ANIMAL PHYSIOLOGY

KNUT SCHMIDT-NIELSEN

FOUNDATIONS OF MODERN BIOLOGY

Animal Physiology

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Foundations of Modern Biology Series

The science of biology today is *not* the same science of fifty, twenty-five, or even ten years ago. Today's accelerated pace of research, aided by new instruments, techniques, and points of view, imparts to biology a rapidly changing character as discoveries pile one on top of the other. All of us are aware, however, that each new and important discovery is not just a mere addition to our knowledge; it also throws our established beliefs into question, and forces us constantly to reappraise and often to reshape the foundations upon which biology rests. An adequate presentation of the dynamic state of modern biology is, therefore, a formidable task and a challenge worthy of our best teachers.

The authors of this series believe that a new approach to the organization of the subject matter of biology is urgently needed to meet this challenge, an approach that introduces the student to biology as a growing, active science, and that also *permits each teacher of biology to determine the level and the structure of his own course*. A single textbook cannot provide such flexibility, and it is the authors' strong conviction that these student needs and teacher prerogatives can best be met by a series of short, inexpensive, well-written, and well-illustrated books so planned as to encompass those areas of study central to an understanding of the content, state, and direction of modern biology. The FOUNDATIONS OF MODERN BIOLOGY SERIES represents the translation of these ideas into print, with each volume being complete in itself yet at the same time serving as an integral part of the series as a whole.

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1 Food and Energy

All living organisms need a supply of energy, which they must obtain from outside sources. Most plants use the energy of sunlight to build carbon dioxide from the atmosphere into sugar (by the process of *photosynthesis*) and, indirectly, into all the complicated compounds that constitute a plant. All animals, on the other hand, obtain their energy from plants, either directly by eating them, or indirectly by eating other animals that depend on plants.

Let us look at the food and energy requirements of animals, who need food for three major purposes: (1) movements, muscle contraction, etc., (2) growth and synthesis of body substances, and (3) energy and material for maintenance. The two first categories seem obvious, but the third deserves some comment. Even when the organism is at rest, many physiological processes continue. Some organs, such as the heart, work continuously, but even so-called resting organs—resting muscles, for example—continue to use nutrients and oxygen. All cells continuously expend energy, and if the process is stopped, death soon follows.

All the food requirements of animals are satisfied by the intake of organic material of plant or animal origin. The bulk of this food consists of three major groups of compounds; *carbohydrates, fats,* and *proteins*. In addition, there is a need for a wide variety of minerals, vitamins, and various other organic compounds. The intake of food is called

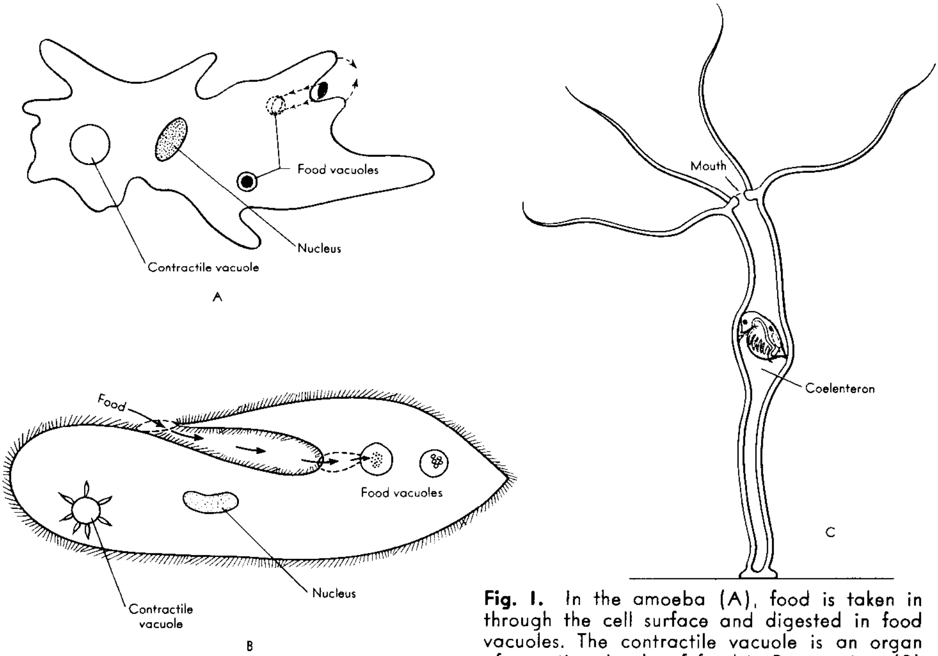

Fig. 1. In the amoeba (A), food is taken in through the cell surface and digested in food vacuoles. The contractile vacuole is an organ of excretion. Intake of food in Paramecium (B) is restricted to one part of the cell surface, the oral groove, but digestion takes place in food vacuoles similar to those of the amoeba. In the larger, multicellular Hydra (C), digestion begins in the coelenteron but is completed inside the cells of the body wall.

feeding; the breakdown of food into simpler compounds that can be used by the body is *digestion;* and the specific needs of an animal for certain types of food or compounds belong to the field of *nutrition.*

Digestion

In the most primitive way of feeding, food particles are taken into the cell for digestion (Fig. 1). Such *intracellular digestion* is found in protozoans and sponges, but is also employed by more complex animals. For example, mussels filter particles out of the water, and small algae and other organisms are caught and taken into the cells of the digestive gland and digested intracellularly. In animals that feed on larger hunks of food, intracellular digestion is not possible unless the food is disintegrated beforehand. In a *Hydra,* prey that is caught by the tentacles is partly digested in the coelenteron, and the disintegrated fragments are completely digested after they have been taken into the cells. The development of a digestive tract permits a more complete *extracellular digestion.*

A few animals accomplish partial digestion before ingestion. The spider, for instance, pierces its prey with its hollow fangs and pumps digestive fluids (from the poison gland) into the victim. This liquefies the softer parts, enabling the spider to suck back the semi-digested fluid. The digestion is completed in the digestive system, as it is in other animals with extracellular digestion.

ENZYMATIC HYDROLYSIS

Most food materials cannot be utilized directly by the organism before they have been broken down to simpler compounds—starches and complex sugars to simple sugars, fats to fatty acids and glycerol, and the extremely complex protein molecules to simple amino acids. This breakdown is called *hydrolysis* because water is taken up in the process. Hydrolysis is a spontaneous reaction, and as it progresses a small amount of energy is released as heat. However, the spontaneous hydrolysis of most materials proceeds extremely slowly. In general, the rate of chemical processes can be speeded up by catalysts, and the catalysts that are produced by living organisms are called *enzymes*. Virtually all metabolic processes in the body—breakdown, synthesis, and certain types of transfers—are catalysed by enzymes, which, therefore, are extremely important in all metabolic processes. All enzymes are protein in nature, are produced by cells, and each cell contains probably hundreds of them.

Biochemists have isolated enzymes in pure form, have studied their action in detail, and have found that each enzyme usually acts on a single substance, the *substrate,* or on a group of closely related substances. The enzymes that act on only one particular substrate are called highly *specific.*

An enzyme is described by the *substrate* it acts on, or by the *reaction* it catalyzes, and its activity by the *rate* of the reaction. Many factors influence the activity, and those that alter the protein of the enzyme destroy its activity. Since heat usually makes proteins coagulate, it also inactivates enzymes; on the other hand, increased temperature also speeds up chemical reactions, and a moderate increase in temperature gives an increased rate of enzymatic action. With a further temperature increase, however, the thermal destruction of the enzyme catches up with the increase in reaction rate, and at some temperature we will observe a maximum reaction rate, or *temperature optimum,* as we call it. Since the degree of thermal destruction increases with time, we will find a high temperature optimum in experiments that last for a short time, and a low optimum in long-lasting experiments with the same enzyme. Thus, since the temperature optimum changes with duration, it is not a specific characteristic of a given enzyme. Most enzymes are rapidly inactivated by temperatures above 45°C or 50°C, but a few are resistant to boiling. One of these, the proteolytic enzyme, papain, from the papaya fruit, is used as a meat tenderizer because it continues its proteolytic action even at the high temperatures of cooking.

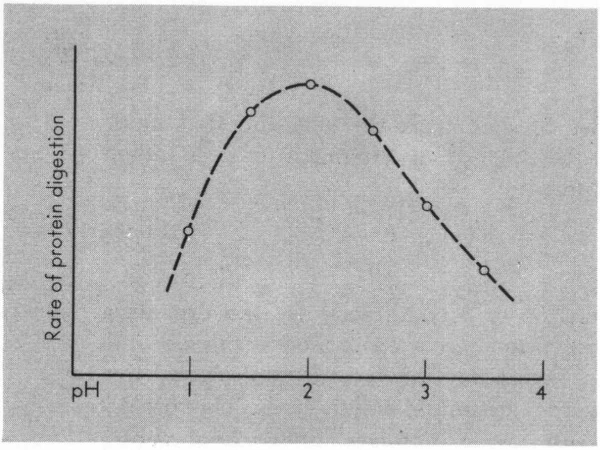

Fig. 2. The digestive action of the enzyme, pepsin, depends on the acidity, or pH. This particular enzyme has its greatest effect in acid solution about pH 2, but other enzymes have different pH optima, frequently around neutrality (pH = 7).

The activity of enzymes is greatly influenced by *acidity* or *alkalinity*. Acids dissociate in water to yield hydrogen ions, H^+, and the concentration of the H^+ indicates the strength of the acid. To designate the acidity of a solution we use the symbol pH. A neutral solution has pH = 7; an acid solution has pH below 7 (e.g., the acid gastric juice has a pH of about 1.5); and alkaline solutions have pH above 7. The pH scale is widely used in physiology and chemistry because it gives accurate information about the hydrogen ion concentration. The pH has a profound influence on enzyme action. The curve in Fig. 2 shows that the action of the enzyme, pepsin, from the vertebrate stomach is greatest in a highly acid solution, about pH = 2, which is the *optimum pH* for pepsin. The pH optimum is characteristic for each enzyme, and many have pH optima in neutral or slightly alkaline solutions. Excessive acidity or alkalinity causes destruction or *denaturation* of enzymes, just as high temperature causes heat denaturation.

DIGESTION IN MAMMALS

Mammals are meat eaters (carnivores), plant eaters (herbivores), or mixed-food eaters (omnivores). The main phases of digestion are alike in these groups (Fig. 3), although there are some notable variations. The *mouth and teeth* serve to some extent to tear the food to pieces, and herbivores and omnivores frequently masticate the food better than carnivores. Dry food cannot be swallowed before it has been mixed with *saliva,* secreted by the salivary glands. The saliva contains water, a small amount of salts and protein, and a digestive enzyme, *amylase,* that acts on starch (the name is derived from the Latin word for the substrate, amylum). The pH optimum of amylase is neutral or slightly alkaline, and in the range of the normal pH of saliva.

The *stomach* serves as a reservoir for food as well as for digestion. Glands in its wall secrete the protein-splitting, or proteolytic, enzyme, *pepsin*, and hydrochloric acid in a concentration of about 0.5 per cent. The pH optimum of pepsin is about 2, and the enzyme therefore works well in the acid stomach juice. When the food comes in contact with the acid, the salivary amylase is inactivated, and starch digestion is stopped; thus the only major digestion in the stomach is proteolytic. The strong acid also inhibits bacterial growth, which otherwise would be excessive during the several hours the food stays in the stomach.

From the stomach, small portions of semi-liquid food enter the upper intestine, where the acid is neutralized by sodium bicarbonate in the secretion from the *pancreas*. The pancreatic juice also contains enzymes; one is a powerful proteolytic enzyme, ***trypsin***, which has a pH optimum of about 8. It is secreted in an inactive form, trypsinogen, which is activated by another enzyme, *enterokinase*, secreted by the intestinal wall. Other important pancreatic enzymes are fat-digesting *lipase* and starch-digesting *amylase*, which both have pH optima near the normal pH of the intestinal contents.

The other main digestive gland in vertebrates is the *liver*. Its secretion, the bile, contains no enzymes, but it does contain the important

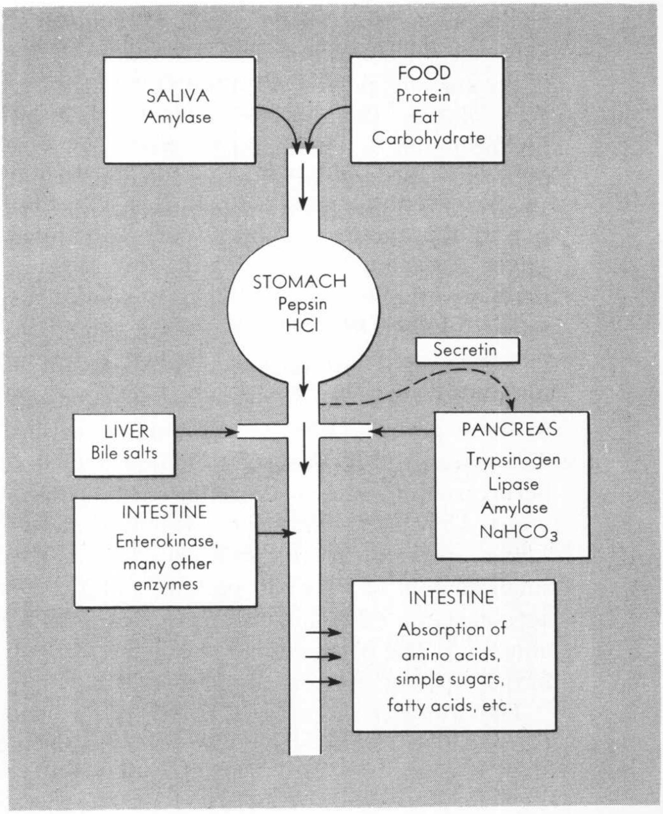

Fig. 3. The most important steps in vertebrate digestion. Ingested food is exposed to a succession of digestive enzymes and broken down to simple components that are absorbed in the intestine.

bile salts, which chemically act in the same manner as detergents. They help emulsify fats, which otherwise would remain as insoluble droplets quite inaccessible to lipase action. Bile salts are essential for fat digestion, and also for absorbing the breakdown products, the fatty acids, as well as certain other substances insoluble in water. One of these is the fat-soluble vitamin K, which is necessary for blood coagulation.

The *intestine* also secretes digestive juices. Its enzymes complete the hydrolysis of the breakdown products formed by the action of pepsin and trypsin on proteins, and they complete the hydrolysis of maltose, which was formed by amylase action on starch; other enzymes digest sucrose (table sugar), lactose (milk sugar), nucleic acids, and so on.

CONTROL OF THE DIGESTIVE GLANDS. The activity of the salivary glands is controlled by nerves. When food comes in contact with the mouth, a nerve reflex stimulates secretion, particularly if the food is appetizing and tasty. Mental processes play a great role in this reflex, and the smell or the mere expectation of food causes stimulation of the salivary glands and literally makes the "mouth water." Secretion of gastric juice in the stomach is also under nervous control, but, in addition, it is influenced by a substance, *gastrin,* which is formed in the wall of the stomach and during digestion circulates in the blood and causes the glands to secrete.

The pancreas has a nerve supply, but its secretion is mainly stimulated by a substance, *secretin,* that is released from the wall of the upper intestine into the blood when the acid food from the stomach enters the intestine. When the secretin reaches the pancreas via the circulation, pancreatic juice containing sodium bicarbonate is secreted into the intestine to neutralize the acid. In this way, the release of secretin assures that an appropriate amount of pancreatic juice is secreted. Such a "messenger" substance circulating in the blood is called a *hormone.* The secretion of bile from the liver is continuous and is not restricted to periods of digestion, and the bile is stored in the gall bladder. During digestion, the gall bladder is emptied as a result of the action of another hormone, *cholecystokinin.*

INTESTINAL ABSORPTION

When a final product of digestion—for example, glucose (the simple sugar formed in starch digestion)—has been formed in the intestine, it is absorbed through the intestinal wall and enters the blood. The natural tendency for dissolved substances is to migrate, or *diffuse,* from a place with a high concentration to a place with low concentration. When the concentration of glucose in the intestine is high, it may enter the blood by such diffusion, for the concentration in the blood is only 0.1 per cent. But glucose is completely absorbed from the intestine, and this cannot be explained by diffusion alone, for when the glucose molecules are completely removed, they would tend to diffuse from the blood back to the intestine.

Such movement of substances against the direction in which they tend to diffuse passively requires energy and is called *active transport,* which is defined as a movement against the concentration gradient. This transport has been compared to moving a wheelbarrow full of rocks: when the rocks are moved uphill, against their tendency to roll down, we must expend energy to push the wheelbarrow. From the laws of thermodynamics, we can calculate the amount of work needed, which depends on the steepness of the hill (the concentration gradient) and the amount of substance moved. Since the intestinal wall has the ability to transport many substances actively, these substances can be removed from the intestinal contents even though they may be present in the blood in a higher concentration. Some substances, on the other hand, penetrate passively and diffuse through the intestinal wall. This is the case with alcohol, which is absorbed and distributes itself evenly throughout all body water.

ELIMINATION. Undigested material—for example, plant fibers, the bodies of dead bacteria, epithelial cells from the intestine, etc.—are eliminated from the lower part of the intestine in the form of *feces.* The characteristic brown color of the feces is due to the excretion of bile pigments from the liver.

DIGESTION IN INVERTEBRATES

The invertebrates have the same main foodstuffs to digest as vertebrates, and thus they have proteases, lipases, and amylases, as well as other hydrolytic enzymes. However, the structure of the digestive system is different, and there is a great variation in the details of the digestive processes. One characteristic difference is that no invertebrate has a proteolytic enzyme that acts in highly acid solution, as does the pepsin of vertebrates. It is possible that the evolution of peptic digestion is associated with the ingestion of large prey, where skeletal material is more easily disintegrated in a strong acid. Pepsin and hydrochloric acid are found throughout all higher vertebrate classes from the fishes on up.

In other respects, invertebrate digestive enzymes are similar to the vertebrate digestive enzymes, although some invertebrates can digest substances indigestible to vertebrates. For example, the clothes moth can digest hair and wool, which are completely resistant to vertebrate digestion. Cellulose can be digested by many invertebrates. Some of them have cellulases, but others depend on microbes that live in their digestive tract and that attack cellulose.

SYMBIOTIC DIGESTION

Microbes (bacteria and protozoans) that live in the digestive tract attack certain materials that cannot be hydrolyzed by the animal's enzymes and change them into substances that can be digested. A relationship between two organisms that is mutually beneficial is called *symbiosis,* and we therefore speak about *symbiotic digestion.* Several examples of symbiotic digestion are given below.

CELLULOSE DIGESTION IN TERMITES. Termites feed on wood, although they do not secrete cellulase. Their intestine, however, is crowded with protozoans that carry out fermentation of cellulose. Each termite species carries characteristic protozoans, and the newly-hatched young are infected by feeding from older termites, and will die if isolated before this occurs. It can be shown that the protozoa, and not bacteria, are responsible for the cellulose digestion. If adult termites are subjected to high oxygen concentration, the protozoans in the intestine are killed but the bacteria survive, and these termites will starve to death unless reinfected.

CELLULOSE DIGESTION IN MAMMALS. Cellulase is not produced by any vertebrate, and herbivores depend on microbes for cellulose digestion. In the horse, the fermentation takes place in an enormous pouch of the intestine, the *caecum.* In the cow and other ruminants, the true stomach is preceded by a large sac, the *rumen* (usually designated as the first of the four ruminant "stomachs"). The food enters the rumen and undergoes heavy fermentation, the decomposition products (mostly acetic, propionic, and butyric acid) are absorbed and utilized, and the remaining food is regurgitated, masticated, and swallowed again. It re-enters the rumen and undergoes continued fermentation. Gradually the food passes to the other parts of the stomach and is subjected to the usual digestive juices (in the cow the rumen contains no glands).

The concentration of microbes in the rumen is very high and equals that of bacterial cultures in the laboratory. Their participation in cellulose digestion is only one phase of their important function. If ammonium salts are added to the food, the bacteria utilize the ammonia for the synthesis of protein. These bacteria are digested, and while animals in general cannot synthesize protein from inorganic nitrogen, the symbiotic bacteria permit the cow to utilize ammonia for protein formation. This process has been utilized in animal husbandry, where part of the high protein supply required by dairy cows can be replaced by cheaper ammonium salts.

In a similar fashion, inorganic sulfates are utilized by microbes for