necessarily followed by negatively charged ions so as to maintain electroneutrality. In turn, water follows the ions, probably by osmosis, and various other substances—sugars, amino acids, and urate ions—also enter the primary urine by diffusion from the blood.

The primary urine, together with soluble products of digestion and insoluble indigestible matter from the midgut, then passes to the rectum. There (or in some insects at an earlier stage) the urine is acidified and the soluble urate is thereby converted to insoluble uric acid, which comes out of solution. Water is then reabsorbed together with the soluble products of digestion and other useful substances, including the bulk of the ions that entered the primary urine. In insects that live in dry surroundings the rectum has remarkable powers of reabsorption, its contents finally being voided as hard, dry pellets containing solid uric acid.

The activity of the excretory system in insects is under hormonal control. This has been most clearly demonstrated in the case of *Rhodnius,* a bloodsucking bug. Immediately after the ingestion of a blood meal there is a rapid flow of urine whereby most of the water taken in with the blood meal is eliminated. The distension of the body after ingestion is the stimulus that causes certain cells in the central nervous system to release a hormone that acts upon the malpighian tubules to promote a brisk flow of primary urine.

VERTEBRATE EXCRETORY SYSTEMS

The kidney and its associated ducts are the excretory system of the mammal, and, as already noted, most of the nitrogenous waste arising in the mammalian body is excreted as urea. Other nitrogenous compounds regularly present in the urine in smaller amounts are uric acid (or the closely related compound allantoin) and creatinine; both of these arise mainly as by-products of the renewal and repair of tissues.

In birds, reptiles, and amphibians the kidneys are compact organs, as they are in mammals, but in fishes they are narrow bands of tissue running the length of the body (see below under *Evolution of the vertebrate excretory system*). In amphibians, as in mammals, the main excretory product is urea. In birds and reptiles it is uric acid. In most fishes the main excretory product is ammonia.

Mammals. The mammalian kidney (Figure 2) is a compact organ with two distinct regions: cortex and medulla. The functional unit of the kidney is the nephron. Each nephron (Figure 2) is a tubular structure consisting of four regions. It arises in the cortex as a small vesicle about one-fifth of a millimetre (0.008 inch) in diameter, known as Bowman's capsule, into which projects a tuft of capillary blood vessels, the glomerulus. Bowman's capsule is continuous with the proximal convoluted tubule, which also lies in the cortex. Following the proximal convoluted tubule is the loop of Henle, which descends into the medulla and then runs straight up again to the cortex where it continues as the distal convoluted tubule. A collecting tubule, into which several nephrons open, courses through the medulla to open a wide cavity, the pelvis of the kidney. From the pelvis the ureter leads to the bladder, and from the bladder the urethra leads out of the body.

From J.M. Forrester, R. Passmore, and J.S. Robson (eds.), *A Companion to Medical Studies*, vol. 1, 3rd ed. (1985); Blackwell Scientific Publications Ltd

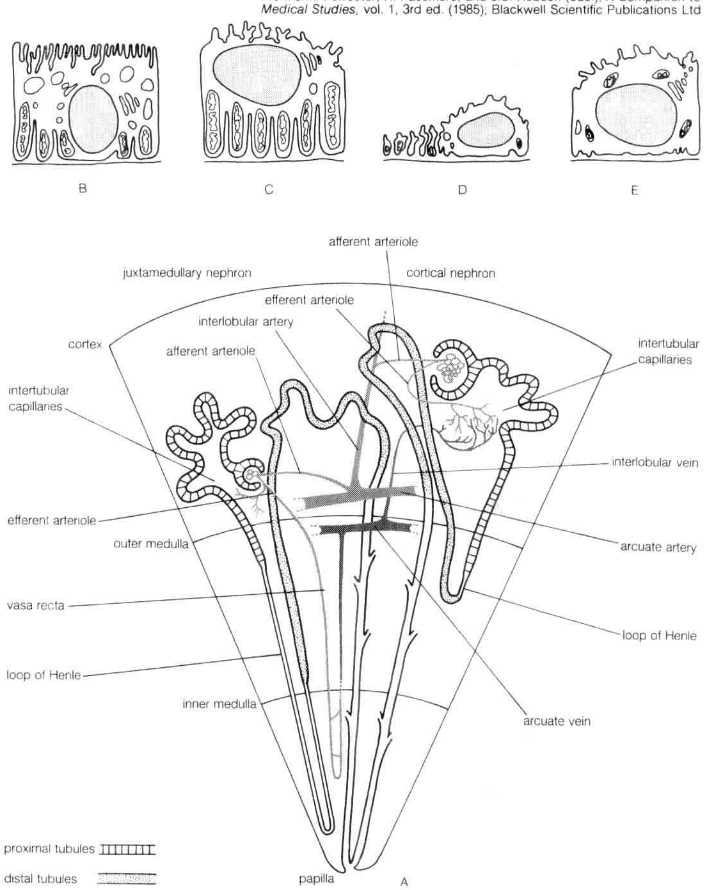

Figure 2: *The histology of the mammalian kidney.*
Diagram (A) shows the constituent parts of nephrons and their blood supply. Typical cells of the nephron are shown from (B) the proximal convoluted tubule; (C) the distal convoluted tubule; (D) the thin limb of the loop of Henle; and (E) the collecting duct. In each case the cell's luminal surface is at the top and the external surface is at the bottom.

Mechanism of urine formation in mammals

The mechanism of urine formation involves three processes: filtration, reabsorption, and secretion. Primary urine is formed by filtration from the blood. From this primary urine certain substances are reabsorbed into the blood and other substances are secreted into the primary urine from the blood. The word secretion is used by renal physiologists to imply transport, other than by filtration, from the blood to urine. Filtration implies that all molecules below a certain size are allowed to pass nonselectively into the primary urine; reabsorption and secretion imply the existence of specific mechanisms for the transport of specific substances.

The membrane covering the glomerulus allows the passage of water and all the constituents of the blood plasma except proteins. The glomerular capillaries are intercalated in the course of an artery, with the consequence that the pressure of the blood in these capillaries is higher than in the capillaries in other parts of the kidney. Opposed to the blood pressure are the pressure of the fluid within Bowman's capsule and the osmotic pressure exerted by the proteins of the blood plasma; but the blood pressure is sufficiently in excess of the sum of these to ensure a rapid flow of fluid, the glomerular filtrate or primary urine, into Bowman's capsule. The glomerular filtrate contains the nitrogenous compounds ultimately to be excreted in the urine. As the glomerular filtrate passes through the proximal tubule, 80 percent of the water, and many substances of value to the body (*e.g.,* glucose), is reabsorbed into the blood capillaries surrounding the tubule. This reabsorptive process is accomplished without any change in the concentration of the tubular fluid, which remains the same as that of the blood plasma.

After traversing the loop of Henle, the remaining 20 percent of the glomerular filtrate passes into the distal tubule, where further reabsorption, notably of salts, takes place. If this is accompanied by a proportionate reabsorption of water, the tubular fluid remains at the same concentration as the blood plasma, but if the reabsorption of water is restricted, as it may be in certain circumstances (see below), the tubular fluid becomes more dilute than the blood plasma. Under normal physiological conditions some 15 percent of the glomerular filtrate is reabsorbed in the distal tubule. Most of the remaining 5 percent is reabsorbed in the collecting tubule. The amount of fluid, at this point called urine, that reaches the pelvis of the kidney is only 1 percent of the volume originally filtered at the glomerulus; but it contains nearly all the nitrogenous waste of the filtrate in concentrated solution. A few substances are also secreted from the blood through the walls of the tubule into the tubular fluid.

The action of the loop of Henle is more difficult to describe, and a full account is given below under *The human excretory system.*

Characteristics of the uric acid of birds and reptiles

Birds and reptiles. The main excretory product of birds and reptiles is uric acid. Since their glomeruli are relatively small, so also is their daily volume of urine. Not highly concentrated by mammalian standards—although it may be turbid with crystals of uric acid—the urine of birds and reptiles is conducted not to a urinary bladder but to the terminal portion of the alimentary canal, the cloaca; from the cloaca it is voided with the feces. Like mammals, and unlike the lower vertebrates, birds and reptiles have skins impermeable to water and thus are well adapted to terrestrial life. The relative inability of the kidney to produce concentrated urine is compensated for in birds that possess salt glands, which remove excess salt from their bodies. These organs are modified tear glands that discharge a concentrated solution of sodium chloride through the nostrils. Salt glands enable marine birds to drink seawater with no ill effects.

Amphibians. Direct evidence for the occurrence of filtration at the glomerulus was first provided by experiments on the amphibian kidney. Although amphibians are formally given the status of terrestrial animals, they are poorly adapted to life on land. They excrete nitrogen in the form of urea and cannot produce urine more concentrated than the blood. Their skins are permeable to water. On land amphibians are liable to lose water very rapidly by evaporation. In fresh water they suffer entry of water by osmosis, which is counteracted by the excretion of a large volume of dilute urine. The urine is stored in a large bladder before being voided, providing a reserve of water the animal can use when it comes on land.

When an amphibian leaves the water, a number of physiological adjustments are made that have the effect of conserving water. The rate of glomerular filtration is reduced by restriction of the blood supply, and this together with an increased release of antidiuretic hormone results in the production of a small volume of urine of the same concentration as the blood. Antidiuretic hormone (ADH, also known as vasopressin, which increases the permeability of the distal and collecting tubules to water) also increases the permeability of the bladder to water and allows the stored urine to be reabsorbed into the body.

Fishes. The homeostasis problem is the same for freshwater fishes as for other freshwater animals. Water enters the body by osmosis and salts leach out. To compensate, the kidney (which has large glomeruli) produces a relatively large amount of dilute urine (about 20 percent of the body weight per day). This serves to remove the water but by itself is insufficient to prevent gradual loss of salts. Extremely diluted salts are taken up from the fresh water and transported directly into the blood by certain specialized cells in the gills. Nitrogenous excretion is no problem: some ammonia is carried away in the large volume of dilute urine, but most of it simply escapes to the external medium by diffusing through the gills.

Excretion in marine fishes

By contrast, the homeostasis problem of marine fishes is unlike that of most marine animals. The salt content of the blood of marine fishes is less than half that of seawater (see below *Evolution of the vertebrate excretory system*); consequently, marine fishes tend to lose water and gain salt. This, it would seem, could be compensated most easily by the excretion of urine more concentrated than the blood, but the kidneys of fishes are not able to do this. In marine bony fishes the kidney has small glomeruli and produces only a small amount (about 4 percent of the body weight per day) of urine, which is of the same concentration as the blood. The fish replaces its lost water by continually swallowing seawater, and the special cells of the gills, working in reverse, reject salt to the external medium. Nitrogen is excreted mostly as ammonia but also as another detoxication product, trimethylamine oxide.

In sharks and rays ammonia is converted to urea, and urea plays an important role in homeostasis. Urea is retained in the blood to such an extent that the blood is slightly more concentrated than seawater. Thus loss of water by osmosis is prevented and these fish have no need to swallow seawater. Any excess of salt in their bodies is removed via the rectal gland, functionally analogous to the salt gland of birds.

Osmotic and ionic regulation in fishes is under hormonal control. This has been studied particularly in fishes such as eels and salmon, which are able to move between fresh water and seawater.

Evolution of the vertebrate excretory system. Studies of the embryonic development of primitive vertebrates, such as the dogfish shark, clearly show that the excretory system arises from a series of tubules, one pair in every segment of the body between the heart and the tail. This continuous series of tubules constitutes the archinephros, the name implying that the kidney of the ancestral vertebrate had some such form as this. Each tubule opens internally to the body cavity and may, in the remote past, have opened separately to the exterior; but in all living vertebrates the tubules open on each side into a longitudinal duct, the archinephric duct. At the posterior end of the body cavity the two archinephric ducts unite before opening to the exterior. Later in development, Bowman's capsule arises as a diverticulum of each tubule, subsequently becoming indented by the glomerulus. Eventually, the tubules usually lose their internal openings to the body cavity. The most anterior tubules of the archinephros (pronephros) usually degenerate in the adult.

Relationship between excretory and reproductive systems

These ducts and tubules also subserve the reproductive function, and for this reason they are also called the urogenital system. The extent to which the ducts and tubules are shared is greater in the male than in the female. In the male the spermatic tubules of the testis connect with the kidney tubules in the middle region of the archinephros (mesonephros), and in some vertebrates (*e.g.*, the frog) where there is no development of the posterior region (metanephros), the tubules of the mesonephros serve to convey both urine and sperm. In the reptiles, birds, and mammals there is greater separation of function, the mesonephros being exclusively genital and the metanephros being exclusively urinary (see Figure 3).

In the female, even in the lower vertebrates, the two systems are confluent only at the posterior end. It has been held that the oviduct is a derivative of the archinephric duct, but the evidence for this is not compelling.

In primitive marine animals the blood is almost identical with seawater in composition; in typical freshwater animals the concentration of the blood is about half that of seawater. Many originally marine animals have evolved the ability to live in fresh water; relatively few animals, after having thus evolved, have returned to the sea, and in none of them has the blood returned to its original "seawa-

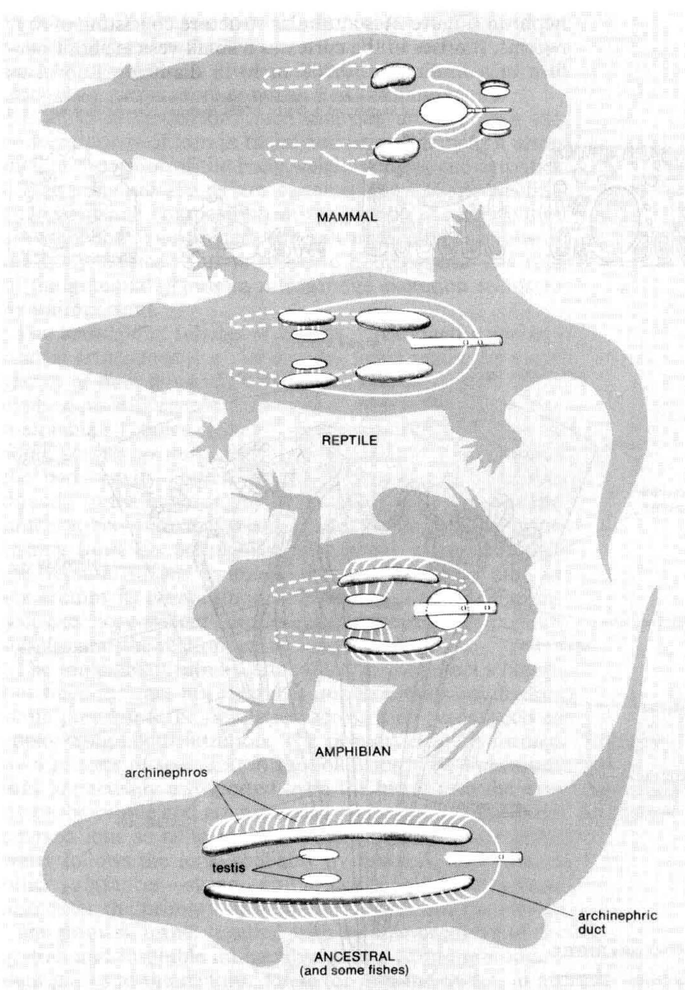

Figure 3: *Evolution of the urogenital system in male vertebrates.* The ancestral archinephric condition has evolved in different patterns for the amphibians, reptiles, and mammals (birds have a pattern similar to reptiles). The broken lines indicate the change in ancestral plan in each of the major vertebrate classes.

ter" concentration. The earliest fossil vertebrates are found in marine deposits, but the fossil record shows clearly that the early evolution of fishes took place in fresh water. It is assumed that the blood of early freshwater fishes, like that of other freshwater animals, was osmotically equivalent to half-strength seawater. The sharks and rays returned to the sea during the Carboniferous Period, and no doubt at that time they evolved the device of urea retention. The bony fishes returned to the sea later, in the Mesozoic Era, and solved their problem by swallowing seawater and rejecting excess salt at the gills. (J.A.R./Ed.)

The human excretory system

In many respects the human excretory, or urinary, system resembles those of other mammalian species, but it has its own unique structural and functional characteristics. The terms excretory and urinary emphasize the eliminatory function of the system. The kidneys, however, both secrete and actively retain within the body certain substances that are as critical to survival as those that are eliminated.

The system contains two kidneys, which control the electrolyte composition of the blood and eliminate dissolved waste products and excess amounts of other substances from the blood; the latter substances are excreted in the urine, which passes from the kidneys to the bladder by way of two thin muscular tubes called the ureters. The bladder is a sac that holds the urine until it is eliminated through the urethra (Figure 4).

THE KIDNEYS

General description and location. The kidneys are bean-shaped, reddish brown paired organs, concave on one long side and convex on the opposite. They are normally located high in the abdominal cavity and against its back wall, lying on either side of the vertebral column between the levels of the 12th thoracic and third lumbar vertebrae, and outside the peritoneum, the membrane that lines the abdomen.

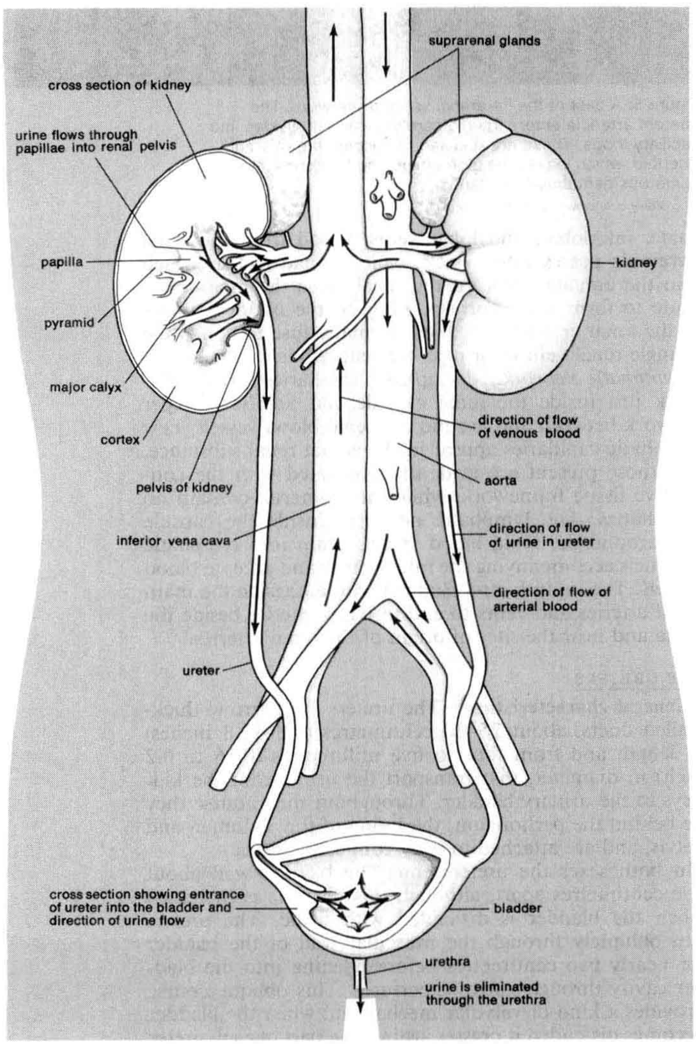

Figure 4: Human renal excretory system.

The long axes of the kidneys are aligned with that of the body, but the upper end of each kidney (pole) is tilted slightly inward toward the backbone (vertebral column). Situated in the middle of the medial concave border is a deep vertical cleft, the hilus, which leads to a cavity within the kidney known as the renal (kidney) sinus. The hilus is the point of entry and exit of the renal arteries and veins, lymphatic vessels, nerves, and the enlarged upper extension of the ureters.

Renal vessels and nerves. The renal arteries arise, one on each side, from the abdominal aorta at a point opposite the upper border of the second lumbar vertebra (*i.e.*, a little above the small of the back). Close to the renal hilus each artery gives off small branches to the adrenal gland and ureter and then branches into anterior and posterior divisions. The large veins carrying blood from the kidneys usually lie in front of the corresponding arteries and join the inferior vena cava almost at right angles. The left vein is longer than the right vein because the inferior vena cava lies closer to the right kidney.

The kidneys are supplied with sympathetic and parasympathetic nerves of the autonomic nervous system, and the renal nerves contain both afferent and efferent fibres (afferent fibres carry nerve impulses to the central nervous system; efferent fibres, from it).

Internal configuration. A cross section of a kidney reveals the renal sinus and two layers of kidney tissue distinguishable by their texture and colour. The innermost tissue, called the renal medulla, forms comparatively dark cones, called renal pyramids, with bases outward and apexes projecting, either singly or in groups, into the renal sinus. Each projection of one or more pyramid apexes into the sinus is known as a renal papilla. The bases of these pyramids are irregular, with slender striations extending toward the external kidney surface. The paler, more granular tissue external to the medulla is the cortex. It arches over the bases of the pyramids and fills gaps between the pyramids. Each group of pyramids that projects into a papilla, together with the portion of cortex that arches over the group, is called a renal lobe.

Types of kidney tissue

The renal sinus includes the renal pelvis, a funnel-shaped expansion of the upper end of the ureter, and, reaching into the kidney substances from the wide end of the funnel, two or three extensions of the cavity called the major calyxes. The major calyxes are divided in turn into four to 12 smaller cuplike cavities, the minor calyxes, into which the renal papillae project. The renal pelvis serves as the initial reservoir for urine, which flows into the sinus through the urinary collecting tubules, small tubes that open into the sinus at the papillae.

Minute structure. The structural units of the kidneys that actually produce urine are the nephrons, of which there are approximately 1,000,000 in each kidney. Each nephron is a long tubule (or extremely fine tube) that is closed, expanded, and folded into a double-walled cuplike structure at one end. This structure, called the renal corpuscular capsule, or Bowman's capsule, encloses a cluster of capillaries (microscopic blood vessels) called the glomerulus. The capsule and glomerulus together constitute a renal corpuscle, also called a malpighian body. Blood flows into and away from the glomerulus through small arteries (arterioles) that enter and exit the glomerulus through the open end of the capsule. This opening is called the vascular pole of the corpuscle.

The nephrons

The tubules of the nephrons are 30–55 millimetres (1.2–2.2 inches) long. The corpuscle and the initial portion of each tubule, called the proximal convoluted tubule, lie in the renal cortex. The tubule descends into a renal pyramid, makes a U-shaped turn, and returns to the cortex at a point near its point of entry into the medulla. This section of the tubule, consisting of the two parallel lengths and the bend between them, is called the loop of Henle or the nephronic loop. After its reentrance into the cortex, the tubule returns to the vascular pole (the opening in the cuplike structure of the capsule) of its own nephron. The final portion of the tubule, the distal convoluted tubule, leads from the vascular pole of the corpuscle to a collecting tubule, by way of a short junctional tubule. Several of the collecting tubules join together to form a somewhat wider tubule, which carries the urine to a renal papilla and the renal pelvis.

Although all nephrons in the kidney have the same general disposition, there are regional differences, particularly in the length of the loops of Henle. Glomeruli that lie deep in the renal cortex near the medulla (juxtamedullary glomeruli) possess long loops of Henle that pass deeply into the medulla, whereas more superficial cortical glomeruli have much shorter loops. Among different animal species the length of the loops varies considerably and affects the ability of the species to concentrate urine above the osmotic concentration of plasma.

The successive sections of the nephron tubule vary in shape and calibre, and these differences, together with differences in the cells that line the sections, are associated with specific functions in the production of urine.

Intrarenal network of blood vessels. The intrarenal network of blood vessels forms part of the blood-processing apparatus of the kidneys.

Arteries and arterioles. The anterior and posterior divisions of each renal artery, mentioned earlier, divide into lobar arteries, each of which enters the kidney substance through or near a renal papilla. Each lobar artery gives off two or three branches, called interlobar arteries, which run outward between adjacent renal pyramids. When these reach the boundary between the cortex and the medulla they split almost at right angles into branches called arcuate arteries that curve along between the cortex and the medulla parallel to the surface of the kidney. Many arteries, called interlobular arteries, branch off from the arcuate arteries and radiate out through the cortex to end in networks of capillaries in the region just inside the capsule. En route they give off short branches called the afferent arterioles, which carry blood to the glomeruli where they divide into four to eight loops of capillaries in each glomerulus (Figure 5).

Near and before the point where the afferent arteriole enters the glomerulus, its lining layer becomes enlarged and contains secretory granules. This composite structure is called the juxtaglomerular apparatus (JGA) and is believed to be involved in the secretion of renin (see below *The role of hormones in renal function*). They are then reconstituted near the point of entry of the afferent arteriole to become the efferent arterioles carrying blood away from the glomeruli. The afferent arterioles are almost twice as thick as the efferent arterioles because they have thicker muscular coats, but the sizes of their channels are almost the same.

Throughout most of the cortex the efferent arterioles redivide into a second set of capillaries, which supply blood to the proximal and distal renal tubules.

Arterioles in the juxtamedullary zone

The efferent glomerular arterioles of juxtaglomerular glomeruli divide into vessels that supply the contiguous tubules and vessels that enter the bases of the renal pyramids. Known as vasa recta, these vessels run toward the apexes of the pyramids in close contact with the loops of Henle. Like the tubules they make hairpin bends, retrace their path, and empty into arcuate veins that parallel the arcuate arteries.

Normally the blood circulating in the cortex is more abundant than that in the medulla (amounting to over 90 percent of the total), but in certain conditions, such as those associated with severe trauma or blood loss, cortical vessels may become constricted while the juxtamedullary circulation is preserved. Because the cortical glomeruli and tubules are deprived of blood, the flow of urine is diminished, and in extreme cases may cease.

Veins and venules. The renal venules (small veins) and veins accompany the arterioles and arteries and are referred to by similar names. The venules that lie just beneath the renal capsule, called stellate venules because of their radial arrangement, drain into interlobular venules. In turn these combine to form the tributaries of the arcuate, interlobar, and lobar veins. Blood from the renal pyramids passes into vessels, called venae rectae, which join the arcuate veins. In the renal sinus the lobar veins unite to form veins corresponding to the main divisions of the renal arteries, and they normally fuse to constitute a single renal vein in or near the renal hilus.

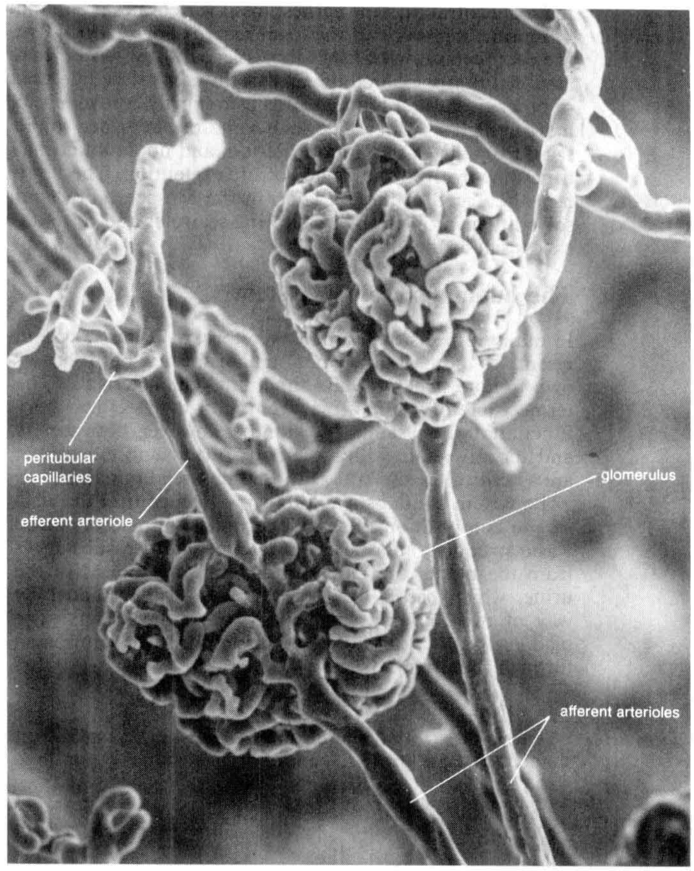

Figure 5: A cast of the intrarenal vascular network. The afferent arteriole enters the glomerulus, where it divides into capillary loops. These are rejoined to become the efferent arteriole, which leaves the glomerulus and branches into numerous peritubular capillaries.

By courtesy of Andrew P. Evan and Vincent H. Gattone II

Lymphatic network. Lymphatic capillaries form a network just inside the renal capsule and another, deeper network between and around the renal blood vessels. Few lymphatic capillaries appear in the actual renal substance, and those present are evidently associated with the connective tissue framework, while the glomeruli contain no lymphatics. The lymphatic networks inside the capsule and around the renal blood vessels drain into lymphatic channels accompanying the interlobular and arcuate blood vessels. The main lymph channels run alongside the main renal arteries and veins to end in lymph nodes beside the aorta and near the sites of origin of the renal arteries.

THE URETERS

General characteristics. The ureters are narrow, thick-walled ducts, about 25–30 centimetres (9.8–11.8 inches) in length and from four to five millimetres (0.16 to 0.2 inch) in diameter, that transport the urine from the kidneys to the urinary bladder. Throughout their course they lie behind the peritoneum, the lining of the abdomen and pelvis, and are attached to it by connective tissue.

In both sexes the ureters enter the bladder wall about five centimetres apart, although this distance is increased when the bladder is distended with urine. The ureters run obliquely through the muscular wall of the bladder for nearly two centimetres before opening into the bladder cavity through narrow apertures. This oblique course provides a kind of valvular mechanism; when the bladder becomes distended it presses against the part of each ureter that is in the muscular wall of the bladder, and this helps to prevent the flow of urine back into the ureters from the bladder.

Structure of the ureteric wall. The wall of the ureter has three layers, the adventitia, or outer layer; the intermediate, muscular layer; and the lining, made up of mucous membrane. The adventitia consists of fibroelastic connective tissue that merges with the connective tissue behind the peritoneum. The muscular coat is composed of smooth (involuntary) muscle fibres and, in the upper two-thirds of the ureter, has two layers—an inner layer of fibres arranged longitudinally and an outer layer disposed circularly. In the lower third of the ureter an additional longitudinal layer appears on the outside of the vessel. As each ureter extends into the bladder wall its circular fibres disappear, but its longitudinal fibres extend almost as far as the mucous membrane lining the bladder.

The mucous membrane lining increases in thickness from the renal pelvis downward. Thus, in the pelvis and the calyxes of the kidney the lining is two to three cells deep; in the ureter, four to five cells thick; and in the bladder, six to eight cells. The mucous membrane of the ureters is arranged in longitudinal folds, permitting considerable dilation of the channel. There are no true glands in the mucous membrane of the ureter or of the renal pelvis. The chief propelling force for the passage of urine from the kidney to the bladder is produced by peristaltic (wavelike) movements in the ureter muscles.

Peristalsis in the ureters

THE URINARY BLADDER

General description. The urinary bladder is a hollow muscular organ forming the main urinary reservoir. It rests on the anterior part of the pelvic floor (see below), behind the symphysis pubis and below the peritoneum. (The symphysis pubis is the joint in the hip bones in the front midline of the body.) The shape and size of the bladder vary according to the amount of urine that the organ contains. When empty it is tetrahedral and lies within the pelvis; when distended it becomes ovoid and expands into the lower abdomen. It has a body, with a fundus, or base; a neck; an apex; and a superior (upper) and two inferolateral (below and to the side) surfaces, although these features are not clearly evident except when the bladder is empty or only slightly distended.

The neck of the bladder is the area immediately surrounding the urethral opening; it is the lowest and most fixed part of the organ. In the male it is firmly attached to the base of the prostate, a gland that encircles the urethra.

The superior surface of the bladder is triangular and is covered with peritoneum. The bladder is supported on the levator ani muscles, which constitute the major part of the floor of the pelvic cavity. The bladder is covered, and to a certain extent supported, by the visceral layer of the pelvic fascia. This fascial layer is a sheet of connective tissue that sheaths the organs, blood vessels, and nerves of the pelvic cavity. The fascia forms, in front and to the side, ligaments, called pubovesical ligaments, that act as a kind of hammock under the inferolateral surfaces and neck of the bladder.

Blood and nerve supplies. The blood supply of the bladder is derived from the superior, middle, and inferior vesical (bladder) arteries. The superior vesical artery supplies the dome of the bladder, and one of its branches (in males) gives off the artery to the ductus deferens, a part of the passageway for sperm. The middle vesical artery supplies the base of the bladder. The inferior vesical artery supplies the inferolateral surfaces of the bladder and assists in supplying the base of the bladder, the lower end of the ureter, and other adjacent structures.

The nerves to the bladder

The nerves to the urinary bladder belong to the sympathetic and the parasympathetic divisions of the autonomic nervous system. The sympathetic nerve fibres come from the hypogastric plexus of nerves that lie in front of the fifth lumbar vertebra. Sympathetic nerves carry to the central nervous system the sensations associated with distention of the bladder and are believed to be involved in relaxation of the muscular layer of the vesical wall and with contraction of sphincter mechanism that closes the opening into the urethra. The parasympathetic nerves travel to the bladder with pelvic splanchnic nerves from the second through fifth sacral spinal segment. Parasympathetic nerves are concerned with contraction of the muscular walls of the bladder and with relaxation of its sphincter. Consequently they are actively involved in urination and are sometimes referred to as the emptying, or detrusor, nerves.

Structure of the bladder wall. The bladder wall has a serous coat over its upper surface. This covering is a continuation of the peritoneum that lines the abdominal cavity; it is called serous because it exudes a slight amount of lubricating fluid called serum. The other layers of the bladder wall are the fascial, muscular, submucous, and mucous coats.

The fascial coat is a layer of connective tissue, such as that which covers muscles. The muscular coat consists of coarse fascicles, or bundles, of smooth (involuntary) muscle fibres arranged in three strata, with fibres of the outer and inner layers running lengthwise, and with fibres of the intermediate layer running circularly; there is considerable intermingling of fibres between the layers. The smooth muscle coat constitutes the powerful detrusor muscle, which causes the bladder to empty.

The circular or intermediate muscular stratum of the vesical wall is thicker than the other layers. Its fibres, although running in a generally circular direction, do interlace. The internal muscular stratum is an indefinite layer of fibres that are mostly directed longitudinally. The submucous coat consists of loose connective tissue containing many elastic fibres. It is absent in the trigone, a triangular area whose angles are at the two openings for the ureters and the single internal urethral opening. Slim bands of muscle run between each ureteric opening and the internal urethral orifice; these are thought to maintain the oblique direction of the ureters during contraction of the bladder. Another bundle of muscle fibres connects the two ureteric openings and produces a slightly downwardly curved fold of mucous membrane between the openings.

The mucous coat of the bladder

The mucous coat, the innermost lining of the bladder, is an elastic layer impervious to urine. Over the trigone it firmly adheres to the muscular coat and is always smooth and pink whether the bladder is contracted or distended. Elsewhere, if the bladder is contracted, the mucous coat has multiple folds and a red, velvety appearance. When the bladder is distended, the folds are obliterated, but the difference in colour between the paler trigonal area and the other areas of the mucous membrane persists. The mucous membrane lining the bladder is continuous with that lining the ureters and the urethra.

THE URETHRA

The male urethra

General description. The urethra is the channel that conveys the urine from the bladder to the exterior. In the male it is about 20 centimetres long and carries not only the urine but also the semen and the secretions of the prostate, bulbourethral, and urethral glands. During urination and ejaculation it opens up, and its diameter then varies from 0.5 to 0.8 centimetre along its length, but at other times its walls touch and its lining is raised into longitudinal folds. The male urethra has three distinguishable parts, the prostatic, the membranous, and the spongy, each part being named from the structures through which it passes rather than from any inherent characteristics.

The prostatic section of the male urethra commences at the internal urethral orifice and descends almost vertically through the prostate, from the base of the gland to the apex, describing a slight curve with its concavity forward. It is about 2.5 to three centimetres long and is spindle-shaped; its middle portion is the widest and most dilatable part of the urethra. The membranous part of the male urethra is in the area between the two layers of a membrane called the urogenital diaphragm. The urethra is narrower in this area than at any other point except at its external opening and is encircled by a muscle, the sphincter urethrae. The two small bulbourethral glands are on either side of it. The membranous urethra is not firmly attached to the layers of the urogenital diaphragm. The spongy part of the male urethra is that part of the urethra that traverses the penis. It passes through the corpus spongiosum of the penis. The ducts of the bulbourethral glands enter the spongy urethra about 2.5 centimetres below the lower layer of the urogenital membrane; except near its outer end, many mucous glands also open into it.

The female urethra

The female urethra is much shorter (three to 4.5 centimetres) and more distensible than the corresponding channel in males and carries only urine and the secretions of mucous glands. It begins at the internal opening of the urethra into the bladder and curves gently downward and forward through the urogenital diaphragm, where it is surrounded, as in the male, by the sphincter urethrae. It lies behind and below the symphysis pubis. Except for its uppermost part, the urethra is embedded in the anterior wall of the vagina. The external urethral orifice is immediately in front of the vaginal opening, about 2.5 centimetres behind the clitoris, and between the labia minora, the inner folds at the outer opening of the vagina.

Structure of urethral wall. The urethra of the male is a tube of mucous membrane supported on a submucous layer and an incomplete muscular coat. The membrane forms longitudinal folds when the tube is empty; these folds are more prominent in the membranous and spongy parts. There are many glands in the mucous membrane, and they are more common in the posterior wall of the spongy part. The submucous layer is composed of fibroelastic connective tissue containing numerous small blood vessels, including more venules than arterioles. The thin muscular coat consists of smooth (involuntary) and striated (voluntary) muscle fibres. The smooth muscular layer, longitudinally disposed, is continuous above with the detrusor muscle of the bladder and extends distally as far as the membranous urethra, where it is replaced and partly surrounded by striated muscle of the external sphincter. The somatic nerves to the external sphincter are the efferent and afferent components of the pudendal nerve, arising from the second, third, and fourth sacral segments of the spinal cord.

The female urethra has mucous, submucous, and muscular coats. As in the male, the lining of the empty channel is raised into longitudinal folds. It also shows mucous glands, mentioned in the preceding paragraphs as existing in the male urethra. The submucous coat resembles that in the male, except that the venules are even more prominent. In both sexes, but especially in females, this layer appears to be a variety of erectile tissue. The muscular coat extends along the entire length of the female urethra and is continuous above with the musculature of the bladder. It consists of inner longitudinal and outer circular layers, and fibres from the latter intermix with those in the anterior wall of the vagina, in which the urethra is embedded.

(G.A.G.M./J.S.Ro.)

Human excretion

GENERAL FUNCTION OF THE KIDNEY

The kidney has evolved so as to enable humans to exist on land where water and salts must be conserved, wastes excreted in concentrated form, and the blood and the tissue fluids strictly regulated as to volume, chemical composition, and osmotic pressure. Under the drive of arterial pressure, water and salts are filtered from the blood through the capillaries of the glomerulus into the lumen, or passageway, of the nephron, and then most of the water and the substances that are essential to the body are reabsorbed into the blood. The remaining filtrate is drained off as urine. The kidneys, thus, help maintain a constant internal environment despite a wide range of changes in the external environment.

Regulatory functions. The kidneys regulate three essential and interrelated properties of the tissues—water content, acid-base balance, and osmotic pressure—in such a way as to maintain electrolyte and water equilibrium; in other words, the kidneys are able to maintain a balance between quantities of water and the quantities of such chemicals as calcium, potassium, sodium, phosphorus, and sulfate in solution. Unless the concentrations of mineral ions such as sodium, crystalloids such as glucose, and wastes such as urea are maintained within narrow normal limits, bodily malfunction rapidly develops leading to sickness or death.

The removal of both kidneys causes urinary constituents to accumulate in the blood (uremia), resulting in death in 14–21 days if untreated. (The term uremia does not mean that urea is itself a toxic compound responsible for illness and death.) Whenever the blood contains an abnormal constituent in solution or an excess of normal constituents including water and salts, the kidneys excrete these until normal composition is restored. The kidneys are the only means for eliminating the wastes that are the end products of protein metabolism. They do not themselves modify the waste products that they excrete, but transfer them to the urine in the form in which they are produced in other parts of the body. The only exception to this is their ability to manufacture ammonia. The kidneys also eliminate drugs and toxic agents. Thus, the kidneys eliminate the unwanted end products of metabolism, such as urea, while limiting the loss of valuable substances, such as glucose. In maintaining the acid-base equilibrium, the kidneys remove the excess of hydrogen ions produced from the normally acid-forming diet and manufacture ammonia to remove these ions in the urine as ammonium salts.

Volumes of blood, water, and urine processed by kidneys

To carry on its functions the kidney is endowed with a relatively huge blood supply. The blood processed in the kidneys amounts to some 1,200 millilitres a minute, or 1,800 litres (about 475 gallons) a day, which is 400 times the total blood volume and roughly one-fourth the volume pumped each day by the heart. Every 24 hours 170 litres (45 gallons) of water are filtered from the bloodstream into the renal tubules; and by far the greater part of this—some 168.5 litres of water together with salts dissolved in it—is reabsorbed by the cells lining the tubules and returned to the blood. The total glomerular filtrate in 24 hours is no less than 50–60 times the volume of blood plasma (the blood minus its cells) in the entire body. In a 24-hour period, an average man eliminates only 1.5 litres of water, containing the waste products of metabolism, but the actual volume varies with fluid intake and occupational and environmental factors. With vigorous sweating it may fall to 500 millilitres (about a pint) a day; with a large water intake it may rise to three litres, or six times as much. The kidney can vary its reabsorption of water to compensate for changes in plasma volume resulting from dehydration or overhydration.

Nonexcretory functions. The kidneys also perform certain nonexcretory functions. They secrete substances that enter the blood. These are of three kinds: renin, which is concerned indirectly with the control of electrolyte balance and blood pressure; erythropoietin, which is important for the formation of hemoglobin and red blood cells, especially in response to anemia or deficiency of oxygen reaching the body tissues; and 1,25-dihydroxycholecalciferol, which is the metabolically active form of vitamin D. Finally, although the kidneys are subject to both nervous and humoral (hormonal) control, they do possess a considerable degree of autonomy; *i.e.*, function continues in an organ isolated from the nervous system but kept alive with circulating fluid. Indeed, if this were not so kidney transplantation would be impossible.

RENAL BLOOD CIRCULATION

Intrarenal blood pressures. The renal arteries are short and spring directly from the abdominal aorta, so that arterial blood is delivered to the kidneys at maximum available pressure. As in other vascular beds, renal perfusion is determined by the renal arterial blood pressure and vascular resistance to blood flow. Evidence indicates that in the kidneys the greater part of the total resistance occurs in the glomerular arterioles. The muscular coats of the arterioles are well supplied with sympathetic vasoconstrictor fibres (nerve fibres that induce narrowing of the blood vessels), and there is also a small parasympathetic supply from the vagus and splanchnic nerves that induces dilation of the vessels. Sympathetic stimulation causes vasoconstriction and reduces urinary output. The vessel walls are also sensitive to circulating epinephrine and norepinephrine hormones, small amounts of which constrict the efferent arterioles and large amounts of which constrict all the vessels; and to angiotensin, which is a constrictor agent closely related to renin. Prostaglandins may also have a role.

Factors that affect renal flow. The kidney is able to regulate its internal circulation regardless of the systemic blood pressure, provided that the latter is not extremely high or extremely low. The forces that are involved in maintaining a circulation of the blood in the kidneys must remain constant if the monitoring of the water and electrolyte composition of the blood is to proceed undisturbed. This regulation is preserved even in the kidney cut off from the nervous system and, to a lesser extent, in an organ removed from the body and kept viable by having salt solutions of physiologically suitable concentrations circulated through it; it is commonly referred to as autoregulation.

The exact mechanism by which the kidney regulates its own circulation is not known, but various theories have been proposed: (1) Smooth muscle cells in the arterioles may have an intrinsic basal tone (normal degree of contraction) when not affected by nervous or humoral (hormonal) stimuli. The tone responds to alterations in perfusion pressure in such a way that when the pressure falls the degree of contraction is reduced, preglomerular resistance is lowered, and blood flow is preserved. Conversely, when perfusion pressure rises, the degree of contraction is increased and blood flow remains constant. (2) If the renal blood flow rises, more sodium is present in the fluid in the distal tubules because the filtration rate increases. This rise in the sodium level stimulates the secretion of renin from the JGA with the formation of angiotensin, causing the arterioles to constrict and blood flow to be reduced. (3) If systemic blood pressure rises, the renal blood flow remains constant because of the increased viscosity of the blood. Normally, the interlobular arteries have an axial (central) stream of red blood cells with an outer layer of plasma so that the afferent arterioles skim off more plasma than cells. If the arteriolar blood pressure rises, the skimming effect increases, and the more densely packed axial flow of cells in the vessels offers increasing resistance to the pressure, which has to overcome this heightened viscosity. Thus, the overall renal blood flow changes little. Up to a point, similar considerations in reverse apply to the effects of reduced systemic pressure. (4) Changes in the arterial pressure modify the pressure exerted by the interstitial (tissue) fluid of the kidney on capillaries and veins so that increased pressure raises, and decreased pressure lowers, resistance to blood flow.

The renal blood flow is greater when a person is lying down than when standing; it is higher in fever; and it is reduced by prolonged vigorous exertion, pain, anxiety, and other emotions that constrict the arterioles and divert blood to other organs. It is also reduced by hemorrhage and asphyxia and by depletion of water and salts, which is severe in shock, including operative shock. A large fall in systemic blood pressure, as after severe hemorrhage, may so reduce renal blood flow that no urine at all is formed for a time; death may occur from suppression of glomerular function. Simple fainting causes vasoconstriction and reduced urine output. Urinary secretion is also stopped by obstruction of the ureter when back pressure reaches a critical point.

Glomerular pressure. The importance of these various vascular factors lies in the fact that the basic process occurring in the glomerulus is one of filtration, the energy for which is furnished by the blood pressure within the glomerular capillaries. Glomerular pressure is a function of the systemic pressure as modified by the tone (state of constriction or dilation) of the afferent and efferent arterioles, as these open or close spontaneously or in response to nervous or hormonal control.

In normal circumstances glomerular pressure is believed to be about 45 millimetres of mercury (mmHg), which is a higher pressure than that found in capillaries elsewhere in the body. As is the case in renal blood flow, the glomerular filtration rate is also kept within the limits between which autoregulation of blood flow operates. Outside these limits, however, major changes in blood flow occur. Thus, severe constriction of the afferent vessels reduces blood flow, glomerular pressure, and filtration rate, while efferent constriction causes reduced blood flow but increases glomerular pressure and filtration.

FORMATION AND COMPOSITION OF URINE

The urine leaving the kidney differs considerably in composition from the plasma entering it (Table 1). The study of renal function must account for these differences; *e.g.*, the absence of protein and glucose from the urine, a change in the pH of urine as compared with that of plasma, and the high levels of ammonia and creatinine in the urine, while sodium and calcium remain at similar low levels in both urine and plasma.

Table 1: Relative Composition of Plasma and Urine in Normal Men

	plasma g/100 ml	urine g/100 ml	concentration in urine
Water	90–93	95	—
Protein	7–8.5	—	—
Urea	0.03	2	× 60
Uric acid	0.002	0.03	× 15
Glucose	0.1	—	—
Creatinine	0.001	0.1	× 100
Sodium	0.32	0.6	× 2
Potassium	0.02	0.15	× 7
Calcium	0.01	0.015	× 1.5
Magnesium	0.0025	0.01	× 4
Chloride	0.37	0.6	× 2
Phosphate	0.003	0.12	× 40
Sulfate	0.003	0.18	× 60
Ammonia	0.0001	0.05	× 500

A large volume of ultrafiltrate (*i.e.*, a liquid from which the blood cells and the blood proteins have been filtered out) is produced by the glomerulus into the capsule. As this liquid traverses the proximal convoluted tubule, most of its water and salts are reabsorbed, some of the solutes completely and others partially; *i.e.*, there is a separation of substances that must be retained from those due for rejection. Subsequently the loop of Henle, distal convoluted tubule, and collecting ducts are mainly concerned with the fine control of water and electrolyte balance (Figure 6).

From J.M. Forrester, R. Passmore, and J.S. Robson (eds.), *A Companion to Medical Studies*, vol. 1, 3rd ed. (1985); Blackwell Scientific Publications Ltd

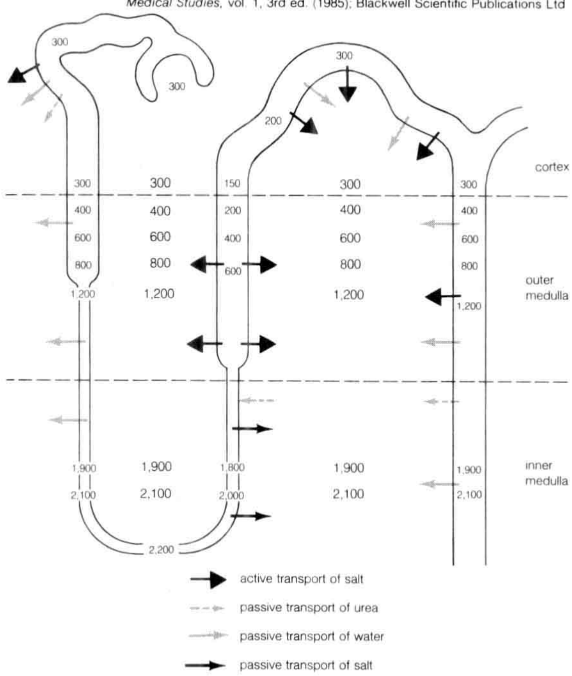

Figure 6: The modes of action of the countercurrent mechanism for concentrated urine production. The values indicated are given in mosmoles of solute/kilogram.

Glomerular filtration. Urine formation begins as a process of ultrafiltration of a large volume of blood plasma from the glomerular capillaries into the capsular space, colloids such as proteins being held back while crystalloids (substances in true solution) pass through. In humans, the average capillary diameter is five to 10 micrometres (a micrometre is 0.001 millimetre). The wall of each loop of capillaries has three layers (Figure 7). The inner layer